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MECHANISMS OF GAZE AND ATTENTION GUIDANCE IN VISUAL EXPLORATION

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Mechanisms of gaze and attention guidance in visual exploration

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Table of contents

I	INTRODUCTION	11
I.1	EXPLORING THE VISUAL ENVIRONMENT: SACCADIC, ATTENTION AND SALIENCE	11
I.1.1	<i>Exploring with the eyes</i>	11
I.1.1.1	Goal-directed factors of eye guidance	13
I.1.1.2	Stimulus-driven factors of eye guidance	17
I.1.1.3	The processing time for saccadic target selection	19
I.1.2	<i>Exploring with the mind</i>	21
I.1.2.1	Guidance of attention in covert visual search	22
I.1.2.1.1	Indirect evidence	22
I.1.2.1.1.1	The attention-guiding “features”	23
I.1.2.1.1.2	The effect of target-distractor similarity	26
I.1.2.1.1.3	The role of stimulus-driven and goal-directed factors	29
I.1.2.1.1.4	Implicit assumptions in the use of visual search to study attentional allocation	33
I.1.2.1.2	Direct measurement of attentional allocation during visual search	36
I.1.2.2	Attentional guidance in cueing experiments	38
I.1.2.2.1	Endogenous cueing	38
I.1.2.2.1.1	Do informative location cues guide attention?	39
I.1.2.2.1.2	Spatial selection by features, feature selection or object selection?	39
I.1.2.2.2	Exogenous cueing	42
I.1.3	<i>Which item to scrutinize next? a definition of salience</i>	44
I.2	THE SALIENCE MAPS	45
I.2.1	<i>Models of salience map</i>	45
I.2.2	<i>Are salience maps necessary?</i>	48
I.2.3	<i>An operational definition of the salience map</i>	50
I.3	THE REPRESENTATION OF SALIENCE IN THE BRAIN	53
I.3.1	<i>Parietal cortex</i>	53
I.3.1.1	Area 7a	53
I.3.1.1.1	Anatomy	53
I.3.1.1.2	Physiology	55
I.3.1.1.3	In humans	60
I.3.1.1.4	Summary	65
I.3.1.2	Lateral Intraparietal Area (LIP)	66
I.3.1.2.1	Anatomy	66
I.3.1.2.2	Physiology	66
I.3.1.2.3	In humans	75
I.3.1.2.4	Summary	76
I.3.2	<i>Frontal eye fields (FEF)</i>	79
I.3.2.1	Anatomy	79
I.3.2.2	Physiology	80
I.3.2.3	In humans	87
I.3.2.4	Summary	89
I.3.3	<i>Superior colliculus</i>	91
I.3.3.1	Anatomy	91
I.3.3.2	Physiology	92
I.3.3.3	In humans	97
I.3.3.4	Summary	97
I.3.4	<i>The network</i>	99
I.3.5	<i>Conclusion</i>	107
I.4	CONTENT OF THE FOLLOWING CHAPTERS	109
II	ARTICLES	111
II.1	SPATIAL AND TEMPORAL DYNAMICS OF ATTENTIONAL GUIDANCE DURING INEFFICIENT VISUAL SEARCH	111
II.1.1	<i>Abstract</i>	111
II.1.2	<i>Introduction</i>	112
II.1.3	<i>Materials and Methods</i>	116

II.1.3.1	Experiment 1	116
II.1.3.1.1	Subjects.....	116
II.1.3.1.2	Task.....	116
II.1.3.1.3	Control task A: letter detection only.....	117
II.1.3.1.4	Control task B: target detection only.....	117
II.1.3.1.5	Data analysis	117
II.1.3.1.6	Statistical analysis.....	117
II.1.3.2	Experiment 2	117
II.1.3.3	Experiment 3	118
II.1.4	<i>Results</i>	118
II.1.4.1	Experiment 1	118
II.1.4.1.1	General performance.....	118
II.1.4.1.2	Influence of goal-directed salience on attentional allocation.....	119
II.1.4.1.3	Influence of stimulus-driven factors and spatial location on attentional allocation.....	121
II.1.4.2	Experiment 2	123
II.1.4.3	Experiment 3	126
II.1.5	<i>Discussion</i>	128
II.1.5.1.1	Influence of goal-directed salience on attentional allocation.....	128
II.1.5.1.2	Role of stimulus-driven salience in attentional allocation.....	128
II.1.5.1.3	Effect of spatial location on attentional allocation	128
II.1.5.1.4	Relationship between attentional selection and target detection.....	129
II.1.5.1.5	Grouping phenomena.....	130
II.1.5.1.6	Conclusions.....	130
II.1.6	<i>Acknowledgments</i>	131
II.2	ATTENTIONAL GUIDANCE RELIES ON A WINNER-TAKE-ALL MECHANISM.	133
II.2.1	<i>Abstract</i>	133
II.2.2	<i>Introduction</i>	134
II.2.3	<i>Experiment 1</i>	135
II.2.3.1	Methods	136
II.2.3.1.1	Subjects.....	136
II.2.3.1.2	Task.....	137
II.2.3.1.3	Control task: target detection only.....	138
II.2.3.1.4	Data analysis	138
II.2.3.1.5	Statistical analysis.....	138
II.2.3.2	Results	139
II.2.3.2.1	The influence of ITS on attention allocation	141
II.2.3.2.2	The influence of spatial configuration on attention allocation	142
II.2.3.3	Discussion	143
II.2.4	<i>Experiment 2</i>	145
II.2.4.1	Methods	145
II.2.4.2	Results	146
II.2.4.3	Discussion	149
II.2.5	<i>General discussion</i>	150
II.3	VISUAL SEARCH WITHOUT ATTENTIONAL DISPLACEMENT	153
II.3.1	<i>Abstract</i>	153
II.3.2	<i>Introduction</i>	154
II.3.3	<i>Experiment #1: Covert feature search</i>	155
II.3.3.1	Methods	155
II.3.3.1.1	Participants.....	155
II.3.3.1.2	Behavioral procedure.....	155
II.3.3.1.3	Control Experiment A.....	156
II.3.3.1.4	Data analysis	156
II.3.3.2	Results	157
II.3.3.2.1	Lack of attentional shift in feature CVS	159
II.3.3.2.2	Interactions between CVS and letter reporting.....	160
II.3.3.3	Discussion	161
II.3.4	<i>Experiment #2: Covert conjunction search</i>	162
II.3.4.1	Methods	162
II.3.4.1.1	Control Experiments B and C.....	163
II.3.4.2	Results	163
II.3.4.3	Discussion	164
II.3.5	<i>Experiment #3: Covert cued attention task</i>	164

II.3.5.1	Methods	165
II.3.5.2	Results	165
II.3.5.3	Discussion	167
II.3.6	<i>General Discussion</i>	167
II.4	SALIENCE REPRESENTATION IN THE PARIETAL AND FRONTAL CORTEX	171
II.4.1	<i>Abstract</i>	171
II.4.2	<i>INTRODUCTION</i>	172
II.4.3	<i>Experiment 1</i>	173
II.4.3.1	Materials and methods	173
II.4.3.1.1	Participants	173
II.4.3.1.2	Task	173
II.4.3.1.3	Transcranial magnetic stimulation	174
II.4.3.1.4	Data acquisition and analysis	176
II.4.3.1.5	Inefficiency of the VS task: control task	176
II.4.3.1.6	Stimulus-driven effect of horizontally and vertically oriented items: control task	176
II.4.3.1.7	Statistical analysis	176
II.4.3.2	RESULTS	177
II.4.3.2.1	TMS experiment: behavioral results	177
II.4.3.2.2	TMS experiment: effect of TMS	177
II.4.3.2.3	Control task B: Stimulus-driven effect of horizontally and vertically oriented items	178
II.4.3.3	Discussion	179
II.4.4	<i>Experiment 2</i>	180
II.4.4.1	Materials and methods	180
II.4.4.1.1	Participants	180
II.4.4.1.2	Task	181
II.4.4.1.3	Transcranial magnetic stimulation	183
II.4.4.2	RESULTS	183
II.4.4.2.1	Results of the goal-directed letter reporting task	183
II.4.4.2.2	Results of the stimulus-driven letter reporting task	185
II.4.4.3	Discussion	185
II.4.5	<i>GENERAL DISCUSSION</i>	186
II.4.6	<i>Acknowledgments</i>	188
II.5	CELL ACTIVITY IN AREA 7A CORRELATES WITH THE PROBABILITY TO MAKE AN EYE MOVEMENT TO A SINGLETON.	189
II.5.1	<i>Introduction</i>	189
II.5.2	<i>Experimental procedure</i>	190
II.5.2.1.1	Subjects and surgery	190
II.5.2.1.2	Behavioral procedure	190
II.5.2.1.3	Data collection	191
II.5.2.1.4	Analysis of neural activity	192
II.5.3	<i>RESULTS</i>	192
II.5.3.1	Behavior	192
II.5.3.2	Neural activity	193
II.5.4	<i>Discussion</i>	199
III	CONCLUSIONS	201
IV	REFERENCES	204

I INTRODUCTION

I.1 Exploring the visual environment: saccades, attention and salience

I.1.1 EXPLORING WITH THE EYES

Many living creatures on earth, from unicellular organisms to mammals have acquired the ability to perceive light. For these animals, this faculty is an immense evolutionary advantage, allowing to perform tasks ranging from orienting itself as a function of light intensity (Hegemann, 1997), to interpreting the emotional state of another organism based on its visual features (Parr, 2003). However, light sensitive systems, or eyes, cannot perceive light from the entire visual surroundings simultaneously but have to sample light from a small portion of the environment. Consequently, most light perceiving organisms have developed the ability to move their eyes, to allow sampling of the visual environment in its entirety. It appears that in most case, the most effective way to explore the visual environment is by making rapid discontinuous movements of the gaze, called saccades, while maintaining the gaze stable between these movements (M. F. Land, 1999). Movements of the eyes themselves, of the head or of the body are used to achieve gaze shifts.

In most vertebrates, the retina is composed of two types of photoreceptors called rods and cones. In humans, the former represents 94% of retinal photoreceptors, i.e. approximately 120 million cells (V. Bruce & Gree, 1990). In the periphery of the retina, the rods greatly outnumber the cone photoreceptors while cones are more numerous in the center, in a region referred to as the fovea. Given their high light sensitivity, the large number of rods found in the periphery of the retina is useful for seeing in low illumination conditions, but visual acuity in this portion of the visual field is quite poor and the discrimination of color is much reduced. In the fovea, high-resolution cone photoreceptors are packed tightly together and are able to discriminate colors. Given these characteristics, the fovea is responsible for high-resolution vision and every potentially relevant visual object in the surrounding must be foveated in order to be properly perceived. On average, humans execute over 150,000 saccades each day (Babcock, Lipps, & Pelz, 2002). Because of the small visual angle subtended by the fovea (between 0.3° and 2° (Steinman, 2003)), exhaustive exploration of the visual surroundings, i.e. complete sampling of the whole visual field, would be much ineffective. Consequently, the decision of where to move the gaze in order to optimize visual information gathering is critical. How the brain achieves this computational conundrum is the central question addressed in the present work.

Since the early work of Yarbus 50 years ago (Yarbus, 1967), the question of the factors that determine where to move the gaze has been the subject of intense research. Yarbus was the first to demonstrate that gaze allocation is much influenced by task-dependent cognitive factors. In his most famous paradigm, he asked subjects to look at a painting and to perform different tasks in relation to this painting. Their eye movements were recorded (see Fig. I.1.1). Yarbus observed that the patterns of fixations differed according to the task performed. He concluded that the selection of

the next location to look at depended crucially on the current cognitive state of the observer and not only on the visual features of the scene.

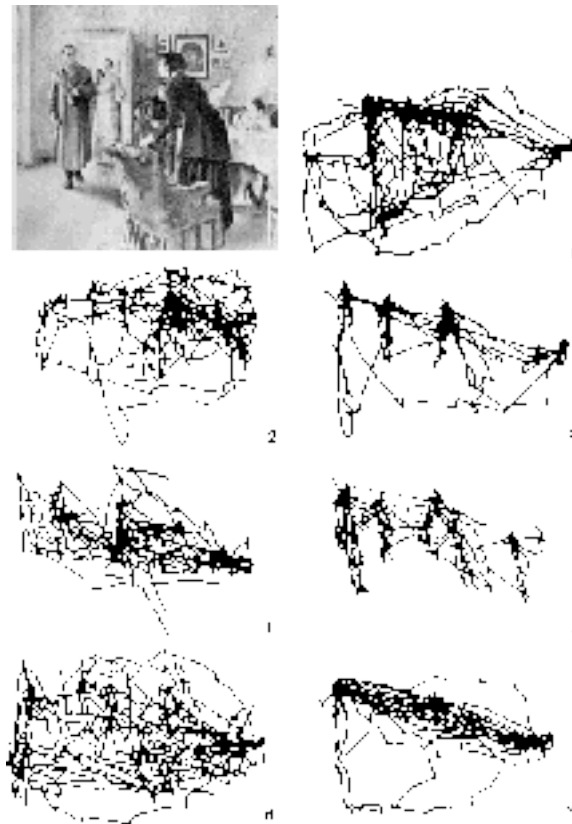


Figure I.1.1

Patterns of eye fixations during different tasks instructed to the subjects: 1) Free examination; 2) estimate of the material circumstances of the family; 3) estimate the ages of the people; 4) guess what the family had been doing before the arrival of the "unexpected visitor;" 5) remember the clothes worn by the people; 6) remember the position of the people and objects in the room; 7) estimate how long the "unexpected visitor" had been away from the family. From (Yarbus, 1967).

Many studies having investigated the factors that determine saccadic goal selection since Yarbus have used so-called visual search tasks. In these tasks the subjects are required to find a given visual object, called the "target", in an unpredictable location, amongst irrelevant items, called distractors. Very early in the history of visual search investigations, it was found that the eyes do not explore the visual scene randomly. In 1967, Williams found that the eyes of the observers, when required to search for a target in a cluttered display, land mainly on visual items and not between them, i.e. on blank locations (Williams, 1967), a result later confirmed by other studies (Motter & Belky, 1998a). Moreover, he found that the features used to define the target with respect to distractors had an influence on the pattern of fixation; for example, when instructing the observers to search for a red target, their fixations were more often located on red items. This finding suggested that the target features guided the eye movements during visual search performance.

Further studies led to the distinction of two different types of factors influencing the guidance of eye movements. The first factor of guidance, introduced by Yarbus and Williams, is a cognitive factor leading eye movements to land on the most relevant

items with respect to the task at hand. This factor of guidance is called either top-down, goal-directed (Egeth & Yantis, 1997) or endogenous (Posner, Snyder, & Davidson, 1980). The second factor of guidance is independent of the current task and refers to the conspicuity of the visual items displayed, depending on their physical characteristics, e.g. on their contrast with respect to the surrounding, on their rarity, on their sudden onset, ... This factor is called bottom-up, stimulus-driven (Egeth & Yantis, 1997) or exogenous (Posner, et al., 1980). Goal-directed factors of guidance are usually assumed to be voluntary, whereas stimulus-driven factors are automatic and not under the control of will. Since several decades, the question of the respective role of each of these factors in the guidance of eye movements was much debated. Some investigators think that goal-directed factors are the most important and usually override stimulus-driven factors, while others state that stimulus-driven factors are crucial in guiding eye movements.

In addition to visual information, auditory and tactile cues are known to influence saccadic and attentional exploration as well (Butter, Bachtel, & Santucci, 1989; Corneil & Munoz, 1996; Engelken & Stevens, 1989; Mazza, Turatto, Rossi, & Umiltà, 2007; Sullivan, Fitzmaurice, & Abel, 2004; Zambbarbieri, Schmid, Magenes, & Prablanc, 1982) and this phenomenon plays certainly an important role in ecological conditions. However, in the present thesis, I chose to focus on the role of visual information in guiding visual exploration. This specific topic has been much more extensively studied and is better understood than the mechanisms involved in crossmodal visual exploration.

1.1.1.1 Goal-directed factors of eye guidance

In order to investigate in greater details the findings of Williams that the features defining the target guide visual exploration, Motter & Belky recorded monkeys eye movements while they were performing a conjunction visual search task, i.e. a task in which the target is defined by the combination of two or more features (Motter & Belky, 1998a). In this task, the target had a unique combination of color and orientation, while distractors shared either the same orientation with a different color, or the same color with a different orientation. Motter found that, before the correct saccade, performed to catch the target, around 75% of fixations were located on an item sharing the target color. Other fixations were located on blank locations (around 20%) or distractor sharing the target orientation (around 5%). He also found that the distribution of saccade amplitude was binomial. When the previous eye movement landed next to the intended goal, short corrective saccades brought subsequently the gaze on the target. They constitute the first peak in the amplitude distribution, corresponding to very small saccades with an amplitude inferior to 2°. The remaining of the saccades is represented in the second peak of the distribution, corresponding to eye movements of large amplitude. Authors showed that most of these saccades were longer than the mean distance between neighboring items, suggesting that the eyes scanned the display by jumping from one item to another, bypassing several items in between. More interestingly, they showed that the average saccade amplitude was proportional and larger than the mean distance between stimuli of the same color as the target (three times that distance in 96 items display), suggesting that the nearest relevant distractors (i.e. sharing the target color) were processed covertly before the eyes move to the next location. In another study, using the same task, the authors found that the portion of space around fixation in which the target could be detected covertly, without additional scanning eye movement, also depended on the density of distractors sharing the target color (Motter & Belky, 1998b). The target was usually accurately detected when located in a region smaller than twice the average distance between distractors sharing the target color (in fact

Motter and colleagues found later that this ratio depended on the cortical magnification factor (Motter & Holsapple, 2000)). Altogether, these results suggest that the subjects adopted the following strategy: during each fixation, a portion of space whose radius depends on the density of pertinent stimuli is processed covertly, and if the target is not detected, a saccade is made to bring the gaze outside this area, fixating another stimulus sharing the target color. In other words, the saccades performed during the search process are made towards distant items, a strategy which allows searching covertly inside a new non-processed area. The fact that observers fixate more often items sharing the target features, and that the average saccade amplitude depends on the density of these items only, suggests that other distractors are simply excluded from the visual search process.

The different features that can be used to define a search target lead to different degrees of guidance, i.e. different probabilities of fixating a distractor sharing this feature. Color seems the most prominent factor of guidance (Motter & Belky, 1998a; Rutishauser & Koch, 2007), but shape (Bichot & Schall, 1999b), or orientation (Zelinsky & Sheinberg, 1997), for instance, can be used as well. When the target is defined by multiple features, the use of a given feature to guide search seems to depend on the frequency of this feature in the search array: when a target-defining feature is rare in the array, it is more likely to be used as a guiding feature than when it is shared by many distractors (Shen, Reingold, & Pomplun, 2000; Zohary & Hochstein, 1989). This suggests that observers adapt their strategy on a trial-by-trial basis, to search for the target in the smallest subset of distractors, the other ones being simply ignored. This so-called distractor-ratio effect can be modulated by other task characteristics: when one of the target features is difficult to discriminate, observers will more likely use the other one to guide their search (Shen, Reingold, & Pomplun, 2003).

The results presented so far have been obtained in very specific laboratory conditions in which observers have to search for a target in a display in which the visual items are clearly separated from each other, presented on a black background, at constant disparity, and defined by a small set of features. These conditions are, obviously, totally different from the situation that we face in daily life. That is why some authors investigated the factors of eye guidance in more naturalistic visual conditions such as picture viewing or video watching. Pomplun (Pomplun, 2006) designed a visual search task in which observers are asked to search for 64x64 pixels targets inside greater images from which these targets are sampled (black and white 800x800 pixels pictures). The author then analyzed saccadic distribution with respect to four local feature dimensions: intensity, contrast, spatial frequency and orientation of the image. He found that saccades were more likely to land on portions of the image that had the same feature value as the target. This was true along each of the four dimensions, even though intensity and contrast had the strongest effect. Besides this strong goal-directed effect, he found that contrast and spatial-frequency also had a stimulus-driven effect, influencing saccadic distribution independently of the target value in these dimensions. Finally, he demonstrated that the use of a given visual feature to guide eye movements during the search process depends on its proportion in the image. Observers are much more likely to use target features which are rare in the image to guide their gaze. This 'feature-ratio' effect can be compared with the 'distractor-ratio' effect described above, referring to the finding that the search is conducted only on the smallest subset of items. Altogether, the results from the Pomplun's study are interesting for three main reasons. First, they confirm the importance of both goal-directed and stimulus-driven factors in the guidance of eye movements in a more ecological situation in which real pictures are used instead of arrays of stimuli. Second, they show that goal-directed influence on gaze allocation is not limited to a dichotomic selection preference, as the one found in conjunction search studies (e.g. eyes select only the red items and never the green ones), but

influence saccadic allocation in a gradual way as evidenced by the large spread of visual guidance found in each of the four feature dimensions. Third, they show, in contrast to the findings of Motter and colleagues described above, that eye movements land on portions of the image that are the most alike the target instead of being strategically deployed on successive distant locations. This discrepancy between the results of Motter and Pomplun appears puzzling. The former proposed that successive fixations of the observers were separated by a distance proportional to the radius of the area that they can process covertly; each new fixation bringing new items in the processed area. In contrast, Pomplun found that the factors influencing saccade goal selection was the feature similarity with the target; items similar to the target being more likely to be fixated than other items.

These two observations lead to two different hypotheses about visual exploration, which were formalized and compared experimentally by Najemnik and Geisler in a recent study (Najemnik & Geisler, 2008). The first model of visual search they proposed, called the “Bayesian ideal searcher”, corresponds to the hypothesis of Motter, and assumes that each saccadic goal location is selected to optimize the gain of information with respect to the location of the target. Eyes are strategically deployed to maximize the gain of information about target location, at each new fixation. In the second model, called “maximum *a posteriori* searcher”, and corresponding to the hypothesis of Pomplun, the saccade lands always on the location of maximal target location probability, i.e. on the item that is the most similar to the target. Determining which of these two models is correct is a complicated issue because they both lead, in most cases, to very similar predictions. However, Najemnik & Geisler pointed out that the two models predict different spatial distributions of fixations across the visual field. This difference in spatial distribution comes from the fact that the perceptual performance around fixation is not homogeneous: performance decreases more quickly with eccentricity along the vertical than along the horizontal meridian. The Bayesian ideal searcher, seeking to optimize information gathering, will explore more often eccentric positions located either above or below fixation, because it takes into account the fact that performance is poorer at these locations. In contrast, the maximum *a posteriori* searcher will explore with equal probability all locations around fixation (see Fig. I.1.2). They compared actual fixation distributions observed in two subjects while performing a visual search task, with the predictions associated with the two models. They found that real observers exhibited fixation distribution comparable to the one predicted by the ideal searcher, and different from the one predicted by the maximum *a posteriori* searcher. This suggests that during visual exploration, each saccadic target selection seeks to optimize the difference between the *a priori* and *a posteriori* target location probability. The higher probability of selecting an item sharing target features during visual search would be only a consequence of this general strategy, observed in conditions where it is actually optimal.

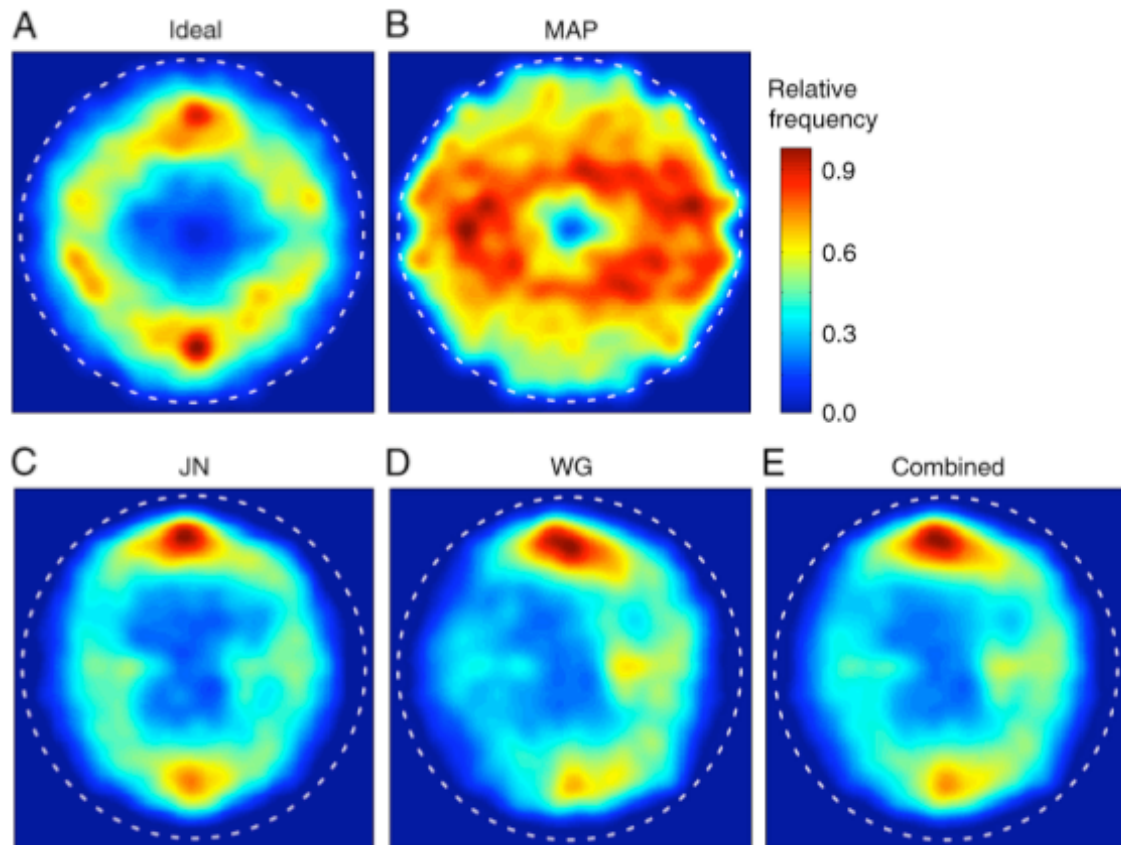


Figure I.1.2

Spatial distribution of fixation locations predicted by the Bayesian ideal searcher (A.), the maximum a posteriori searcher (B.), the two human observers (C. and D.) and the combined data from the two subjects (E.). From (Najemnik & Geisler, 2005).

Recent studies have shown that eye fixation schemes during visuo-motor tasks are very precise and predictable both in space and time. Land & McLeod measured eye movements in three cricket batsmen while playing (M. F. Land & McLeod, 2000). They showed that players fixated the ball at very precise timing during the ball's trajectory and that these timing were optimal in providing information to the player on when and where he would have to hit the ball. Eye movements during daily-living activities, either sedentary like reading, picture viewing, and drawing, or dynamic like walking, driving or doing sport have been extensively studied (reviewed in (M. F. Land, 2006) and (Hayhoe & Ballard, 2005)). The general conclusion from these studies is that eye movements play a crucial role in the organization of actions and are involved proactively to gather information needed for the upcoming action. During the performance of familiar tasks, the eyes go, with very few errors, directly on the appropriate objects (M. Land, Mennie, & Rusted, 1999). When making tea, for example, the proportion of task-irrelevant objects fixated is under 5% (M. Land, et al., 1999). In a task performed under virtual reality, eyes are directed on conspicuous irrelevant parts of the screen during only 0.2% of the time (Rothkopf, Ballard, & Hayhoe, 2007). This demonstrates the crucial role of cognitive factors in the guidance of eye movements.

I.1.1.2 Stimulus-driven factors of eye guidance

The next important question to address is whether eye movements can be attracted involuntarily by the conspicuity of visual items. Theeuwes and collaborators asked subjects to perform a very simple feature search task (make a saccade towards the only grey circle amongst red circles), but in half of the trials, an additional distractor was displayed at an unpredictable location simultaneously with the target (J. Theeuwes, Kramer, Hahn, & Irwin, 1998). This location was never the target's location. In addition, observers were asked to report the orientation of a 'C' letter displayed inside the target. They found that in about half of the trials, the appearance of a new, abrupt onset stimulus disrupted the planning of the saccade towards the target. Erroneous saccades were made mostly toward the new stimulus (see Fig. I.1.3), followed by rapid (≈ 150 ms latency) corrective saccades toward the target. Subjects, questioned a posteriori, seemed to be completely unaware of these errors, confirming the automatic nature of the saccadic capture.

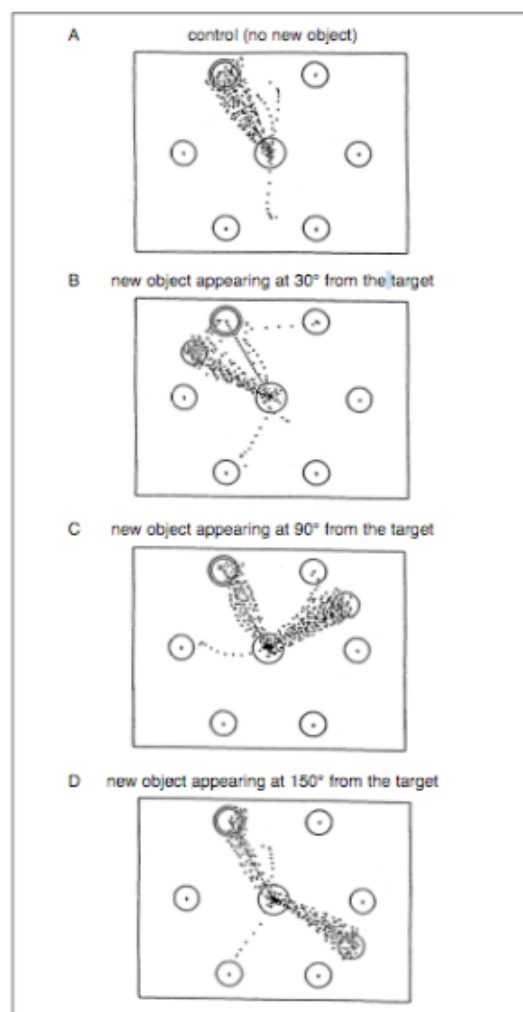


Figure I.1.3

First saccades in trials with no new stimulus onset (A), or new stimulus onset at 30° (B), 90° (C) or 150° (D) from the target. From (J. Theeuwes, et al., 1998).

In their Experiment 2, Theeuwes and colleagues (J. Theeuwes, et al., 1998) added an informative cue, which indicated with 100% accuracy the location of the upcoming

target. In this case, the effect of the new stimulus was completely suppressed, all saccades going directly to the target. This result was interpreted as evidence that goal-directed factors, i.e. information given by the cue in the present case, can override stimulus-driven capture. In a recent study, Van Zoest and colleagues looked at the proportion of saccades made to the target or to a conspicuous distractor as a function of saccade latency (van Zoest, Donk, & Theeuwes, 2004). They found that early saccades were equally likely to land on the target than on the conspicuous distractor, whereas later saccades accurately selected the target most of the time. This suggests that stimulus-driven factors are involved in the early part of the selection process, but are later overridden by goal-directed factors, which are slower to set up.

The existence of such an overriding of stimulus-driven influence by goal-directed factors has been much debated in the literature. However, most studies on this topic have been conducted in covert conditions, in which no eye movement is allowed. Hence, this issue will be discussed further in the chapter addressing covert visual search.

Numerous studies investigated the role of stimulus-driven factors in eye guidance during exploration of natural images (Kienzle, Wichmann, Schölkopf, & Franz, 2007; D. Parkhurst, Law, & Niebur, 2002; D. J. Parkhurst & Niebur, 2003, 2004; Reinagel & Zador, 1999; Tatler, Baddeley, & Gilchrist, 2005; Tatler, Baddeley, & Vincent, 2006). They all tried to determine the correlation between fixation probability and different factors of conspicuity, such as luminance or color contrast for example. Many of them, instead of assessing the role of each conspicuity factors separately, used a model of visual saliency, developed by Itti and colleagues, which is a complex integration of multiple factors. The details of this model will be discussed later on. They all concluded that features such as luminance contrast, orientation contrast, color contrast, texture contrast, or any complex combination of these different features contribute to eye guidance, in free viewing or in various visual search conditions. However, these factors can only explain, at best, around 50% of the variability in the eye fixation patterns (D. Parkhurst, et al., 2002), and the importance of these low-level factors are strongly dependent on the task at hand, suggesting that their influence is not purely stimulus-driven. But the main issue with these studies is that the relationship they observe between stimulus-driven factors and eye movements is correlational but not necessarily causal. For example, subjects will fixate more often the eyes in human faces. Because eyes usually have contrasted features this will induce a strong correlation between eye fixation pattern and stimulus-driven factors. However, it is likely that the preferential fixation of eyes is determined by goal-directed instead of stimulus-driven factors. Tatler and colleagues showed that an important part of the correlation between conspicuity factors and fixation probability can be explained by the central bias of visual exploration (Tatler, et al., 2005): both fixation probability and image contrast are higher on average in the most central portions of the image. Hence the correlation between these two variables could be artefactual. The effect of the context on the importance of stimulus-driven factors in gaze guidance has been investigated by Underwood and collaborators. In a visual search task performed on natural images, when manipulating the conspicuity and the context congruency of items in the scene, they found that only congruency and not conspicuity influenced fixation probability (Underwood & Foulsham, 2006). In contrast, when subjects are asked to explore pictures in a memory task, and they know they will have to perform a recognition test afterwards, stimulus-driven factors are critical in guiding eye movements (Foulsham & Underwood, 2007; Underwood & Foulsham, 2006). In this case, fixating conspicuous features could help memorizing the image. Finally, when the explored pictures are modified so that they appear less natural (e.g. by modification of the hue), the influence of first-order stimulus features in the guidance of eye movements

disappear (Frey, Konig, & Einhauser, 2007). However, second-order stimulus features, i.e. texture contrast, still significantly affect eye target selection. In summary, here again, while stimulus-driven factors might be important in certain conditions, they are usually overridden by goal-directed factors, preponderant in the guidance of eye movements in most active exploration conditions.

1.1.1.3 The processing time for saccadic target selection

Usually, the latencies of the saccades performed during visual search experiments are constant and independent of the difficulty of the task (J. M. Findlay, 1997). However, in a conjunction task where subjects were required to detect the target at the first saccade, and were hence discouraged to explore the visual fields with multiple eye movements, Bichot and colleagues (Bichot & Schall, 1999b) observed that the latency of this first saccade was a linear function of the number of items displayed, or set-size. This finding of crucial importance, so-called the set-size effect, was in fact the replication of a result observed in numerous earlier covert visual search studies, i.e. search performed without moving the eyes (see section 1.2). This effect is at the core of the dichotomy between inefficient searches, which exhibit the set-size effect, and efficient searches, which do not exhibit this effect. Zelinsky studied these two categories of search tasks in a condition where the target did not have to be detected at first saccade and saccades were thus freely performed (Zelinsky & Sheinberg, 1997). Subjects were asked to press a button to indicate whether the target was present or not in the display. Authors then measured the reaction time (RT) in button press in different search conditions (efficient or inefficient) and set-sizes (5 or 17 items) and investigated whether the RT was explained better by the number of saccades performed during the search or by the duration of the fixations between saccades. Authors found two opposite effects concerning the number of saccades performed. First, they observed unexpectedly that the number of trials in which no saccade was performed before target detection increased with the set-size. Second, they found that the mean number of saccades performed increased with the set-size in difficult search conditions. Regarding the duration of fixations they found also opposite results for the first saccade and for subsequent saccades. While the latency of the first saccade was clearly dependent on both the set-size and difficulty (see also (Shen, et al., 2000)), subsequent fixation durations were independent of these factors. When computing the correlation between manual RT in the task and either first fixation duration or number of saccades, authors found that the latter explained a much greater fraction of the variability in RT (up to 67%) than fixation duration. This suggests that the inter-fixation processing leading to the selection of the next saccadic goal is performed during a fixed amount of time, independent of the difficulty of the task. Consequently, with increasing difficulty, the probability of making a saccade to the target decreases, and more saccades are needed in order to detect the target.

The most surprising finding, however, came from Experiment 3 of the Zelinsky study, in which the authors asked subjects to perform the same tasks covertly, by maintaining steady fixation throughout the task duration. Instead of increasing the difficulty of the task, this experimental manipulation led to shorter RTs, with a similar rate of error in inefficient search tasks (see also (Klein & Farrell, 1989)). In contrast, in efficient searches, performance was equal in eye-free and steady-fixation conditions. This finding questions the actual role of eye movements during search. Authors propose that saccades are used as a default search procedure in ecological conditions and subjects keep using this strategy when performing a visual search task in which covert search is actually more efficient. This hypothesis is also in

agreement with their surprising observation that trials in which subjects make no eye movements become more frequent as the set-size increases. Covert visual search tasks, in which eye movements are prevented, either by instruction, or by using short display durations, are discussed in the next section.

I.1.2 EXPLORING WITH THE MIND

As already mentioned, eye movements are critical to compensate for the poor resolution of our peripheral vision by placing relevant stimuli onto the fovea, and therefore, they are used heavily and systematically in ecological conditions of visual exploration. However, in laboratory conditions, a great number of complex visual tasks can be performed with a surprising efficiency in the complete absence of eye movements. In some situations, visual tasks can be conducted even more efficiently covertly, i.e. when eyes remain still, than in overt condition, when they are allowed to scan the visual scene (Zelinsky & Sheinberg, 1997). In covert condition, instead of eye movements, the selection of relevant stimuli is thought to be achieved by an internal selection process called visual attention. The term “selection” means here that the processing of attended visual items will be enhanced whereas other items will receive less processing resources. The term “internal” refers to the fact that the selection occurs without any modification of the sensory input, in contrast to selection performed by means of eye movements. Attention is thought to be able to select either a portion of space (spatial attention), a given visual feature (feature-based attention) or a visual object (object-based attention).

In the investigation of attention mechanisms, the issue of which factors are used to determine what must be selected and what must be excluded is crucial. This question is similar to the question addressed in the previous section, i.e. which factors determine where to look. In fact, as we will see, there are many reasons to believe that the factors of guidance of eye movements and the factors of guidance of attention are identical, depend on the same processes, and are controlled by the same neural structures.

Attention has been investigated by means of a huge number of different experimental paradigms, but most of them can be included in one of the following categories:

1. Cueing paradigms, in which a cue indicates the location in space where to allocate attention, or the feature on which attention must be focused, or any information relevant for the allocation of attention;
2. Covert visual search, in which observers have to search for the presence of a visual target amongst a set of distractors without moving the eyes;
3. Rapid serial visual presentation (RSVP), where observers have to detect the occurrence of targets in a continuous stream of stimuli;
4. Change detection, where observers have to detect the occurrence of changes in the display;
5. Multiple object tracking, in which several visual items have to be tracked while they move randomly amongst distractors, independently from each other.

In the following chapters we will mainly describe tasks belonging to the two first of these categories (i.e. cueing paradigms and covert visual searches) because they are the most pertinent with respect to the question of attentional guidance.

I.1.2.1 Guidance of attention in covert visual search

In his very influential model of visual search, called Guided Search Theory, Jeremy Wolfe proposes that during visual search, so-called preattentive mechanisms are involved first, to process the whole visual field in parallel. They lead to the building of an activation map, in which stimulus-driven and goal-directed factors are integrated. This map is subsequently used to select the target of the next attentional shift: the location with the maximal activation in the map (i.e. either high conspicuity, relevance with respect to the task, or both) is selected for the next shift (J. M. Wolfe, Cave, & Franzel, 1989). Hence the parallel stage is used to guide the second stage of the model, which consists in the serial deployment of attention. This model was able to predict the classical difference found in visual search tasks between so-called efficient searches, in which performance does not depend on the number of items displayed, and inefficient searches, in which performance drops proportionally to the number of items (see section 1.1.3). The idea was that, in efficient searches, preattentive mechanisms are able to guide attention directly on the correct item, making subsequent shifts unnecessary, whereas in inefficient searches, preattentive mechanisms alone are unable to identify the target, and several shifts are needed, proportionally to the number of items, in order to detect the target. Each additional attentional shift induces a constant increase in the global RT. The main model preceding Guided Search Theory, namely the Feature Integration Theory proposed by Treisman and Gelade in 1980 (A. M. Treisman & Gelade, 1980), explained the dichotomy between efficient and inefficient searches by the fact that attention was needed to bind multiple features together. This model was based on the observation that conjunction searches were always inefficient while feature searches were always efficient. Later studies challenged this view by showing that both efficient conjunction searches and inefficient feature search were possible (J. M. Wolfe, et al., 1989). While Feature Integration Theory was unable to account for these more recent findings, Guided Search Theory, assuming no clearcut boundary between conjunction and feature searches, remained able, with several subsequent updates (J. Wolfe, 2007), to predict many experimental results up to now.

Two distinct bodies of evidence are found in the literature to support the existence of preattentive mechanisms, as proposed in Guided Search Theory. In the first body of evidence, the modification of performance (mainly RT) induced by modification of the set-size, the similarity between target and distractors, the pre-knowledge of target information, etc... during visual search *implies* the existence of attentional guidance. In the second set of evidence, attentional allocation is assessed by measuring *directly* perceptual performance at critical locations during visual search performance. These two bodies of evidence will be discussed in different chapters of the present work, entitled accordingly.

I.1.2.1.1 Indirect evidence

According to Guided Search Theory, efficient searches lead to flat set-size slopes (no RT increase as a function of the number of distractors in the display) thanks to the ability of preattentive mechanisms to guide attention directly on the target. Hence, according to this theory, studying the factors that lead to flat set-size slopes is equivalent to studying the factors that guide attention. In most visual search experiments, the visual items are made from a combination of so-called visual features, which are elementary visual characteristics like orientation, color, luminosity, etc... These visual features, because they are elementary, are assumed to be processed early in the visual system hierarchy. Guided Search Theory

proposed that these basic features guide attention during visual search. Hence, identifying these basic guiding features is critical.

I.1.2.1.1.1 The attention-guiding “features”

In two thorough reviews, Wolfe discusses the evidence gathered throughout the visual search literature, helping to determine which visual features can be used to guide attention (J. M. Wolfe, 1998a; J. M. Wolfe & Horowitz, 2004). He distinguishes five categories of visual features, on the basis of the confidence he has on their role in attentional guidance. The features that, according to him, are the most undoubtedly involved in attentional guidance are color, orientation, motion and size. In addition to the fact that search in these feature dimensions is efficient (as long as the difference between target and distractors is large enough and the difference between distractors is small enough, cf. below), another strong argument for the role of these features in guidance is that the boundary between two sets of texture elements differing between each other along these dimensions are effortlessly perceived (see Fig. I.1.4). This immediate texture segregation is believed to occur preattentively (Julesz, 1986). Even though Wolfe demonstrated in an earlier study that preattentive texture segregation and preattentive target detection in visual search are not the same thing (J. M. Wolfe, 1992) (see also (H. C. Nothdurft, 1990)), he considers effortless texture segregation as a marker of guidance.

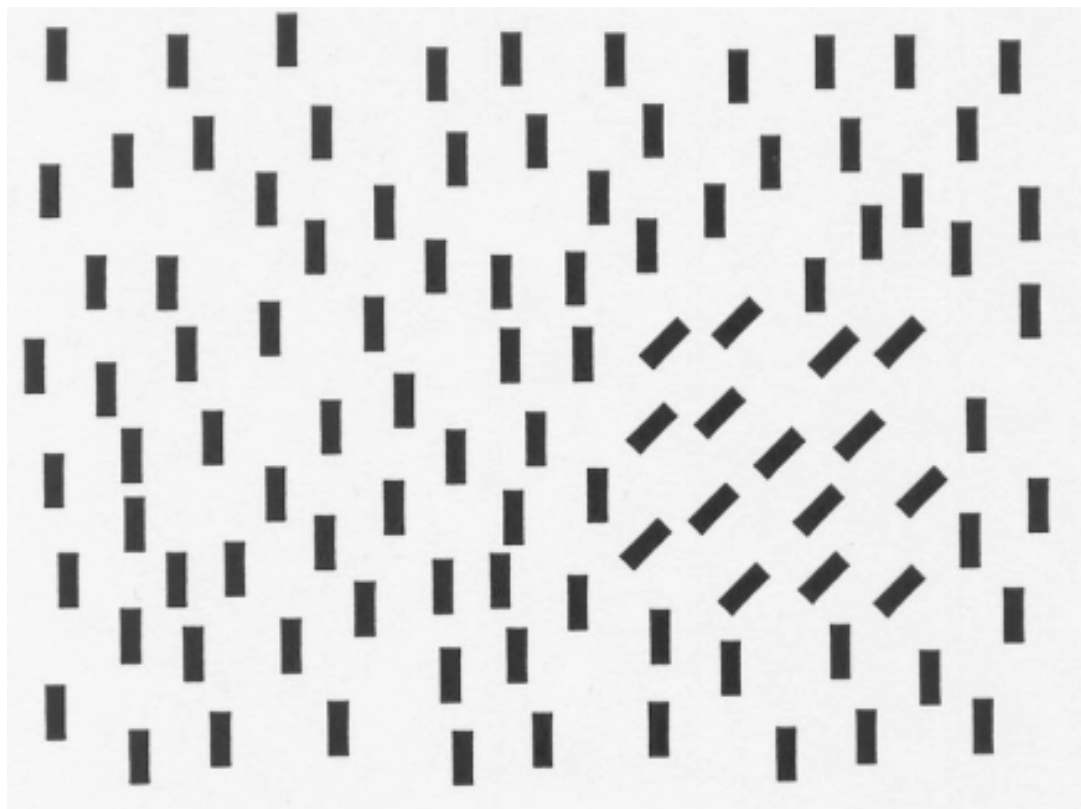


Figure I.1.4

Texture made from two sets of elements differing along the orientation dimension. The boundary between the two sets is effortlessly perceived (from (J. M. Wolfe, 1992)).

In the two Wolfe's reviews, other experimental findings that are considered as evidence for the implication in visual guidance of a given feature dimension are

illusory conjunctions (incorrect binding between features of neighboring items), visual search asymmetry (difference in set-size effect between searches for the presence or the absence of a given feature), and resistance to heterogeneity (search that remains inefficient despite heterogeneity of the distractors). However, the reason why these phenomena would be markers of the guiding features is not clear.

In addition to classifying the features as a function of their importance in attentional guidance, Wolfe & Horowitz propose in their review the interesting idea that the mechanisms that guide attention are distinct from the processes of low-level vision. In other words, they argue against the linear model that assumes that preattentive vision, acting in parallel across the whole visual field and responsible for the elementary analysis of the scene and the guidance of attention would be *followed* by an attentional stage of visual processing. Instead, they propose that elementary visual processing and extraction of the features that are used to guide attention act in parallel, or independently (see Fig. 1.1.5). The main reason for this distinction is that, sometimes, information available to early or attentive vision is not available to guide the deployment of attention - like intersection for example (J. M. Wolfe & DiMase, 2003). Conversely, some of the characteristic of attentional guidance are not reflected in attentive vision - e.g. as will be seen further on, guidance by color or orientation appears to be coarse and categorical, whereas attentive vision has access to much more fine-grained color and orientation information (see chapter 1.2.1.1.2).

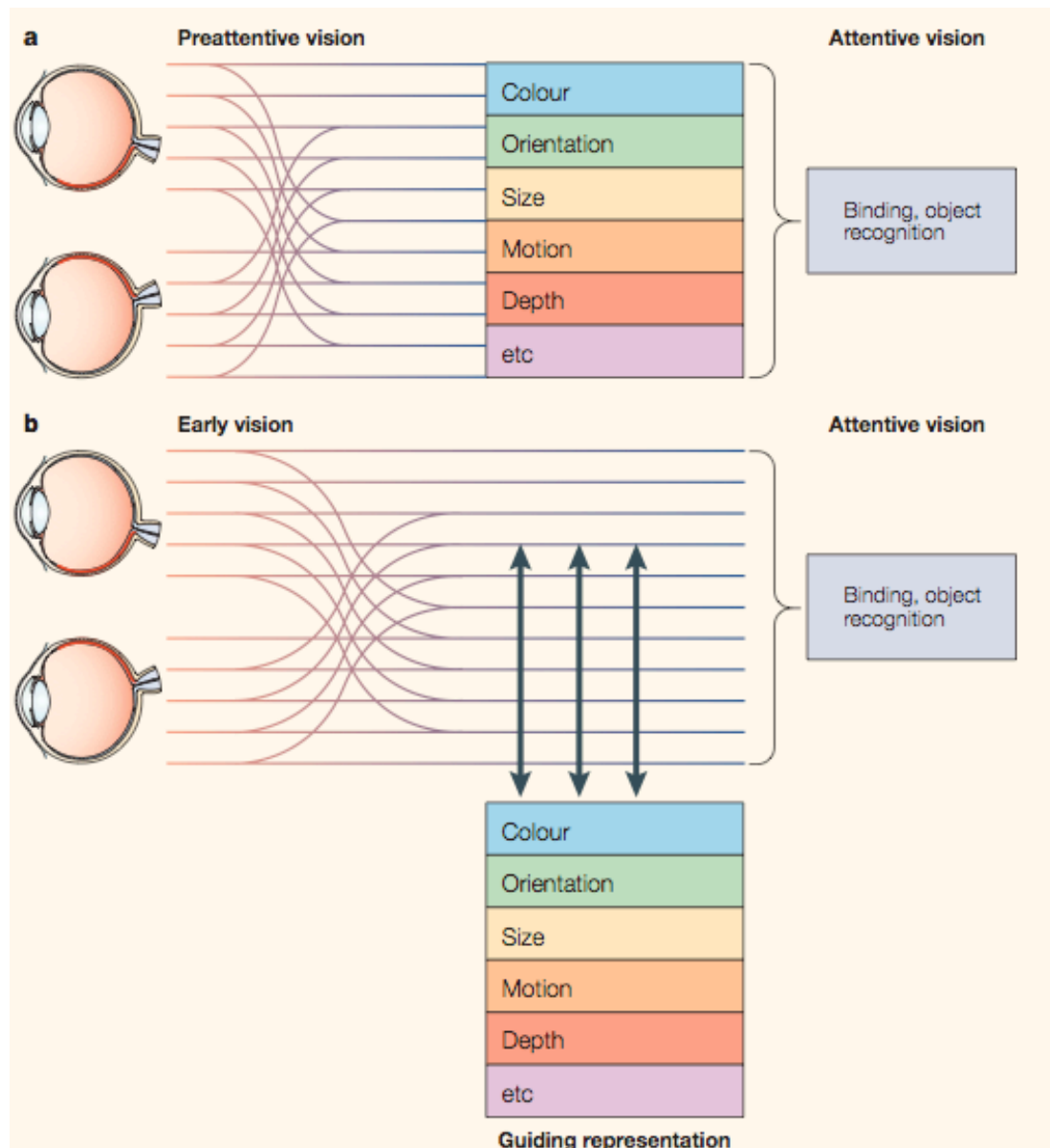


Figure I.1.5

- A. A standard linear two-stage model with a parallel preattentive stage followed by a serial attentional process.**
- B. B. The model proposed by Wolfe & Horowitz, in which low-level vision and guiding feature extraction act independently. From (J. M. Wolfe & Horowitz, 2004).**

The concept of attentional guidance by basic features has been very fruitful in explaining the results obtained in experiments performed on artificial visual items that are made from simple combinations of these features. However, it is known that object identification relies at least partly on holistic processing and not only on a simple combinatorial analysis of features (Logothetis, 2000; Pelli & Tillman, 2007; Tanaka & Farah, 1993). Hence, it might be that the evidence - which we will discuss in the following paragraphs - for the role of these elementary features in guiding attention would not be valid in ecological conditions but would only result from a strategy adopted by subjects when confronted to the specific requirements of the task they have to perform in the laboratory. The special case of shape in the feature

classification of Wolfe, which he defines as a “probable attribute”, is interesting because it points out the limitation of the “featural” approach (Duncan, 1987). Indeed, do we have to consider shape as a distinct feature (circle, square, diamond, ...), or as a combination of simple features like orientation, curvature, closure, line termination, etc...? In summary, the ecological validity of the feature approach of attentional guidance remains an open experimental question.

I.1.2.1.1.2 The effect of target-distractor similarity

Obviously, as stated above, a guiding feature will lead to efficient search only if the difference between target and distractors for this particular feature is great enough. This effect of similarity between the target and distractors has been extensively studied by Duncan & Humphreys. In their initial study, they used a letter search task (mainly rotated T and L) in which they modified the similarity between the target and distractors and the heterogeneity of the distractors (Duncan & Humphreys, 1989). They found that the interaction between these manipulations had a strong effect on search efficiency: search efficiency decreased importantly in case of a low distractor-distractor (D-D) similarity and a high target-distractor (T-D) similarity. However, the T-D similarity had almost no effect on search efficiency in case of a high D-D similarity, the search being efficient in all cases. Likewise, D-D similarity had no influence on search efficiency in case of a low T-D similarity (see Fig I.1.6).

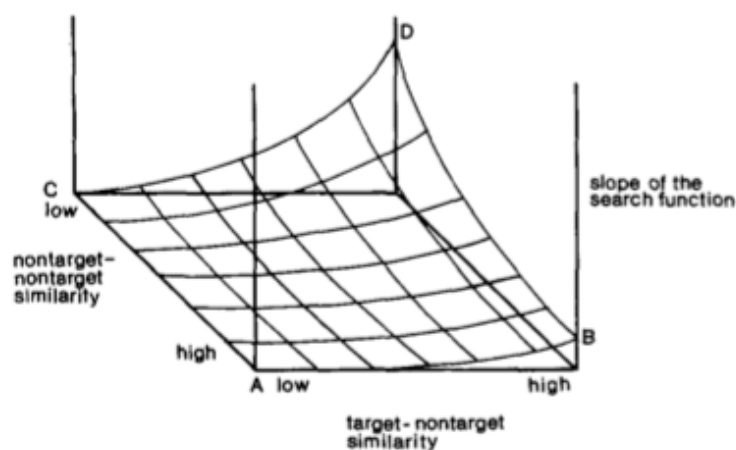


Figure I.1.6

Schematic representation of the interaction between target-distractor and distractor-distractor similarity on search efficiency. From (Duncan & Humphreys, 1989).

To explain their findings, Duncan & Humphreys proposed a model in which visual items compete to access to visual short-term memory. Each item receives a certain weight, depending on its relevance to the task, or resemblance to the target, and which determines its access priority to visual short-term memory. Moreover, when the D-D similarity is high, grouping occurs between the distractors, which can then be suppressed altogether from further processing. In fact, this theory exhibits many similarities with the Guided Search Theory, which was published at the same time. In the Guided Search Theory, each item is represented in a priority map, and the activation corresponding to this item in the map is proportional to its conspicuity and its relevance to the task. A critical addition to Guided Search in the model of Duncan & Humphreys is the inclusion of grouping phenomena, which was omitted in Wolfe’s theory.

These results suggest that similarity is a critical factor that determines efficiency of the search, and hence, presumably attentional guidance. However, similarity is a relative notion. In particular, which level of T-D and D-D similarity is needed to achieve efficiency in a visual search task? This specific question was addressed by Nagy and Sanchez with respect to color (Nagy & Sanchez, 1990). They first measured the minimal color difference that observers are able to discriminate. This difference can be represented by the MacAdam ellipse, which corresponds to the region in the color space containing all colors that are indistinguishable from the color at the center of the ellipse. Then they measured the minimal color difference between target and homogeneous distractors that yields an efficient search, they computed ellipses representing this difference in the color space and compared them to the MacAdam ellipses. They found that the search ellipses were much larger, and had a different shape than the MacAdam ellipses, suggesting that the mechanisms involved in attentional guidance are different, and much coarser than the mechanisms involved in visual discrimination (see section 1.2.1.1.1).

It appears that beyond the quantitative difference in the relevant feature between target and distractors, the visual category to which they belong is a factor that strongly affects search efficiency. For example, in a study by Jeremy Wolfe, subjects had to perform a feature search task in which the target was defined by its orientation (J. M. Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992). Distractors were heterogeneous, i.e. could have multiple different orientations, and while keeping T-D similarity constant, they manipulated the category in which both target and distractors could be included. For example, in their experiment 3, the target could either be -10° with -50° and $+50^\circ$ distractors; 10° with -30° and 70° distractors; or 20° with -20° and 80° distractors (see Fig. 1.1.7). In the first case, the target is the only item belonging to the category "steep". In the second case, the target is the steepest but the -30° distractor is considered steep as well. And in the third category, the target is just as steep as one of the distractor. They found that the "steep target" condition was clearly the most efficient one. Moreover, they confirmed that this category effect could be found with other categories such as "leftward oriented" or "tilted". Color category was also found to influence search efficiency (Daoutis, Pilling, & Davies, 2006).

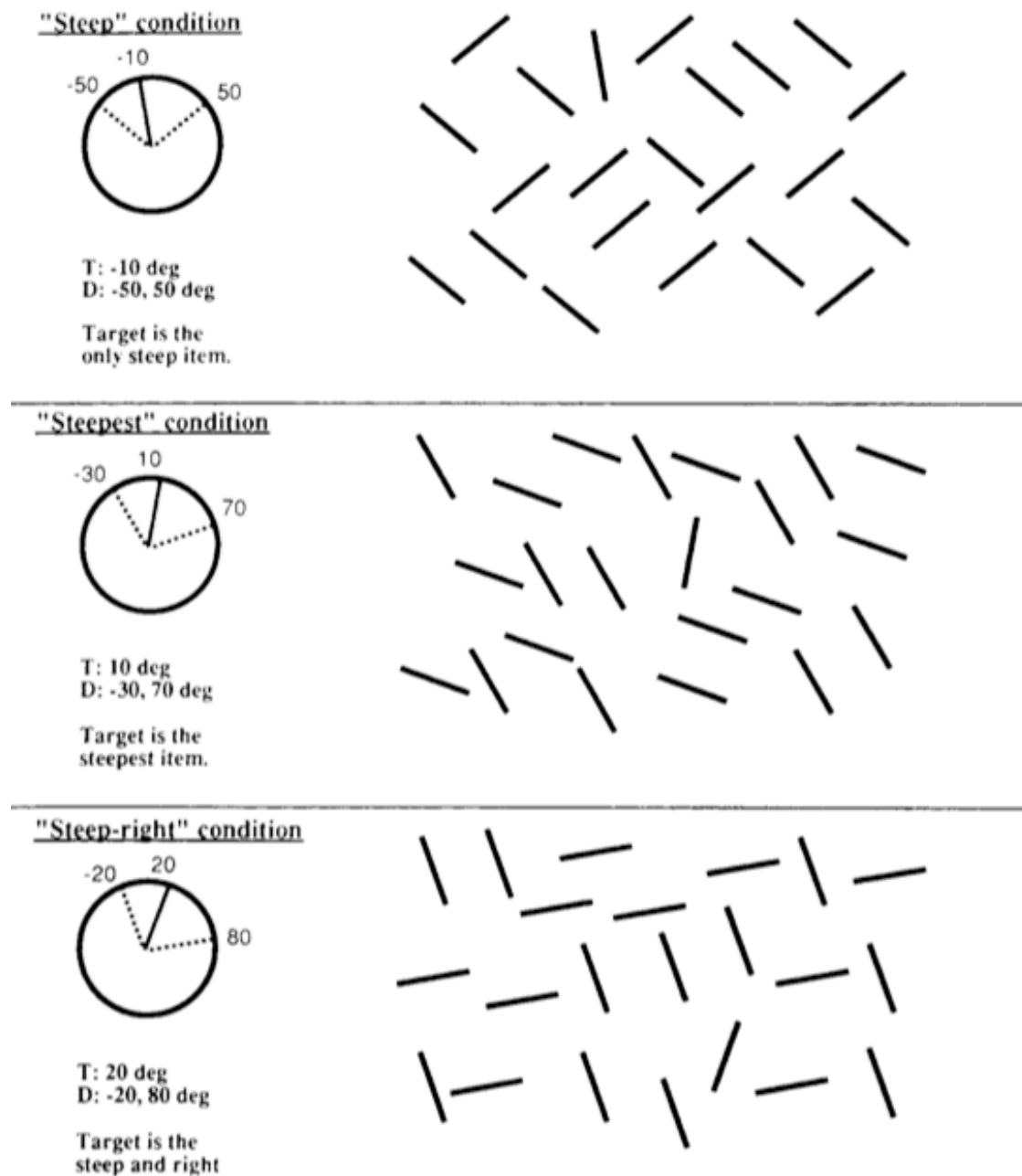


Figure I.1.7.

The three conditions compared in the Experiment 3 of the Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992 study. Note that there is a mistake in the middle part of the figure. Instead of 70° oriented bars as indicated in the circle on the left, -70° oriented bars are shown in the sample of visual search display on the right.

Concerning the quantitative analysis of the role of D-D similarity, an interesting theory has been proposed by D'Zmura with respect to color (D'Zmura, 1991). He suggested that search efficiency was greatly affected by whether the target could be linearly separable from the distractors in the color space. For example, if the target color is orange and distractors are either red or yellow, no line can be drawn to separate the target from the distractors because distractors color "surround" target's color. In

contrast, if the target is red and the distractors are either orange or yellow, a line can separate the target from the more yellow distractors and the search is more efficient. The validity of the concept of linear separability was confirmed in a more recent study, where complex combinations of target and distractors colors were used (Bauer, Jolicoeur, & Cowan, 1999) and was also extended to the shape and the size dimensions (Hodsoll & Humphreys, 2001; Saumier & Arguin, 2003).

I.1.2.1.1.3 The role of stimulus-driven and goal-directed factors

In the above chapters, we discussed the nature of the factors that determine the efficiency of visual search. In efficient visual search, the target is often conspicuous, because strikingly different from the distractors but it contains also target-specific features that are easier to differentiate from the features of the distractors, hereby making goal-directed guidance more effective. Hence, it is difficult to determine whether factors supposed to affect attentional guidance toward the target in this case are stimulus-driven, or goal-directed. A way to investigate the role of these two factors is by controlling the amount of information defining the target. This manipulation can be done in odd singleton searches, as described in section 1.2.1.1.3.1. Another useful approach to investigate stimulus-driven factors of attentional guidance is to study the effect of irrelevant conspicuous distractors during visual search, a phenomenon known as attentional capture, addressed in the section 1.2.1.1.3.2.

I.1.2.1.1.3.1 Singleton search

In singleton search, i.e. search in which the target is presented amongst homogeneous distractors differing from the target by a single feature, information on target identity can be limited. In some cases, subjects do not know in advance what will the target be like but they know only that it will differ from the surrounding distractors. Therefore, in this case, they have to search for the odd item (Bravo & Nakayama, 1992; Friedman-Hill & Wolfe, 1995). From trial to trial, either the feature value (e.g. red or green, (Bravo & Nakayama, 1992)), the feature dimension (orientation or color, (H. J. Muller, Heller, & Ziegler, 1995)), or both the feature value and dimension (J. M. Wolfe, Butcher, Lee, & Hyle, 2003) that differentiate the target from the distractors can change. Hence, the identification of the target must rely at least partly on conspicuity. In other cases, however, the features and dimensions that identify the target are constant across blocks of trials. Results from all these studies show that in singleton search, the efficiency of the search is usually not affected by whether target characteristics change from trial to trial, or remain constant throughout each block. This suggests that removing the information on target identity does not alter the efficiency of attentional guidance and therefore, that stimulus-driven factors must play an important role in attentional guidance in efficient feature searches. However, the pre-knowledge of the target feature and dimension speeds up search by a fixed amount of time. This indicates that goal-directed factors influence the search processes involved either before or after the attentional bottleneck stage. Finally, in cases where either target feature value or dimension changes on a trial-by-trial basis, the performance is greatly influenced by the characteristics of the previous trial. When the target feature/dimension remains identical in two successive trials, RT is reduced, a phenomenon called priming of pop-out (Maljkovic & Nakayama, 1994). Previous target location also induces a strong priming effect on detection performance: when the target appears successively at the same location, the target detection occurs much faster (Maljkovic & Nakayama, 1996). These results indicate that, even in cases where this strategy is not efficient because target characteristics

change on every trial, observers automatically use previous trial information in their search strategy. In addition, in their study, Maljkovic & Nakayama demonstrated that priming of pop-out could not be prevented, even when the subjects know that the upcoming target is different than the previous one.

Theeuwes and colleagues (J. Theeuwes, Reimann, B. & Mortier, K 2006) used a singleton task in which the feature dimension (shape or color) of the target was cued at the beginning of every trial, by displaying the corresponding word (“shape”, “color” or “equal”) on the screen, with 83% validity (replicating an earlier experiment by Muller (H. J. Muller, Reimann, & Krummenacher, 2003)). They showed a beneficial effect of valid cues and a detrimental effect of invalid cues on RT, demonstrating that observers used the cue information to adapt their search strategy. They also observed strong priming of pop-out effects, which did not interact with the effect of the cues, suggesting that priming could not be influenced by goal-directed factors. The most interesting experimental manipulation was in Experiment 2, where observers, instead of responding merely to target presence or absence, had to report the orientation of a line displayed inside the target. In this case, the cue validity effect completely disappeared, suggesting that the beneficial effect of the cue on RT observed in Experiment 1 was not explained by attentional guidance. Indeed, if this were the case, attention would be guided more quickly to the target following valid cues, and the discrimination of the line orientation should be enhanced as well, in contrast to Theeuwes’s findings. Interestingly, the intertrial priming of popout effect remained, confirming that it relies on attentional factors. Finally, when using the singleton item itself as a cue at the beginning of each trial (Experiment 4 & 5), the cue validity effect reappeared, but even in cases where it was totally non informative or even counter-productive (Experiment 5). This finally shows that some cues can have an automatic effect on attentional allocation, which cannot be overdriven by goal-directed factors of guidance. This study of Theeuwes points out two important conclusions. First, it shows that conspicuity seems preponderant in the control of attentional guidance during singleton search, and hence presumably during feature search. Second, it demonstrates that using efficiency and RT measurements in visual search tasks as a way to study attention allocation might be flawed because they also depend on other factors related to signal detection, decision, and response selection. This issue will be the topic of the last paragraph of this section.

In summary, it appears that attention during the performance of singleton search is guided by conspicuity and that the knowledge of the target feature might affect search performance through its influence on non-attentional processes. However, in this case, conspicuity is a relevant feature since it can be used to identify the target and hence, cannot be considered as a stimulus-driven factor. To assess the role of stimulus-driven factors in singleton search, one must determine whether singletons attract attention when they are not the target of the search. This is the topic of the attentional capture literature.

I.1.2.1.1.3.2 Attentional capture

Whether conspicuous items are able to attract attention automatically seems at first sight a straightforward and easy to address question. However, and surprisingly, this question has been intensely debated in the literature since 20 years and did not receive a consensual view yet. In attentional capture experiments, an irrelevant conspicuous distractor is displayed during a visual search task. The conspicuity of this distractor is induced either by its abrupt onset or by its difference in visual features with respect to the other items (singleton capture). The classical result

described in these experiments is that, when the conspicuous distractor is displayed, RT for target detection increases (Jonides & Irwin, 1981; Pashler, 1988). This finding has been regarded as evidence that the conspicuous distractor captures attention and hence, delays target detection. The critical question, however, is whether or not this capture occurs in a purely stimulus-driven way, with no possible control from goal-directed factors. Against this view, Folk and colleagues showed that capture occurred only when the irrelevant distractor shared some feature with the target (Folk, Remington, & Johnston, 1992), and proposed the concept of contingent capture, in which attentional capture is contingent on the current task sets: if one searches for a red target, a red distractor will capture attention, but not otherwise. Along the same line, Bacon & Egeth proposed that earlier findings of attentional capture were caused by a specific strategy adopted by subjects (Bacon & Egeth, 1994). When they are asked to find a singleton target, and they do not know the actual feature value of this upcoming target, they adopt a singleton search strategy, in which they search for the conspicuous item. In this case, an irrelevant singleton attracts attention. But when they are asked to find a target with a specific feature, such as the color red, they enter in a feature search mode, and singleton distractor are no longer able to capture attention. Therefore, they propose that stimulus-driven attentional capture is totally under the control of goal-directed factors. While this view remains currently accepted by many authors (reviewed in (Burnham, 2007)), other researchers argue in contrary that stimulus-driven attentional capture is possible, and that conspicuous distractors can attract attention even when goal-directed factors should prevent this capture (Forster & Lavie, 2008; Schreij, Owens, & Theeuwes, 2008; Yeh & Liao, 2008; Yeshurun, Kimchi, Sha'shoua, & Carmel, 2008). In a recent study similar to the one described in the previous chapter, Theeuwes and colleagues used a shape singleton search in which the target feature could either be cued or not at the beginning of the trial (J. Theeuwes & Van der Burg, 2008). These cues could either be word (Experiment 1, "circle" or "diamond") or symbolic cues that were identical to the upcoming target (Experiment 2). Subjects had to report the orientation of a line displayed inside the target. They found that even in trials where the cue indicated the target feature, and in which subjects should hence adopt a feature search strategy, color irrelevant singleton induced a significant increase of the RT. This result was observed in both the word and symbolic cue conditions.

Finally, similarly to singleton search experiments, the attentional capture account of the mere observation that RT increases in the presence of a conspicuous distractor has been questioned (Ester & Awh, 2008; Folk & Remington, 1998). Ester & Awh used a classical attentional capture paradigm in which a singleton target was displayed amongst distractors (Ester & Awh, 2008). The feature of the target (square or circle) was constant (Exp.1) or variable from trial to trial (Exp.2). Occasionally, a conspicuous distractor, with a different color than the other distractors, was displayed. Subjects had to respond to the orientation of a gap in the contour of the target. When subjects were required to make a speeded response, and that display duration was unlimited, classical attentional capture effects were observed, i.e. RT was longer when the conspicuous distractor was displayed. However, if this effect was actually explained by a capture of attention by the distractor, Ester & Awh predicted that, in addition to increasing the RT, the presence of the conspicuous distractor should also impair accuracy of gap discrimination when the display duration is sufficiently short to prevent attention to shift from the attracting distractor to the target. When using such very short display durations (28 ms on average), authors did not find any effect of the conspicuous distractor on accuracy. This result strongly questions the validity of the interpretation that lengthening of the RT in presence of a distractor is explained by attentional capture and suggests instead a critical role of later, post-perceptual processes. In contrast, Chastain and Cheal found that target detection occurs faster when the conspicuous distractor is displayed near

the target (Chastain & Cheal, 2001). This effect of proximity suggests that the attentional spotlight is actually attracted to the distractor and includes the neighboring target, as long as it is close enough. These contradictory findings point out the current lack of clarity regarding the mechanisms involved in the attentional capture phenomenon.

I.1.2.1.1.3.3 Feature contrast

As already explained, one of the factors that determine the conspicuity of a visual object is its difference with respect to other objects. For example, a single vertical line amongst multiple horizontal lines will pop-out. Hans-Christoph Nothdurft studied extensively this effect of feature difference, which he calls “feature contrast” (H. C. Nothdurft, 1993b). He compared the effect of feature contrast for different feature dimensions, such as color, motion and orientation, investigated the spatio-temporal properties of the conspicuity effect and how the different feature contrast dimensions interact with each other.

In order to compare the effect of feature contrast across different combinations of feature dimensions (orientation, color, motion, luminance), Nothdurft used a task in which two line arrays were displayed – one at the left and one at the right of fixation (H. Nothdurft, 2000a, 2000b; H. C. Nothdurft, 1993a). On each side, a single item differed from all other items along one or two feature dimensions, which were different at both sides of fixation. Subjects had to report which of the two single items they perceived as the most conspicuous: the one on the left or the one on the right. This approach is very peculiar in that it relies on a subjective assessment of conspicuity, but the results obtained with this method seem nevertheless rather robust, with reasonable between- and within-subject variability. Nothdurft showed that in most cases, an item was more conspicuous when different from the other items in two than in one feature dimension, but this additivity effect was highly non linear. This suggests that the conspicuity arising from different feature contrast dimensions relies on different and at least partly independent mechanisms.

To study the temporal properties of the conspicuity effect in different feature contrast dimensions, Nothdurft used another interesting methodology. He presented an array of lines, with one line differing from all the others. The feature values of the single items and of the other items were exchanged in successive frames, with a variable rate of frame change. For example, in one frame, the target was oriented at 45° and the distractors at 135°, in the next frame the target was 135° and the distractors were 45° and in the following frame the target was back to 45° and the distractors to 135° again. Nothdurft reasoned that as long as the duration of each frame was below the time needed to process feature contrast in the tested dimension, the single target should not be detected. As the frame rate goes down, and the frame duration goes up, the visual system progressively has more time to process conspicuity, and the target pops out. The results elegantly demonstrate that some feature contrast dimensions are processed more rapidly than others. Amongst the tested dimensions, luminance (median frame duration allowing target localization = 57 ms) and color contrast (64 ms) were processed the most rapidly, orientation contrast (130 ms) the least rapidly and motion contrast processing speed was intermediate (85 ms), but inconsistent across subjects (see Fig. I.1.8). This also confirms that the mechanisms involved in the computation of feature contrast are at least partly different across these feature dimensions.

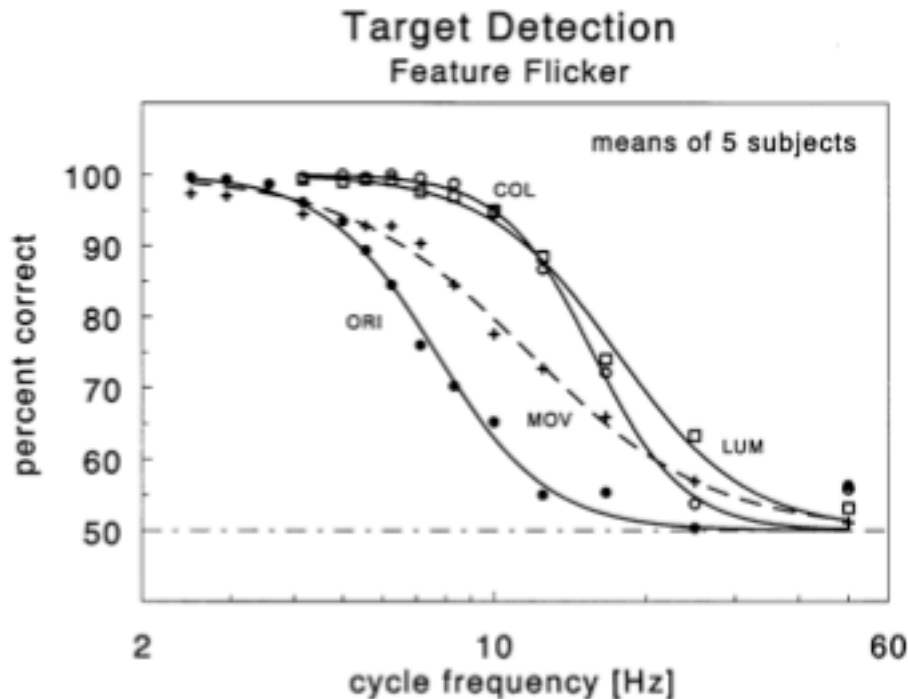


Figure I.1.8

Average performance of the five subjects in the two-alternative forced choice target localization task, as a function of frame change rate (cycle frequency). From (H. Nothdurft, 2000b).

I.1.2.1.1.4 Implicit assumptions in the use of visual search to study attentional allocation

The results described so far used mainly RT and search efficiency as dependent variables to investigate attentional allocation. We will discuss the validity of these two experimental measures with respect to attentional allocation.

The interpretation of RT measurements in most visual search experiments assumes implicitly that any RT modification is explained by attentional allocation mechanisms. However, twenty years ago, Santee and Pashler proposed a theoretical framework that clearly differentiates what can be inferred respectively from RT and accuracy effects in psychology experiments (Santee & Egeth, 1982). They stated that under so-called data-limited viewing conditions, in which exposure duration is short, accuracy depends on perceptual processes, such as attentional allocation, whereas RT depends more on post-perceptual, response-related processes. Moreover, under resource-limited viewing conditions, in which the display duration is not limited - the most common viewing condition used in visual search experiments - both accuracy and RT depend more on post-perceptual processes. This theoretical issue is confirmed by empirical results. We discussed evidence in the two previous sections that the interpretation of RT in singleton search (J. Theeuwes, Reimann, B. & Mortier, K 2006) and attentional capture experiments (Ester & Awh, 2008) in terms of attentional allocation can be flawed.

The use of search efficiency as a mean to investigate attentional allocation relies on the implicit assumption that visual search efficiency depends on attentional allocation: visual search is efficient when attention can be directly guided onto the

target. In contrast, in inefficient search, it is assumed that attention must serially explore the visual items in order to find the target, and hence, that target features cannot be used to guide attention efficiently. However, the theoretical limitations of this assumption have also been pointed out more than 30 years ago (J. Townsend, 1971). More recently, a whole theoretical framework has been developed, using a signal theoretical approach to visual search (see Fig. I.1.9) (Verghese, 2001). In this theory, visual features are represented by noisy signals and solving the visual search task requires to differentiate signals in which the target is present from signals in which the target is absent. Target present and target absent displays are represented by distributions with different means. The distance between these means depends on the target-distractor similarity whereas the spread of the distributions depends on distractor-distractor similarity and on the number of distractors. In her review, Preeti Verghese shows that adding distractors, by increasing the spread of the target-present and target-absent distributions, increases the overlap between these distributions, and decreases performance (see Fig. I.1.9). Hence, this theory gives an account of the set-size effect that relies exclusively on parallel mechanisms. This points out that efficiency of visual search might depend on the signal to noise ratio of the target-defining feature rather than on attentional guidance on the target and that interpretation of all the aforementioned results could be erroneous.

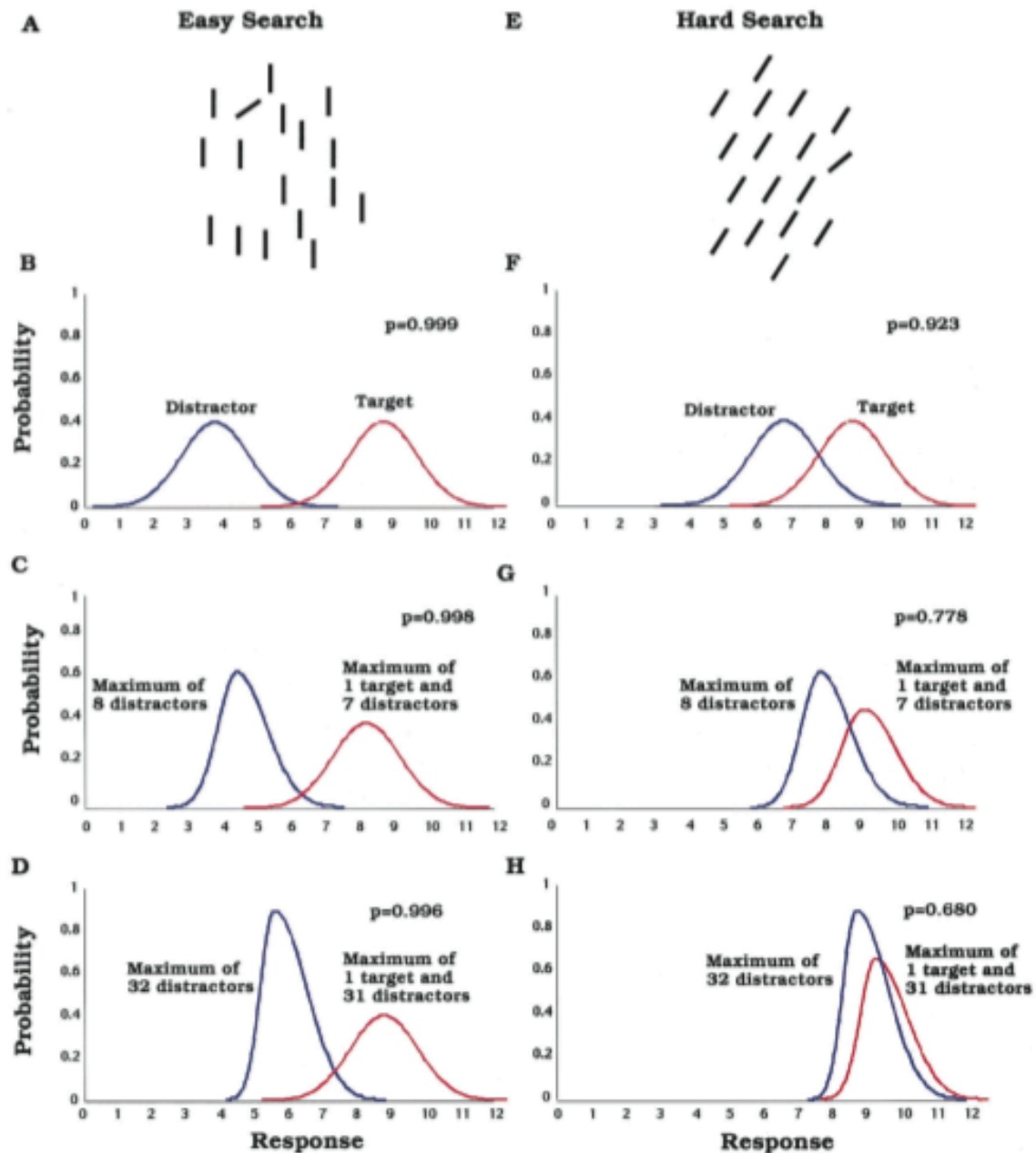


Figure I.1.9

Schematic representation of the signal detection theoretic account of visual search. X-axes represent the response of a putative feature detector and Y-axes, the probability of observation. Left and right traces in each graph are for target absent and target present distributions respectively. The effect of increasing the number of distractors is shown for easy (B, C and D) and difficult (F, G and H) search. From (Verghese, 2001).

The efficiency of parallel mechanisms in vision has been clearly evidenced in other visual tasks than visual search. Observers are able to perform complex visual categorization tasks, e.g. determining whether a picture contains the image of an animal, very rapidly, in around 120 ms (Kirchner & Thorpe, 2006). But more strikingly, this performance remains almost unaffected when two pictures are displayed instead of one (Rousselet, Fabre-Thorpe, & Thorpe, 2002). In addition, when four pictures are displayed, the small magnitude of the performance decrease and the distribution of the reaction times are more compatible with parallel than serial

models of visual processing (Rousselet, Thorpe, & Fabre-Thorpe, 2004). Finally, this task can also be performed in the periphery while another attention-demanding task is performed centrally (F. F. Li, VanRullen, Koch, & Perona, 2002), even though the interpretation of this result is unclear (VanRullen, Reddy, & Koch, 2004). Altogether, these findings point out the efficiency of parallel processing in vision and validate the idea that visual search tasks can be performed in parallel without the need for serial attentional shifts.

However, whereas signal detection theory gives an alternative, potential account of the efficient-inefficient dichotomy, whether inefficient visual search is actually performed serially or in parallel remains unknown. Several studies have compared parallel and serial models in their ability to predict RT, accuracy, or speed-accuracy trade-offs in different visual search tasks, and found support for the validity of the parallel account (Doshier, Han, & Lu, 2004; Eckstein, Thomas, Palmer, & Shimozaki, 2000; McElree & Carrasco, 1999; Palmer, Ames, & Lindsey, 1993; Palmer, Verghese, & Pavel, 2000). However, these studies provide only very indirect evidence for the parallel account of inefficient search. Moreover, some recent evidence for the existence of serial mechanisms during inefficient visual search has also been provided (Bricolo, Ganesini, Fanini, Bundesen, & Chelazzi, 2002; Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Woodman & Luck, 2003). Consequently, the question of the role of the parallel versus serial mechanisms in visual search remains to be clarified.

Finally, it must be clear that parallel models reject the need for *serial* shifts of attention in visual search tasks but do not question the need for attention *per se* in such tasks. Attention can influence performance in search tasks by selecting the most potentially relevant items (Verghese, 2001). This selection helps to reduce the spread of the distribution either by reducing distractors influence (Z. L. Lu & Doshier, 2004) or by enhancing the target signal (Cameron, Tai, & Carrasco, 2002). The necessity of attention during visual search has been experimentally evidenced by means of cueing experiments and dual tasks, even though these results are based on the interpretation of RT. Cueing attention allocation during an efficient visual search task strongly affects RT: when attention is cued to a non-target location, RT is longer than when it is cued to the upcoming target location (J. Theeuwes, Kramer, & Atchley, 1999). Along the same line, it has been shown that efficient search is affected by the concurrent performance of a central, attention-demanding task (Braun, 1994; Joseph, Chun, & Nakayama, 1997) (see however (VanRullen, et al., 2004)). These results provide evidence that attention is involved at some stage, even in efficient visual searches.

1.1.2.1.2 Direct measurement of attentional allocation during visual search

Given the aforementioned remarks, concerning the validity of the interpretation of RT and efficiency with respect to attentional allocation, a different approach to the question of the factors of attentional guidance must be found. As discussed above, spatial attention is a selection mechanism that increases the discriminability of visual items that fall inside the attentional spotlight (Carrasco, 2006; Cave & Bichot, 1999; Z. L. Lu & Doshier, 2004). Therefore, the best way to measure attentional allocation during visual search is to assess perceptual performance on relevant locations concurrently to search performance. Sagi and Julesz provided one of the first attempts to use such an approach to measure attentional allocation, albeit not in a visual search task. They used a dual task in which observers had to discriminate the orientation of a target stimulus and in the same time, report the presence or absence of a near threshold probe stimulus (Sagi & Julesz, 1986). The location of the probe stimulus was varied with respect to the location of the target. They found that the

probe stimulus was more likely to be correctly reported when presented in the vicinity of the target. This is evidence that, even in such a simple task as orientation discrimination, spatial attention selects the location of the target.

Kim & Cave (Kim & Cave, 1995) were the first to use the probe technique to assess the allocation of attention during visual search. They used both dot detection and letter discrimination tasks concurrently to feature and conjunction (shape and color) visual search tasks. In the case of dot detection, a dot followed the visual search presentation in 25% of the trials, and could appear on any of the search locations after a variable amount of time (stimulus-onset asynchrony, SOA). Subjects had to respond to the dot as quickly as possible by pressing a button. Then they were asked whether the target of the search was present or absent. In the case of letter discrimination, letters were displayed on all visual search item locations with a variable SOA. Here, subjects responded first to the visual search task and then indicated which letters they had perceived. In both the dot detection and the letter discrimination dual tasks, the visual search display duration was very short (15 ms in the feature search and 45 ms in the conjunction search) in order to prevent eye movements. Kim & Cave found, both in the dot detection and in the letter discrimination tasks that probes were better reported when presented at the target location, or at locations occupied by distractors sharing either the same color or the same shape as the target (see Fig. 1.1.10). They found no clear effect of the distance with respect to the target, and an effect of SOA only in the dot detection condition. These results converge with the findings described in section 1.1.1 of this thesis, dealing with overt visual search tasks, and suggest that attention, like eye movements, can be guided by visual features when they are pertinent to the task at hand.

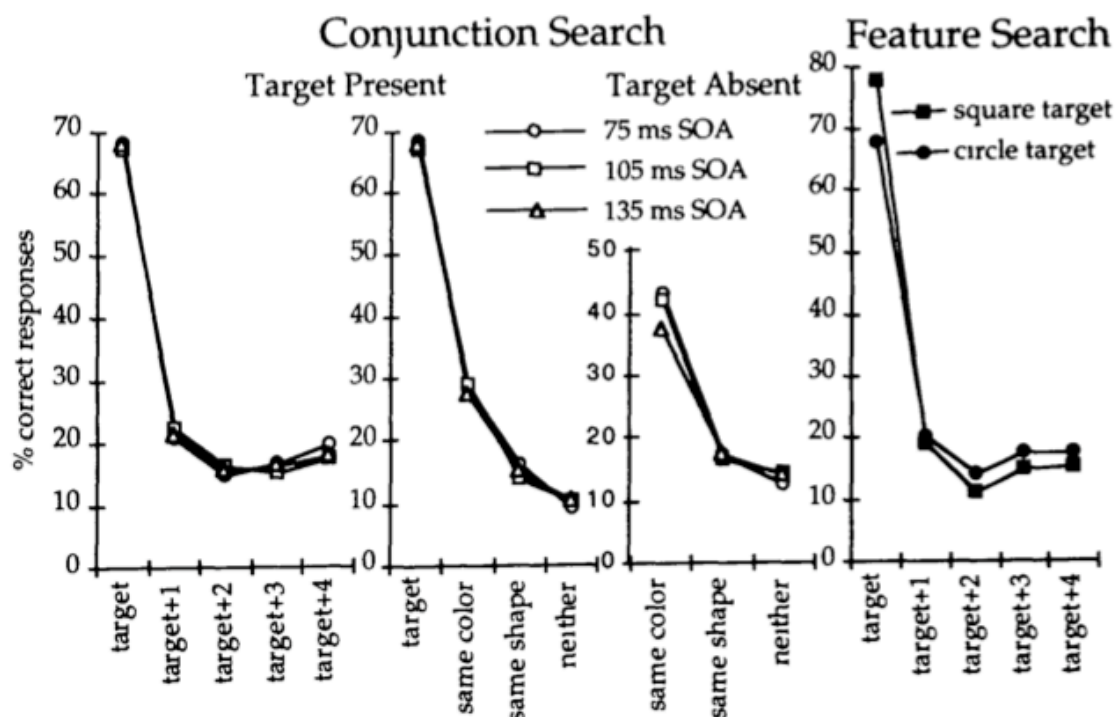


Figure 1.1.10.

Results from the visual search – letter discrimination dual task in the Kim & Cave study (Kim & Cave, 1995).

Percentage of correct letter identification (Y-axis) is indicated as a function of distance

with respect to the target (leftmost graph for conjunction search and rightmost graph for feature search), item features in target present (middle left) and target absent (middle right) conditions. SOA is represented by the shape code.

The probe technique has been used also to address the question of attentional capture (Kim & Cave, 1999b; Lamy, Tsal, & Egeth, 2003) but the conflicting results from these studies do not bring new insights into this complex problematic. However, the observation that probe detection can be enhanced (Kim & Cave, 1999b) or slowed down (Lamy, et al., 2003) by the conspicuity of the co-localized distractor confirms that attentional allocation is involved at least partly in the attentional capture phenomenon described above.

In summary, it appears that using probe detection performance as a mean to measure attentional allocation during visual search performance can prove to be a very valuable tool. Indeed, this approach provides a direct measurement of attention allocation instead of relying on indirect effects on RT.

1.1.2.2 Attentional guidance in cueing experiments

In his pioneering work, Posner asked observers to respond to the onset of a visual stimulus as fast as possible, and a visual cue (a central arrow) was presented before the target and could indicate the correct (valid) or incorrect (invalid) location of the upcoming target (Posner, et al., 1980). The proportion of valid trials was superior to the proportion of invalid trials. Therefore, the cue was informative and indicated the most probable location of the target. Such informative cues are called endogenous, which is equivalent to the term goal-directed that we use throughout the remaining of the present work. The critical observation of Posner was that RTs were faster in the valid than in the invalid condition. This was considered as evidence for attentional allocation on the location indicated by the cue: whereas in the valid condition, attention is already allocated on the right location when the target appears, in the invalid condition attention has to shift to the target appearing at the opposite location, resulting in an RT increase, or an accuracy decrease. Since then, dozens of studies confirmed that beyond detection, stimulus discrimination (Mackeben, 1999; Yeshurun & Carrasco, 1999) and even subjective perception (Carrasco, Ling, & Read, 2004) can be influenced by cueing. There is an abundant literature addressing the question of the mechanisms of selection involved in cueing experiments. It remains currently unclear whether attentional selection induces an enhancement of the selected signal (Carrasco, 2006) or an exclusion of the noise (Z. L. Lu, Lesmes, & Doshier, 2002), i.e. of the non selected signals.

In the following we will examine what kind of information can be used to guide attention in endogenous cueing experiments, and whether stimulus-driven attentional guidance can be achieved by conspicuous cues.

1.1.2.2.1 Endogenous cueing

As discussed above, location cues are known for long to be able to efficiently guide attention (Posner, et al., 1980) to likely target locations. When valid, the cue indicates the upcoming target location, but in many experiments, the cue can also be invalid in some trials, and indicate a wrong location. As long as the proportion of valid cues

exceeds the proportion of invalid cues (in a two alternatives forced choice task), the cue is informative and is assumed to have a goal-directed influence on attentional allocation. The question as to whether uninformative cues can be effective will be addressed in chapter 1.2.2.2.

1.1.2.2.1.1 Do informative location cues guide attention?

Most cueing experiments used RT as dependent variable and infer attentional allocation from the observation of a reduction of RT. Consequently, the same remark as in chapters concerning visual search can be made as to whether this effect is really attentional. In fact, in its original work, Posner already opposed two potential explanations of his results: perceptual enhancement at the cued location induced by an attentional shift, or a shift in the decision criterion (Posner, et al., 1980). Indeed, the information provided by the cues could be used to influence decision processes in addition to, or instead of determining attentional allocation. Cathryn Downing addressed this issue in a very thorough study by using a signal detection approach (Downing, 1988). Subjects had to perform four different tasks, on different blocks of trials: luminance detection, brightness discrimination, form discrimination and orientation discrimination. An endogenous central cue was presented to subjects, indicating in which of the 12 possible locations the target was the most likely to appear. This cue was valid in 80% of the trials. In addition, up to three additional targets were displayed at noncued locations. After array presentation, four locations were successively probed and subjects were asked to determine whether a target occurred at each of these probed locations. Downing estimated perception performance and response bias independently by measuring respectively d' (a signal theoretic measure of performance) and β (a signal theoretic measure of bias) at each location, as a function of the distance with respect to the cue. She found that d' was maximal at the cued location in each of the four possible tasks, and decreased with distance. In addition, she found that β at non-cued locations was not affected by cue presentation and that β at the cued location decreased only partly: the 80% validity of the cue predicted a β value of 0.25 at the cued location (strong bias for target present response), whereas actual β values were between 0.46 and 0.88. This shows that perceptual enhancement (d') explained a much greater part of the effect of the cue than decision criterion shift (β) and hence that location cue influence attentional allocation more than decision criterion.

Beyond location, the visual search literature offers us evidence that cues providing feature information can also influence task performance, as discussed above (J. Theeuwes, Reimann, B. & Mortier, K 2006). However, the interpretation of these results in terms of attentional guidance is problematic (see section 1.2.1.1.4).

In the cueing literature, findings in agreement with the existence of selection on the basis of feature information are numerous. These studies are addressed in the following.

1.1.2.2.1.2 Spatial selection by features, feature selection or object selection?

The precise definition of feature-based attention may vary in the literature but generally speaking, it assumes the selection of visual information on the basis of visual features (color, orientation, motion, ...). An early question that arose in the study of the effect of feature cues was whether they guide spatial attention to locations that contain the cued feature, or whether they involve a non-spatial selection of the visual features proper (Cave & Bichot, 1999; C. M. Moore & Egeth, 1998; Shih & Sperling, 1996; J. Theeuwes, 1989). In many, even recent, studies supposed to investigate feature-based attention, this important distinction is not addressed, so that it is impossible to determine whether the selection process under study is based on spatial or featural information. For instance, in an experiment from

the laboratory of Marisa Carrasco, authors used a Posner-like task, in which observers had to covertly attend to a random dot motion stimulus following a 100% informative cue that indicated either target location or motion direction (Liu, Stevens, & Carrasco, 2007). Subjects had to detect a motion speed change in the target stimulus. Authors argue that the cue indicating motion direction controlled feature-based attention. However, it is equally likely that the direction cue directed spatial attention, instead of feature-based attention, to the stimulus exhibiting the corresponding motion. A similar remark applies to the study of Melcher and colleagues, where the effect of a prime on subsequent motion discrimination is contingent on whether its color matches the attended color (Melcher, Papathomas, & Vidnyanszky, 2005). This effect can be explained by spatial attentional capture by the prime with the matching color (contingent orienting, see section 1.2.1.1.3.2).

In some cases, however, it is clear that spatial information alone is not sufficient to control selection. The simple observation that one of two overlapping stimuli, occupying exactly the same position in space, can be selected on the basis of a distinctive feature is a convincing evidence that observers can rely on feature information to select visual objects, when spatial information is not sufficient (Blaser, Pylyshyn, & Holcombe, 2000). But in that case, the question is whether the attended feature only is selected, not the object containing this feature. Whereas this last point may appear irrelevant, it is the distinctive characteristic that makes feature-based attention different than so-called object-based attention. In order to address this question, Blaser and colleagues, used two superimposed gabor stimuli, each of which changed smoothly in color, orientation and spatial frequency during a trial (Blaser, et al., 2000). Observers were required to focus on one of the two superimposed stimuli and keep track of it despite the feature changes. Subjects were very good in this task (> 90% correct). But critically, when required to report sudden changes in two feature dimensions (e.g. orientation and color), performance was much better when these two changes occurred in the same gabor, than in two different gabors. This indicates that, instead of a single feature, all the features of the tracked gabor were selected altogether. Authors argue convincingly that these results are compatible with object-based attention - the gabor stimulus is selected as a whole - and not feature-based attention.

Finally, according to the purest definition of feature-based attention, when a given visual feature is attended, this feature should be selected wherever it is present in the visual field, potentially leading to its selection at multiple locations at the same time. In an attempt to tackle this issue, Saenz and colleagues used overlapping random fields of different motion direction (up and down), or color (red and green), which occupied the same spatial location (Saenz, Buracas, & Boynton, 2003). Two overlapping random fields were displayed at both sides of fixation (hence, four random dot fields were displayed) and subjects had to detect a speed or luminance change in one of the two random fields at both locations simultaneously (see Fig. I.1.11 a. and c.). The critical experimental manipulation was that in some trials subjects had to detect change in the left and right fields exhibiting different features (motion or color) while in other trials, they had to detect change in the dot fields sharing the same features. For example, in the first condition, they had to detect speed change in the left random field with upward motion direction and in the right random field with downward motion direction. Changes occurring in other random dot fields (distractors) had to be ignored. Authors found that subject performance was better when dividing attention to stimuli sharing the same feature than when they had to detect concurrently feature change in random fields exhibiting different features (see Fig. I.1.11 b.). This effect was no longer observed in the absence of distractor (see Fig. I.1.11 d.). Authors argued that the facilitated detection observed when both attended stimuli shared the same feature was explained by feature-based selection of these stimuli, enhancing their processing. There are two strong arguments against

this account. First, subjects had to detect events occurring in another feature than the attended one (speed in the case of motion direction, and luminance in the case of color). Feature-based attention is supposed to enhance the processing of the attended feature and not other ones. Second, the poorer performance of subjects when having to detect changes in fields of dots exhibiting different features can be explained by executive factors. In such a trial, subjects had to detect change in, say, the left random dot field moving upward, ignore the left random field moving downward, detect change in the right random field moving downward and ignore the right random field moving upward. This is likely to be more demanding than to detect change in both downward moving fields. Hence, Saenz's experiment does not provide convincing evidence that selection on the basis of features is distributed in space. A similar remark applies also to a comparable study by Lu and Itti (J. Lu & Itti, 2005).

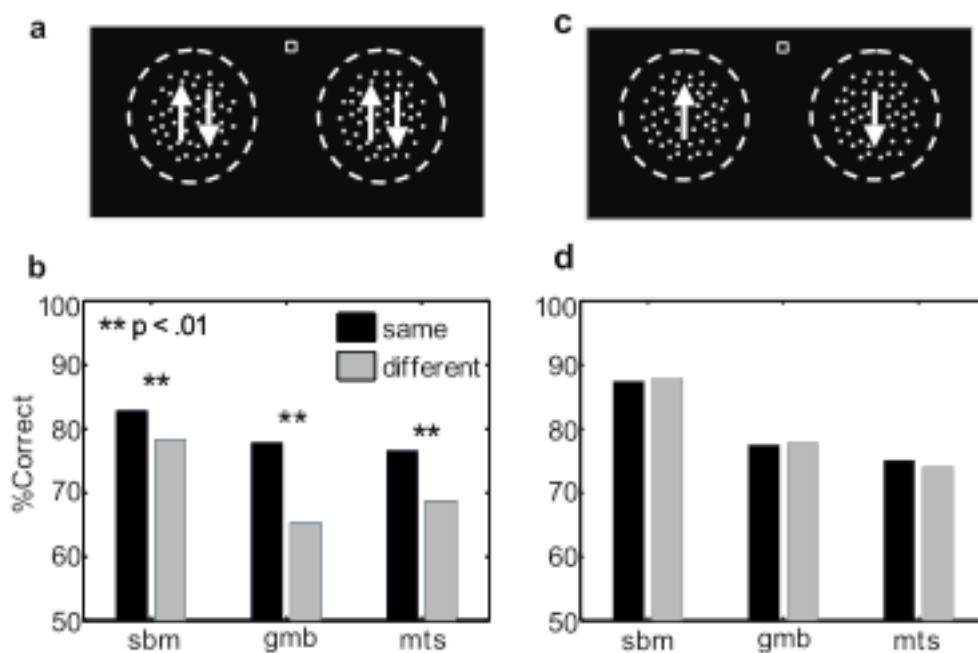


Figure I.1.11

a. and c. schematic representation of the experimental procedure with and without distractors, respectively.

b. and d. task performance for the three different subjects (sbm, gmb and mts) when the attended motion direction was different (gray) or identical (black) on both sides of fixation for the task with (b) and without (d) distractors. From (Saenz, et al., 2003).

Along the same line, Busse and colleagues used similar stimuli than in the Saenz's study (i.e. two times two superimposed random dot fields moving in opposite directions, at the left and right of fixation) to investigate the effect of exogenous location cues and feature cues (in their experiment 2) (Busse, Katzner, & Treue, 2006). A color change occurred randomly in one of the four random dot fields, which exogenously cued a location and a motion direction. Subjects detected faster direction changes in the cued random dot field, than in other fields (i.e. in the case where the cue was valid for both the location and the motion direction). The cue was also effective when indicating the correct location of the change, even though the motion direction was not valid, but importantly, the effect was smaller in this case.

This means that the cue attracted attention to both location and motion direction. However, the cue was ineffective when indicating only the valid motion direction and not the correct location. These results show that exogenous feature cueing do not lead to global selection of the cued feature in the whole visual field, but that when multiple stimuli with different features are co-located in a spatially cued location, exogenous feature-based attention can select one of these stimuli among the others. In other words, they do not demonstrate the existence of feature-based attention like we defined it, but provide evidence for the existence of a feature-based modulation of spatial attention.

In summary, it appears that no clear evidence for feature-based attention, as defined above, can be found in the literature. Feature information is efficient in guiding stimulus selection only when combined with spatial information (Busse, et al., 2006), and this effect is likely to rely on object-based instead of feature-based attention (Blaser, et al., 2000), because in this case, all the features are selected together.

The lack of behavioral evidence for feature-based attention in the literature is in striking contrast with the multiplicity of studies having found that neural activity is modulated by attention to features. In both monkeys (Bichot, Rossi, & Desimone, 2005; Hayden & Gallant, 2005; McAdams & Maunsell, 2000; Treue & Martinez Trujillo, 1999) and humans (Liu, Larsson, & Carrasco, 2007; McMains, Fehd, Emmanouil, & Kastner, 2007; M. M. Muller, et al., 2006; Saenz, Buracas, & Boynton, 2002), it has been demonstrated that feature-specific activity in cells or subpopulation of cells in visual areas are modulated by task constraints, irrespective of their spatial specificity (receptive field). These results correspond to the neurophysiological equivalent of our definition of feature-based attention. This discrepancy can be interpreted in two ways. First, the lack of clear behavioral evidence for feature-based attention so far does not mean that it does not exist. We only showed that the findings currently described in the literature do not provide a convincing demonstration for the existence of spatially distributed feature-based selection. Second, if we assume that the behavioral correlate of feature-based selection in visual areas does not exist, then it follows that the feature-specific enhancement observed in these areas is not accompanied by a corresponding feature-specific enhancement of sensory processing. We might propose that this signal enhancement would be instead a neural correlate of feature relevance, which would guide spatial attentional selection, but would not have an effect on sensory processing *per se*.

1.1.2.2.2 Exogenous cueing

In a variant of the Posner paradigm, an uninformative (50% validity) but very conspicuous cue (typically a brief peripheral onset cue) decreases RT for detecting a target at the cued location and is hence supposed to attract attention in an automatic, exogenous way. To investigate the automatic nature of exogenous shifts, McCormick and colleagues used a Posner paradigm in which a target can appear at two potential locations (McCormick, 1997). The cue is displayed most of the time at the location opposite the target, so that following the cue abrupt onset, supposed to induce an exogenous shift towards the cue, observers have to endogenously shift their attention from the cue to the opposite location in order to detect the target. This reorientation of attention is evidenced by the fact that, for short stimulus-onset-asynchronies (SOA), the target is detected faster at the exogenous cue location (invalid trials), because of the exogenous shift towards the cue, while later on, RT becomes shorter when the target appears at the opposite location (valid trials), where the target is the most likely to appear. The critical experimental manipulation is in the contrast of the cue. Authors added a condition in which the cue contrast was very low. In that condition, observers failed to consciously perceive the cue, and could not

use it anymore to allocate attention on the expected target location. However, McCormick observed that even in this condition, at short SOAs, RT was shorter when the target appeared at the cue location, demonstrating its exogenous effect. They conclude that stimulus-driven orienting can be automatic and completely independent of awareness.

However, as explained above, RT reduction is not an unequivocal evidence for attention allocation, and the hypothesis that exogenous cues might have decisional instead of perceptual effect on detection should be considered as well. Prinzmetal compared the effects of endogenous and exogenous cues on accuracy and RT (Prinzmetal, McCool, & Park, 2005). They opposed two different hypotheses regarding the effect of the cue. The first hypothesis is called “channel enhancement”, and corresponds to the classical view that cues direct attentional selection and leads to an enhancement of the perceptual processing at cued location. The second hypothesis is “channel selection”. Following this hypothesis, the cue influences the decision process underlying the question as to which location should be responded to, but does not affect the perception of the target per se. Consequently, following this hypothesis, a cue will affect target detection or discrimination accuracy only in condition of location uncertainty (e.g. when the target is masked). According to Prinzmetal and colleagues, in the absence of location uncertainty, whereas “channel enhancement” predicts an increase in accuracy, in addition to a decrease in RT, “channel selection” predicts only a decrease in RT and no alteration of accuracy. The probable reason for this (which is not clearly explained in the paper) is that, in the case of channel selection, knowing the location of the target in advance speeds up the detection, but as the perceptual representation of the target remains unchanged, the accuracy is not enhanced. To test their hypotheses, the authors used a series of Posner-like experiments using either visual or auditory cues, letter or face discrimination. Target could appear in one out of four possible locations. A conspicuous cue was displayed before the target, with a variable time interval, and was either informative (80% validity) or not (25% validity). In all experiments tested, Prinzmetal and co-workers found that exogenous cues induced only RT reduction and had no effect on accuracy, whereas endogenous cues affected both variables. Thus, in these experiments, exogenous cues fulfill the criteria for “channel selection” instead of “channel enhancement”. In other words, this suggests that such cues lead to post-perceptual selection (for action or for memorization), instead of selection for perception. This very interesting finding questions the view that exogenous cues are able to capture attention automatically.

I.1.3 WHICH ITEM TO SCRUTINIZE NEXT? A DEFINITION OF SALIENCE

To summarize the previous chapters, it appears that even though goal-directed influence usually overrides stimulus-driven factors, the probability that an eye movement, or attentional shift, land on a given visual item depends on the integration of both factors. Hans-Christoph Nothdurft, for instance, investigated the effect of stimulus-driven factors on goal-directed guidance (H. C. Nothdurft, 2006). He manipulated the conspicuity of the target in a visual search task, while maintaining target-distractor similarity in the search-relevant feature dimension constant. He found that increasing the conspicuity of the target increased search efficiency, suggesting enhanced attentional guidance on the target (considering however that the efficiency argument for attentional guidance can be flawed, see previous sections). In the literature, multiple terminologies are used to refer to the two sources of guidance and to their integration (Serences & Yantis, 2006; VanRullen, 2003). The concept of “saliency” has been used sometimes to refer strictly to the stimulus-driven side of guidance (L. Itti & Koch, 2000; H. C. Nothdurft, 2002), sometimes to the integration of stimulus-driven and goal-directed influence (J. P. Gottlieb, Kusunoki, & Goldberg, 1998). “Saliency” is even used in some cases without any reference to guidance but only with respect to search efficiency: targets that induce pop-out are salient (H. C. Nothdurft, 2006). In the remaining of the present work, the “saliency” of a given part of the visual field will refer to the probability of making an eye movement and/or attentional shift to this location. The respective roles of conspicuity and task relevance in visual guidance will be referred to as stimulus-driven and goal-directed factors of saliency. This terminology is the most straightforward in that it has a clear functional meaning and allows avoiding confusion. Moreover, this definition of saliency is used by most neurophysiological studies that will be discussed further.

In the above definition, I used “and/or” because it remains uncertain whether both attentional and saccadic guidance are controlled by common mechanisms. If not, it would be necessary to distinguish between saccadic saliency and attentional saliency. However, many results in the literature converge to suggest that the mechanisms of attentional shift and saccadic control are shared. One of the most important evidence is that saccadic movements are always preceded by attentional shifts (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995). Moreover, recent results, albeit very indirect, suggest that no covert attentional shift occur between saccades during visual search (Motter & Holsapple, 2007). This implies that in ecological situations, where eye movements are allowed, both attention and eyes land on the same locations, and hence are guided by the same saliency factors. Consequently, in the remaining of this work, the term “saliency” will be used in most cases to refer to both saccadic and attentional guidance.

I.2 The salience maps

The idea that attention and eye movements are guided by preattentive mechanisms conducted to the proposal that a topographical representation of salience, used to guide visual exploration, might exist in the brain. The concept of salience map was proposed in 1985 by Koch & Ullman (Koch & Ullman, 1985). Their model was deeply influenced by the Feature Integration Theory of Treisman and Gelade (A. M. Treisman & Gelade, 1980). They suggested that in the different feature maps in which elementary visual features such as color or orientation are topographically represented, some local competition occurs, so that locations that differ from their surroundings are singled out. They stated that information from these features maps are integrated in a featureless topographic map, and that inside this map, a so-called winner-take-all process selects the most activated location for the next attentional or saccadic shift.

I.2.1 MODELS OF SALIENCE MAP

This compelling idea was further developed into a complete, presumably biologically plausible computational model (L. Itti, Koch C., Niebur E., 1998). In this model, the input image is decomposed into 9 spatial scales (see Figure 2.1). The image passes first a low-pass filter and is then subsampled by a factor of 2. This process is conducted iteratively, in order to obtain nine images with reduction factors ranging from 1:1 (initial image) to 1:256. These images are then decomposed in three feature dimensions: color, orientation and intensity. In these feature dimensions, local contrast is computed by subtracting lower frequencies images from higher frequencies images. Activity in the low frequency maps represents an average of the local activity in the higher frequency maps at corresponding locations. Hence, subtracting low frequency maps from high frequency maps is equivalent to a center-surround computation, in which activities that are higher than their local average are enhanced. This subtraction is achieved on several combinations of spatial scales, which are different for the three feature dimensions (12 combinations for color, 6 for intensity and 24 for orientation). Activities in each of the resulting maps are normalized. The normalization operator is designed to favor maps in which a small number of peaks are present, and inhibit maps in which numerous locations show high activation. When the difference between the highest peak and the map average is large, the most active location stands out, and the map is strongly promoted. When the difference is small, the map contains nothing unique and is suppressed. The resulting maps are then combined with each other and yield three conspicuity maps, corresponding to a topographical representation of feature contrast in the three feature dimensions. Finally, these three conspicuity maps are combined into a unique salience map in which a winner-take-all mechanism selects the most active location to guide the next saccade or attentional shift. This model yields predictions on simple feature and conjunction visual search tasks that are compatible with classical observations in the literature and provides eye scan paths compatible with previous observations during the exploration of natural stimuli, in terms of spatial frequency content (Reinagel & Zador, 1999). A neural network implementation of this model has been provided recently (de Brecht & Saiki, 2006).

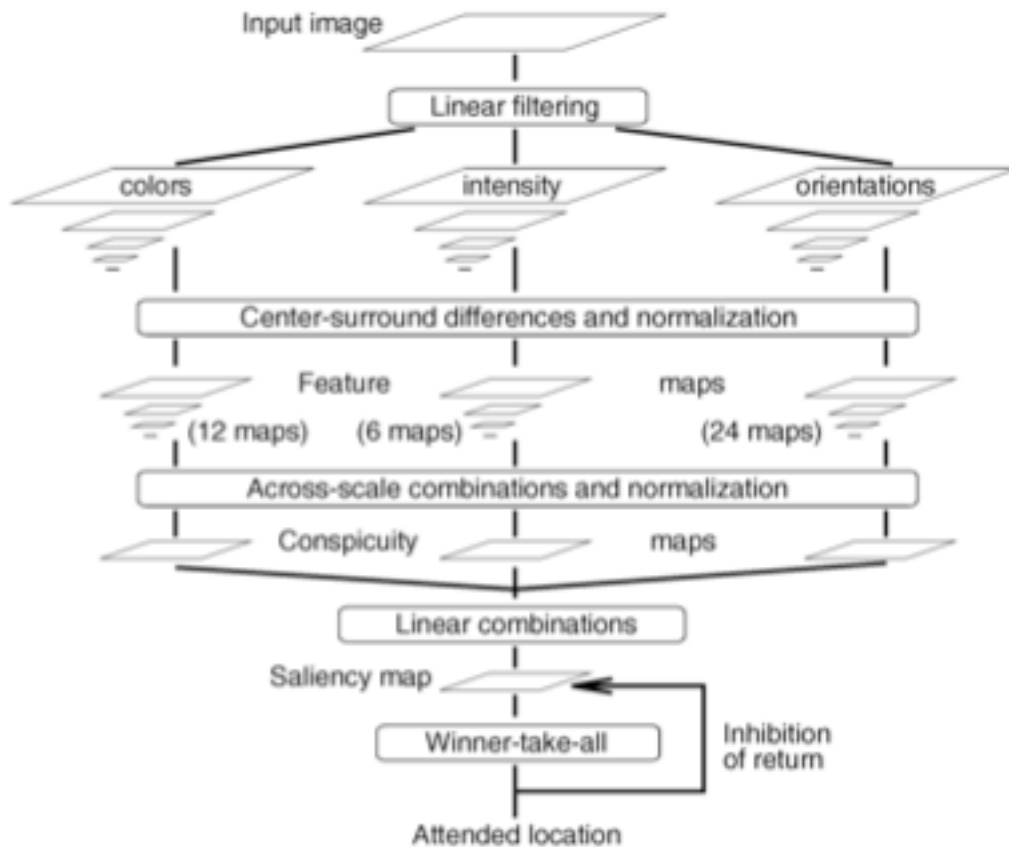


Figure I.2.1.

Architecture of the model proposed by Itti and colleagues, described in the text (L. Itti, Koch C., Niebur E., 1998).

This model has three main drawbacks. First it relies on a great number of peremptory assumptions in the details of the computations (Kienzle, et al., 2007). Second, it takes only stimulus-driven salience, and even more specifically local feature contrast into account. This is a great limitation of this model given the recent view that these factors have only a limited role, if any, in attentional and eye guidance. Evidence of this limitation is provided by the observation that the match between the predictions of this model or its later variants (L. Itti & Koch, 2000) and the actual eye target selection during visual exploration by real subjects is only weak (Einhauser & König, 2003; Kienzle, et al., 2007; D. Parkhurst, et al., 2002; Peters, Iyer, Itti, & Koch, 2005). Third, as explained in a previous chapter, support for this model comes from the finding that saccades land more often on parts of the visual field having a high level of activations in the modeled salience map. This correlational approach can be confounded by hidden covariates, such as the eccentricity of the saccadic endpoint (Underwood & Foulsham, 2006).

The role of goal-directed factors was later added to the model (Navalpakkam & Itti, 2005). Four phases of computation were individuated. In the first phase, the target features are computed on the basis of task specifications stored in working memory. In the second phase, the “attention guidance map” is computed and a winner-take-all mechanism selects the most active location for the next saccade/attention shift. In the third phase, the attended object is identified and its relevance to the task is

assessed. Finally, in the fourth phase, the working memory of the model is updated to take into account the last fixated object and compute the next one. We are here interested mostly in the second phase, in which the salience map is computed (called attention-guidance map by the authors). They implement goal-directed factors, by applying different weights, to each of the feature maps combined in the salience map, so as to promote the target's relevant features and suppress its irrelevant features. These weights are learned directly from training images containing the target. Authors found that biasing for the target accelerated target detection over twofold on average.

Several neural network models of attention have been proposed (Deco, Pollatos, & Zihl, 2002; Deco & Rolls, 2005; Standage, Trappenberg, & Klein, 2005). Describing all these models is outside the scope of the present work. However, one of these neural network models proposes an original view on salience computation and on the mechanisms by which feature cues (e.g. search for the red target) guide spatial attention (Hamker, 2003). In this model, two separate feedback pathways lead to the enhancement of visual activity in visual areas. The first pathway originates from prefrontal cortex, in which a target template is stored, and leads to the activation of the representation of the target feature, i.e. feature-based selection. For example, when searching for a red item, all activities specific for the color red will be enhanced in the color feature map. However, the other features, like orientation, of all the red items are not enhanced at this time. The second pathway comes from feedback connections originating from frontal eye fields, a frontal area involved in eye movement control, which will be described in detail further on. The activation of the red items in feature maps leads to peaks of activity in a salience map. These peaks induce an activation of premotor cells in frontal eye fields, which in turn send feedback signals to corresponding locations in feature maps. This time, all the features of the red items become activated. Finally, strong competition amongst the premotor cells leads to the selection of a single location, and the corresponding location in the feature maps remains the only one activated. In summary, whereas a feature-specific, spatially non-specific mechanism first selects visual items, this turns progressively into a spatially-specific, feature non-specific selection. This framework is interesting in two aspects. First it proposes a mechanism by which feature-based and spatial attention interact. Following Hamker, parallel, feature-based attention would be involved only early in the selection processes and would be replaced progressively by the selection of a single spatial location. This could help explaining why evidence for feature-based selection has repeatedly been found in neurophysiology but remains difficult to demonstrate in psychophysics (see section 1.2.2.1.2). Second, it proposes that, because the salience map exerts a direct feedback to visual areas, as long as multiple locations are activated in the salience map, multiple locations can be selected together, at least transiently. This contrasts with the classical view that winner-take-all mechanisms always lead to the selection of only a single location at a time.

1.2.2 ARE SALIENCE MAPS NECESSARY?

The concept of salience map has proved to be a useful approach to the problem of attentional selection. However, some authors argue that the existence of a salience map in the brain is not mandatory (Z. Li, 2002; VanRullen, 2003). Van Rullen proposes instead that stimulus-driven salience is computed into the ventral visual pathway. From the retina to the highest-level temporal visual areas, visual information is modulated by center-surround computations. Consequently, at each level of the visual hierarchy feature contrast is represented, instead of feature per se. This means that there is no need for an additional representation of stimulus-driven salience, since it is already intrinsically contained in visual representations. Van Rullen argues that this model is more adequate to predict the high rapidity that the visual system is able to achieve (Thorpe, Fize, & Marlot, 1996) because it relies only on feedforward instead of feedback connections. Moreover, he argues, as proposed earlier by Thorpe and colleagues (Thorpe & Gautrais, 1997), that information in the ventral streams is read out by means of spike timing instead of discharge rate. When mixed together, the intrinsic representation of stimulus-driven salience in the ventral visual stream and the reliance on spike timing lead to ultra-rapid processing time predictions, compatible with observed data.

Along the same line, Li Zhaoping proposed that stimulus-driven salience can be computed directly in striate cortex (Z. Li, 2002). Because of the lateral connections linking nearby cells, activity of V1 neurons is modulated by neighboring visual context. Hence, stimulus-driven salience related to feature-contrast is already conveyed in V1. The computational problem raised by salience computation in V1 is that activity in this area is highly feature specific (orientation and color). How both stimulus-driven salience and visual features can be represented together in the neural activity of V1? Li demonstrates theoretically and computationally that this concurrent salience and feature representation is possible. In the cell population, feature is represented by the differential activity of cells tuned to different features, and salience is represented by the difference in activation between optimally tuned cells and other cells. For example, if a vertical bar is displayed on a black background, cells tuned to vertical orientation that contain the vertical bar in their receptive field will discharge more than cells tuned to horizontal orientation. This population activity contains the necessary information to represent the orientation of the bar. If horizontal distractors are added next to the vertical bar, the activity of vertically tuned cells containing the vertical bar in their receptive field will be enhanced and the activity of horizontally tuned cells will decrease. While not altering the coding of the orientation of the bar, the increase of the difference in activity between horizontally and vertically tuned cells contains a representation of the salience of the bar. Using a biologically plausible computational model, Li replicates classical feature and conjunction search results.

These models, while very interesting with respect to their computational efficiency, are not able to explain the strong effect that goal-directed factors have been shown to have on stimulus-driven guidance. Indeed, we have shown along the previous pages, that in many instances (but seemingly not all instances), stimulus-driven factors can be overridden by goal-directed influence. The hard-wired stimulus-driven salience computation proposed by Van Rullen and Li is completely intertwined with feature computation itself, and could hardly be overridden by cognitive demands.

Moreover, there is an important conceptual difference between the notion of salience assumed by Van Rullen and the definition of salience considered in the present work: we consider salience as the guiding factor for attention and gaze whereas Van Rullen

consider salience as a general priority factor for computation which does not necessarily relies on attentional selection. Stimulus-driven salience in Van Rullen's model arises automatically from center-surround computation at each level of the visual hierarchy. This, indeed, induces an enhancement of the visual information that is the most contrasted with respect to the surrounding, but does not necessarily imply attentional or saccadic target selection. To account for attentional and gaze capture phenomena, additional assumptions, which are not discussed by the authors, have to be proposed. It might be hypothesized that under neutral cognitive context (as far as this condition can be achieved), gaze and attention are automatically allocated to the location with strongest activation in visual cortex, corresponding to the stimulus with higher stimulus-driven salience. Specific areas (parietal, frontal,...) would then be responsible for the overriding of this default mechanism under specific cognitive contexts, being able to impose a saccadic or attentional target selection different than the one dictated by feedforwardly computed stimulus-driven factors. These areas could contain a salience map restricted to the representation of goal-directed factors of salience.

I.2.3 AN OPERATIONAL DEFINITION OF THE SALIENCE MAP

The observation that attention and eye movements are not random but are guided by specific factors is sufficient to assume the existence of some form of salience representation in the brain. Consequently, the only remaining question is whether salience is represented topographically in a neural map in the brain. We can state three hypotheses with respect to this question:

1. A single instance of the salience map is represented in the brain in an individuated, isolable brain structure
2. Multiple instances of the salience map are represented in several individuated brain structures. These brain structures contain either different salience factors, different salience maps for attentional and eye guidance, or redundant representation of the same salience factors.
3. No individuated, isolable brain structure is responsible for salience computation, which instead arises from the interplay between several brain structures.

So according to hypotheses 1 and 2, some brain areas are specifically involved in salience representation. We define four criteria that a candidate brain area should fulfill to be considered as a salience map:

- A. **PROPORTIONALITY.** The activity of a given neuron inside the map must be proportional to the probability to make a saccade and/or attentional shift toward a specific spatial location (receptive field). In the case where the salience map would contain only a partial representation of salience (e.g. only goal-directed salience, see hypothesis 2), neural activity inside the map would co-vary with saccadic and/or attentional selection probability only if this probability changes because of a modification of the factor involved. In the case of a goal-directed salience map, for instance, if the probability to make a saccade to a given item changes because of a modification of its conspicuity, the activity inside the map would not be affected.
- B. **CAUSALITY.** The neural activity inside the map must be causally linked to saccadic and/or attentional selection:
 - The discrimination between likely and unlikely saccadic targets in the neural activity must happen before the actual target selection takes place by a saccade or attentional shift.
 - Any modification of the neural activity must have observable consequences on saccadic and/or attentional selection probability.
- C. **SENSORY AND MOTOR ASPECIFICITY.** The activity of the neurons inside the map should be featureless, i.e. should not be influenced by any sensory (e.g. color, orientation, motion, etc...) or motor (e.g. limb involved in the response to a stimulus, see 3.1.2.2) parameters, unless they affect saccadic and/or attentional selection probability.
- D. **TOPOGRAPHY.** The neural activity in the map must be organized topographically with sufficient spatial resolution.

In the next section, we will review evidence from the literature and will try to

determine whether the brain areas that are classically believed to be involved in the representation of salience fulfill the above criteria.

I.3 The representation of salience in the brain

From electrophysiology, neuro-imagery, neuro-disruption, and neuropsychology experiments, four brain structures emerged as the main potential loci of salience representation. These structures are the lateral intraparietal area (LIP) and area 7a in the parietal cortex, frontal eye fields (FEF) in the frontal cortex and Superior Colliculus (SC) in the brainstem. Each of these structures will be reviewed in the following. For each area, we will discuss first the anatomy and physiology of the area in the monkey brain. Then we will discuss whether the properties of the monkey area can be generalized to its homolog in the human brain. Finally, we will address how these structures can work together, in a fronto-parieto-tectal network.

I.3.1 PARIETAL CORTEX

I.3.1.1 Area 7a

I.3.1.1.1 Anatomy

Area 7 is located in the inferior parietal lobule, lying between the intraparietal sulcus, above, and the superior temporal sulcus, below. The anatomy of area 7a is a complex issue, because it suffers from inconsistencies in the terminology. Vogt & Vogt, in 1919, proposed the division of area 7 in a caudal and a rostral part, respectively area 7a and 7b. Functionally, the former of these two parts was considered as a visual area, at the top of the dorsal visual stream, whereas area 7b was regarded as a sensory-motor area, involved in the control of arm and face movements (Andersen, Snyder, Bradley, & Xing, 1997). Another architectonic study, however, led to a different segregation of area 7, defining PF, PFG, PG and Opt areas, from rostral to caudal (Pandya & Seltzer, 1982). A recent study gave valuable insight into the actual subdivision of area 7a based on the investigation of both the architectonic and the connectivity of its subparts (Rozzi, et al., 2006). According to this study, two parts can be distinguished in area 7a, corresponding to the Opt and PG of Pandya & Seltzer. The most caudal Opt is connected to visual areas in temporal cortex (STP and IPa), dorso-lateral prefrontal cortex (46) and FEF, and other parietal areas (LIP, PG, V6a, MST). In contrast, PG shows more extended connections with somatosensory and motor areas, involved in the control of the superior limbs. In addition, authors show that more rostral parts of area 7, corresponding to area 7b according to Vogt & Vogt, or PGF and PF in the Pandya & Seltzer nomenclature, are even more interconnected with pre-motor and somatosensory areas, and much less with visual areas.

The issue is that most electrophysiological and anatomical studies conducted before the study of Rozzi and colleagues did not clearly distinguish between the rostral (PG) and caudal (Opt) parts of area 7a. Consequently, we will have to keep, in the following, the most classical, albeit incomplete terminology, considering area 7a as a single functional and anatomical entity.

Area 7a is connected with high-level visual areas of both the dorsal (LIP, MST, V6) and the ventral visual stream (STP, IPa, TE), and with limbic areas (parahippocampal and posterior cingulate cortices) (Andersen, Asanuma, Essick, & Siegel, 1990; Rozzi, et al., 2006). It has also connections with the frontal cortex, mainly area 46 and the prearcuate cortex. The parietal connections are mostly labeled as feedback, the

temporal connections are mixed and the frontal, cingular and parahippocampal connections are feedforward (Rozzi, et al., 2006). Importantly, its connection with FEF is only very weak, and no connection has been evidenced with the superior colliculus (Andersen, Asanuma, et al., 1990; Asanuma, Andersen, & Cowan, 1985), two structures whose critical role in saccade and attention control has been demonstrated (cf. next sections). Area 7a also projects to medial pulvinar and receives weak projections from the lateral part of the pulvinar (Asanuma, et al., 1985). These projections respect the topographical organization of area 7a. Area 7a is also connected to its contralateral homolog (Andersen, Asanuma, & Cowan, 1985). As already mentioned, the rostral part of area 7a, PG, heavily interconnected to its caudal counterpart, area Opt, displays more extended connections with somatosensory (parietal operculum) and premotor areas (MIP, AIP, F5), involved in the control of the superior limbs (Rozzi, et al., 2006).

In a very interesting study, Jouve and colleagues used a mathematical approach (factorial analysis and clustering techniques) to study the connectivity of visual areas (Jouve, Rosenstiehl, & Imbert, 1998). Authors demonstrate that area 7a, together with FEF, occupy a singular position in the visual network, because they both show equivalent connectivity with both the visual and dorsal visual stream (relay areas, see Fig. I.3.1). However, whereas FEF is heavily connected to many of the visual areas from the lowest (except V1) to the highest levels of the hierarchy, area 7a is only connected to the highest-level areas. This strategic position of area 7a seems particularly adequate to integrate high-level visual information on object identity with visuo-spatial information, motivational factors and executive commands. This situation could be regarded as compatible with a role of area 7a in the computation of goal-directed salience factors, whereas its absence of connections with lower visual areas makes it an unlikely candidate for representing purely stimulus-driven salience.

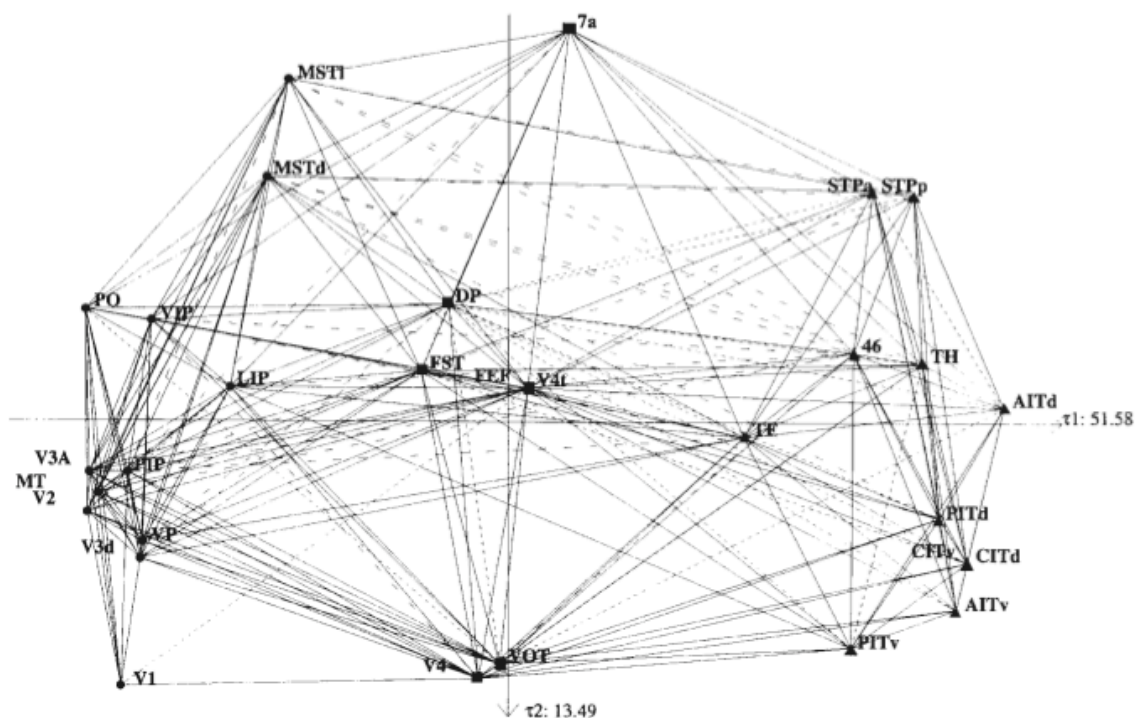


Figure I.3.1

Representation of the visual network from the factorial analysis performed in Jouve et

al., 1998. Ventral stream areas are represented by triangles, dorsal stream areas by circles and relay areas by squares.

1.3.1.1.2 Physiology

In early electrophysiological studies of area 7a, two types of cells were individuated (Hyvarinen, 1981), on the basis of their visual and somatosensory responses, already introducing the distinction found later by Rozzi and colleagues. Some were sensitive to passive or active limb manipulation, whereas others were specifically activated by visual inputs and/or eye movements. The former were more often located in the rostral part of area 7a (area PG), whereas the latter were located in the caudal part (area Opt). Motter & Mountcastle (Motter & Mountcastle, 1981) recorded 1600 cells in area 7a and identified 5 different types of cells. Thirty-one percents of the cells were called light-sensitive because they responded to the presentation of stationary or moving light stimuli. Sixteen percents were fixation or fixation suppression neurons, and responded (fixation cells) or were inhibited (fixation suppression cells) when the animal fixated a “behaviorally relevant” object (e.g. related to reward, or aversive) but were insensitive to visual stimulation *per se*. Ten percents of the cells were labeled as oculomotor cells. Amongst those, saccade neurons were active during and before visually-evoked saccadic eye movements; re-fixation neurons discharged after completion of the saccade; tracking neurons responded to pursuit; and vergence neurons responded to eye movements either toward or away from the face but never both. The visual responsiveness and the oculomotor sensitivity were distributed along a continuum from strictly visual to strictly oculomotor. Twelve percents of area 7a cells were projection or manipulation cells, which were active when the animal projected his arm towards a target, or when the animal manipulated an object, respectively. This last category might correspond to PG cells, recorded more rostrally. Finally, 31% of the cells were classed as unidentified because they exhibited no clear selectivity either for visual stimulation, eye movements or limb movements.

Different types of visual responses were found in light-sensitive neurons. Some discharge continuously during visual stimulation, some exhibit a transient response, some respond to stimuli offset, and some are inhibited by visual stimulation. The latencies of the responses of these neurons varied from 50 to 290 msec, with a mean of 118 msec. Motter & Mountcastle found three remarkable characteristics of the 7a cells: their receptive fields are very large; they are frequently bilateral; and many of them display foveal sparing, i.e. do not respond to foveally presented stimuli (see Fig 1.3.2). However, this last characteristic was not confirmed in more recent studies (Quraishi, Heider, & Siegel, 2007), and as suggested by the authors, was probably induced by the active state of fixation of the monkey during recording in Mountcastle’s study.

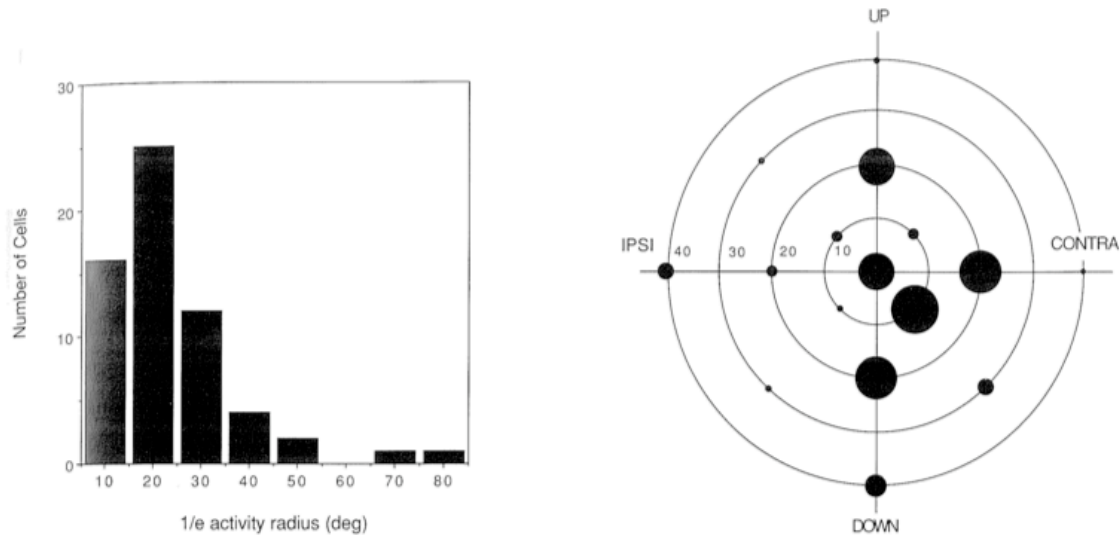


Figure I.3.2

A. Distribution of area 7a receptive fields width from a study by Andersen and colleagues (Andersen, Asanuma, et al., 1990). The radius of the receptive fields is defined as the average distance from the peak of activity to 37% of the peak. B. Each circle represents a location where visual stimuli were flashed. The diameter of the circles represents the number of cells having their peak of activity at the corresponding location.

In a systematic study, Quraishi and colleagues studied the effect of the task performed by the animal on the size and the location of the receptive fields of area 7a cells (Quraishi, et al., 2007). During so-called FIX trials, the fixation target dimmed at some time and the monkey was required to release a lever after the dim to receive a juice reward. In the PROBE condition, the animal had to monitor a peripheral probe stimulus instead of the fixation target, and to report the detection of its dimming by releasing the lever. Therefore, both conditions induced comparable retinal stimulation but manipulated the locus of covert attention (either central or peripheral). Among all visually responsive cells, around 50% responded differently to different stimulus locations (i.e. had a receptive field) and half of them (25% of the total) were modulated by the task. In addition, around 8% of the cells were modulated by the task but exhibited no spatial selectivity. In summary, cells in area 7a have a low spatial selectivity (either very large receptive fields, 60° on average, or no spatial selectivity at all), and are strongly modulated by attentional factors.

The unreliability of the spatial representation in area 7a was further evidenced by studies investigating cell activity in area 7a during maze-solving tasks (Crowe, Averbeck, Chafee, & Georgopoulos, 2005; Crowe, Chafee, Averbeck, & Georgopoulos, 2004). In these studies, while sensitivity to the direction of the paths in the mazes was found in some cells, no congruence was observed between this directional sensitivity and the visual receptive fields or motor fields (preferred saccade direction). In more recent studies, these authors proposed that part of the computation taking place in area 7a is object-centered (Chafee, Averbeck, & Crowe, 2007; Crowe, Averbeck, & Chafee, 2008), giving a potential explanation for the incoherence in spatial selectivity across tasks.

Visual cells in area 7a have been shown to be sensitive to a large variety of stimuli. Some authors argued that area 7a, thanks to its large receptive fields and its sensitivity to motion, might be involved in the computation of optic flow (Steinmetz, Motter, Duffy, & Mountcastle, 1987). This has been the topic of several studies that

evidenced some specificity in the response of area 7a cells to different kinds of optic flows (Merchant, Battaglia-Mayer, & Georgopoulos, 2001; Raffi & Siegel, 2007; Siegel & Read, 1997), even though the functional role of area 7a in optic flow analysis has never been demonstrated by means of stimulation or inactivation studies. Nevertheless, optic flow can be used as efficient stimuli to drive 7a cells response.

Because area 7a lies entirely on the convexity of the cortex, it can be investigated by means of optical imaging. This approach is very helpful to the study of topographical organization. Using this technique, Siegel and colleagues investigated the topography of eye gain fields, i.e. the modulation of neural activity by the position of the eyes in the orbit (Andersen, Asanuma, et al., 1990), in area 7a and area DP. They found that lower eye positions activate area 7a whereas upper eye position gain fields are located in area DP (Siegel, Raffi, Phinney, Turner, & Jando, 2003). Heider and colleagues (Heider, Jando, & Siegel, 2005) used optical imaging to investigate the retinotopy in area 7a and DP, by using optic flow stimuli. In contrast to the clear-cut and stable gain field topography found earlier, the retinotopical organization found in area 7a was highly unstable in time. On any given day, some topographical organization could be observed, but on successive days, the topography changed dramatically, and no systematic organization could be found when regrouping data from several recording days. Raffi & Siegel used also the same technique to investigate the topography in area 7a with respect to the locus of covert attention (Raffi & Siegel, 2005). They used a Posner task with two distinct fixation locations and analyzed the effect of gaze position and cue position (presumably revealing attentional allocation) on neural activity in area 7a and area DP. Here again, the eye-position topography was clear-cut, and stable across time, downward fixation being associated to higher activity in area 7a, and upward fixations activating mostly DP. In contrast, the cue- or attention-dependent topography was patchy: ipsilateral and contralateral cue locations were represented by small and numerous intermingled patches. In addition, and comparably to retinotopical organization, it was highly unstable across days of recording. This complex and variable topographical organization is a striking feature that differentiates area 7a from the other brain structures (LIP, FEF and SC) that we will review in the following.

Area 7a seems not to be involved directly in saccadic control. First, as stated above, it has no or a few connections with SC and FEF, two areas that have a critical importance in the control of saccades. Second, saccadic responses in area 7a are mainly post-saccadic and hence, cannot be involved in the control of saccades. Finally, the findings of early microstimulation studies that saccades can be evoked electrically in area 7a (Shibutani, Sakata, & Hyvarinen, 1984) are now strongly questioned. Indeed, in a more recent study, Thier and colleagues were unable to evoke any saccade in area 7a, while microstimulation in area LIP with the same stimulation parameters evoked saccades reliably (Thier & Andersen, 1998). They explain the discrepancy with the earlier study by the fact that anatomical segregation between area 7a and neighboring area LIP was unclear at that time, and that sites where saccades were evoked probably corresponded to area LIP. The only effect reported following microstimulation in area 7a in the Thier study was eye blinks.

Early studies, using either peripheral (Bushnell, Goldberg, & Robinson, 1981) or central (Mountcastle, Andersen, & Motter, 1981) detection tasks, showed that activity in area 7a was modulated by attentional factors: response to peripheral stimuli is enhanced when the animal is involved in active central fixation or when the stimulus is behaviorally relevant. Bushnell and colleagues showed that the proportion of cells that were modulated in the saccadic task on one hand, and in the peripheral detection or reaching tasks on the other hand, were similar (see Fig. I.3.3). The amplitude of the modulation in these conditions was also comparable. Moreover,

cells that were tested on several tasks and which exhibited a modulation in one of them usually exhibited modulation for the other tasks as well (Bushnell, et al., 1981). These results led Bushnell and colleagues to propose that the same underlying process, namely spatial attention, is the origin of the modulation found in all these cells.

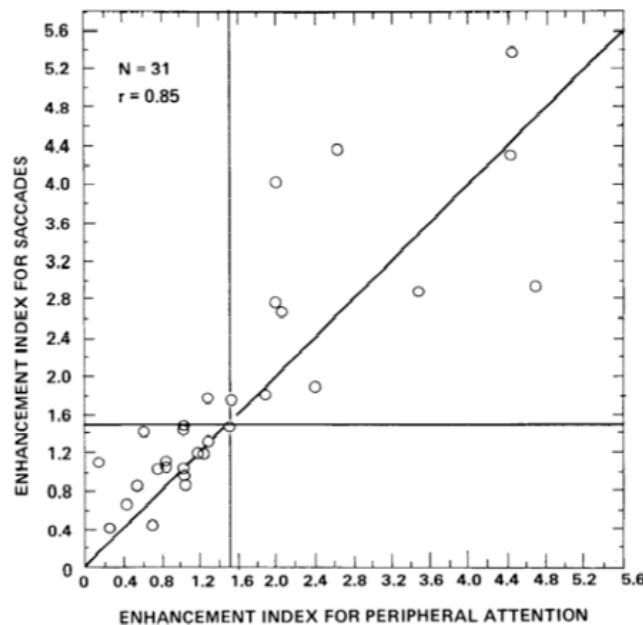


Figure I.3.3

Correlation between the modulation found during the peripheral detection or reaching task (X-axis: enhancement index for peripheral attention) and the modulation found during the saccadic task (Y-axis: enhancement index for saccades). From (Bushnell, et al., 1981).

Whereas stimuli that attract spatial attention induce an enhanced response in area 7a, Steinmetz and Constantinidis showed that responses to stimuli were suppressed when displayed at the current locus of peripheral covert attention (Steinmetz & Constantinidis, 1995). This compelling feature of area 7a cells has also been found in area LIP, as will be seen further, and contrasts with the enhanced activity observed in visual stream areas, or areas MT and MST, when stimuli are displayed inside the attentional focus (McAdams & Maunsell, 1999; Reynolds, Pasternak, & Desimone, 2000; Roelfsema, Lamme, & Spekreijse, 1998; Treue & Maunsell, 1996). This suppression of activity at the attentional locus has been interpreted as strong evidence that area 7a and LIP are involved in the re-direction of spatial attention: they do not respond to stimuli that do not induce attention re-direction (at the current attention locus) but strongly respond to relevant stimuli displayed outside of the attentional locus (peripheral stimuli when attention is at fixation).

In a more recent study, Constantinidis & Steinmetz recorded area 7a neurons during a match-to-sample task in which monkeys had to remember the location of a cue and release a bar whenever a visual stimulus was further displayed at the cued location. The cue could either be a single stimulus or an array of stimuli containing a singleton pop-out stimulus (Constantinidis & Steinmetz, 2001b). They found that 68% of the visually responsive cells in area 7a exhibited a spatial selectivity for the pop-out stimuli. Moreover, they demonstrated that the spatial tuning (size and shape of the receptive fields) was similar in single-stimulus and multiple-stimuli conditions. In

multiple-stimuli condition, while the initial visual response was similar whether a target or a distractor was displayed in the receptive field (a feature which is also observed in LIP and FEF, cf. next sections), after 120 ms, cell activities strongly diverge between these two conditions. Even though the spatial tuning was comparable whether the target was displayed alone or with distractors, the average discharge rate was lower in the multiple-stimuli condition suggesting that distractors and the pop-out target compete for their representation in area 7a. In a companion paper, Constantinidis & Steinmetz confirmed that when the test stimuli following the cue appeared at the cue location, cell response was strongly suppressed (Constantinidis & Steinmetz, 2001a). In contrast, cell response was enhanced when a test stimulus appeared at a non-cued location. Moreover, the response reduction was equal when the cue appeared alone or accompanied by distractors, in the multiple-stimulus condition. This demonstrates that the reduction observed is not a mere effect of stimulus repetition, because cell response was not suppressed when a test stimulus was displayed at a non-cued location.

In the task used by Constantinidis & Steinmetz, the pop-out stimulus is behaviorally relevant because it indicates the location that the monkey has to remember and compare with the location of the test stimuli. Consequently, one cannot interpret these results in terms of either stimulus-driven or goal-directed salience. In another paper, the authors addressed this issue by using a passive task, in which the monkeys just have to maintain fixation, while either single stimuli, or pop-out stimuli inside multiple-stimuli arrays are displayed (Constantinidis & Steinmetz, 2005). They were able to replicate their earlier results in this passive condition. They also compared the characteristics of the cell response in the active and the passive conditions. A smaller percentage of cells (31% vs 68% in the active task) showed spatial selectivity in the multiple-stimuli condition, with a longer latency (180 ms vs 120 ms in the active task) and lower accuracy (area under ROC curve: 0.77 vs 0.86 in the active task).

A big issue in these two studies is that the actual attentional locus during task performance was not assessed. In the first paper, it is assumed that spatial attention is maintained at the cue location during the delay period. In the second paper, we do not know whether attention is captured by the singleton stimulus, and whether the monkey attributes some relevance to the singleton stimulus (which might be the case if the same monkeys have been used in both studies). Consequently, it is impossible to determine whether the modulation observed is related to feature contrast - modulation by feature contrast can be observed in V1 (Hegde & Felleman, 2003) -, to goal-directed or stimulus-driven salience, or to the allocation of attention. This last hypothesis points out a general problem in the interpretation of many studies addressing the question of the representation of salience. Indeed, salience is a gradual value that represents the incentive, or probability to make a gaze or attentional shift to a given location in space. Therefore, a salient item will also attract attention or gaze and assessing whether a given brain structure contains a representation of salience requires to provide evidence that the signal recorded is proportional to the probability of selection and is not an all-or-nothing representation of the current locus of spatial attention. The critical difference between these two hypotheses is that cells in a salience map will represent all relevant and/or conspicuous locations in the visual field simultaneously, or in parallel, independently of the current attentional locus. In contrast, in an area that would control the actual attentional locus and/or saccadic goal, cells would be active only when the attentional spotlight or the upcoming saccadic endpoint crosses their receptive field. The Constantinidis & Steinmetz study does not provide data allowing to distinguish between these two hypotheses: salience representation or attentional allocation control.

It must be pointed out that this distinction assumes the existence of an all-or-nothing selection process. The existence of this process is mandatory in the case of saccadic goal selection. Indeed, even if we assume that, when performed in sequence, two or three saccadic goals can be selected at the same time (Baldauf & Deubel, 2008; Tian, Schlag, & Schlag-Rey, 2000), this still necessitates to transform continuous salience values into a binary selection values. In contrast, the all-or-nothing nature of selection is not that obvious in the case of spatial attention. It could be hypothesized that multiple locations can be selected simultaneously by attention and that visual processing of visual information at these locations would be enhanced proportionally to their salience. This hypothesis will be addressed in section II.2.

1.3.1.1.3 In humans

The question of the homology between monkey and human brain structures is not consensual. Cortical areas in humans and macaques should be considered homologous if they derive from areas present in a common primate ancestor (Orban, Van Essen, & Vanduffel, 2004). This strict criterion for homology is, unfortunately, rarely practically applicable. Instead, various criteria, based on common cyto- and myelo-architecture, connectivity, topography and/or functional properties, are usually employed to determine homologies between macaque and human brains. Another methodology for assessing homologies is surface-based mapping, which uses areas with undisputed homology (e.g. primary areas) as constraints to map the cortical surface of the macaque with the human cortical surface (Van Essen, et al., 2001). However, this approach is useful to study homologies between brain regions, not brain areas. The issue of monkey-human homology is further complicated by the ten-fold increase in cortical surface occurring in humans, when compared to monkeys. This transformation is not merely a matter of scale but involves also differences in the number and the function of distinct areas. Broadly speaking, homology can be inferred rather than proven. Hence, the confidence in the human homology of a given macaque brain area is variable, and some monkey and human areas have simply no corresponding homolog in the other species. This is why care must be taken when comparing human and monkey data, as we will do in the following discussion.

The human cortical area that is the most likely homolog of monkey area 7a is the angular gyrus (Van Essen, et al., 2001). The dorso-ventral angular gyrus exhibits a high connectivity with the para-hippocampal gyrus, similarly to area 7a (Clower, West, Lynch, & Strick, 2001; Rushworth, Behrens, & Johansen-Berg, 2006), but other studies pointed the antero-ventral angular gyrus instead as a potential homolog of area 7a ((Mort, Malhotra, et al., 2003), see below). Caution must prevail to avoid confusion, common in the fMRI literature (Cheng, Fujita, Kanno, Miura, & Tanaka, 1995; Culham, Cavanagh, & Kanwisher, 2001; Peuskens, Sunaert, Dupont, Van Hecke, & Orban, 2001), between monkey Brodmann area 7 and human Brodmann area 7, which corresponds to the superior parietal lobule. Indeed, common Brodmann terminologies across different species do not necessarily indicate homolog regions.

The situation of angular gyrus in human attentional literature is peculiar. As we will see, the angular gyrus is thought to be one of the main areas involved in hemineglect, and its perturbation by transcranial magnetic stimulation (TMS) induces clear attentional deficits. However, paradoxically, it is only exceptionally involved in the networks activated during attentional tasks in functional imagery experiments.

Mort and colleagues conducted a very thorough study to compare lesions exhibited by stroke patients (medial cerebral (MCA) and posterior cerebral arteries (PCA) strokes) with or without neglect (Mort, Malhotra, et al., 2003). Patients were categorized as neglect when exhibiting unilateral bias in either the line bisection task

(in which subjects must indicate the perceived middle position of a line) or the cancellation task (in which subjects must cancel target shapes amongst distractors). Their MRI scans were normalized and compared. The region of maximal overlap between all MCA neglect patients was the antero-ventral part of the angular gyrus (see Fig. I.3.4). All 14 neglect patients had a lesion in this region and only one non-neglect patient exhibited a lesion extending to this area, but to a different sub-part of it. Amongst the five PCA neglect patients, all had a lesion in the para-hippocampal gyrus, which might then be the critical area involved in posterior neglect. Interestingly, as detailed above, area 7a is heavily interconnected with the para-hippocampal gyrus in monkeys.



Figure I.3.4

Overlap of lesions in MCA neglect patients. This region (46,-44,29) corresponds to the antero-ventral part of the angular gyrus. From (Mort, Malhotra, et al., 2003).

Along the same line, transient disruption of angular gyrus function by TMS has been repeatedly shown to lead to attentional deficits (Chambers & Mattingley, 2005). Early parietal TMS studies relied on the 10/20 system (Ashbridge, Walsh, & Cowey, 1997) or on a functional method (Walsh, Ashbridge, & Cowey, 1998) to determine the stimulation site. The functional method, also called hunting procedure, consists in stimulating several locations around a given spot (usually located on the basis of the 10/20 system) and assessing the effect of the stimulation on a behavioral variable (Walsh, Ashbridge, et al., 1998; Walsh, Ellison, Ashbridge, & Cowey, 1999). The site associated to the greatest effect of the TMS on this behavioral variable, in this case an RT increase in a conjunction visual search task, is selected as the target site. A more recent localization technique, called co-registration, allows determining precisely the location of the brain site perturbed by TMS-induced current. In a study using a hunting procedure together with co-registration, Rushworth and colleagues identified the angular gyrus, as the target site (Rushworth, Ellison, & Walsh, 2001), and this location has been systematically targeted in later studies. Classical neglect symptoms, such as bias in line bisection (Fierro, Brighina, Piazza, Oliveri, & Bisiach, 2001), visual extinction (Hilgetag, Theoret, & Pascual-Leone, 2001), or deficit in cancellation (Rushworth, et al., 2006) have been reported following angular gyrus virtual lesion. Effects of angular gyrus disruption on visual search have also been repeatedly reported. Walsh and colleagues showed an increase of RT in

conjunctions search following stimulation of right parietal cortex (using variable localization technique, with a plausibly common target site, later identified as angular gyrus), at 100 ms post-stimulus onset when the target is present and 160 ms when the target is absent (Ashbridge, et al., 1997; Walsh, Ashbridge, et al., 1998; Walsh, et al., 1999). Interestingly, these effects were observed only in conjunction and inefficient feature searches and not in efficient feature search tasks (Rosenthal, et al., 2006; Walsh, Ashbridge, et al., 1998), similarly to what was found in inactivation studies of LIP in monkeys, which will be reviewed below (Wardak, Olivier, & Duhamel, 2004). It is noteworthy that the spatial resolution of the TMS effect, and the technique used to localize the target site, does not allow affirming in these studies that the effect of the stimulation on this region depends on angular gyrus disruption only, and not to the concurrent perturbation of nearby areas such as the human homolog of LIP in the intraparietal sulcus.

Chambers and colleagues assessed the effect of single pulse TMS on a Posner task (Chambers, Payne, Stokes, & Mattingley, 2004). They targeted the left or right angular gyrus and supramarginal gyrus and measured accuracy in a target localization judgment task. An uninformative cue was displayed, prior to target appearance, in 50% of trials at target location and in 50% at a non-target location. They observed a specific effect of right angular gyrus disruption on discrimination accuracy of invalidly cued targets, irrespective of their location. In contrast, no effect was observed following virtual lesion of the left angular gyrus, or left or right supramarginal gyrus. TMS on right angular gyrus affected target detection when applied either at 90-120 ms or at 210-240 ms after target onset (see Fig. 1.3.5). The fact that angular gyrus disruption affects stimulus detection only in invalidly cued trials, replicating earlier findings (Rushworth, et al., 2001), suggests that this area could be involved in the re-allocation of attention, in agreement with the results from monkey experiments described above.

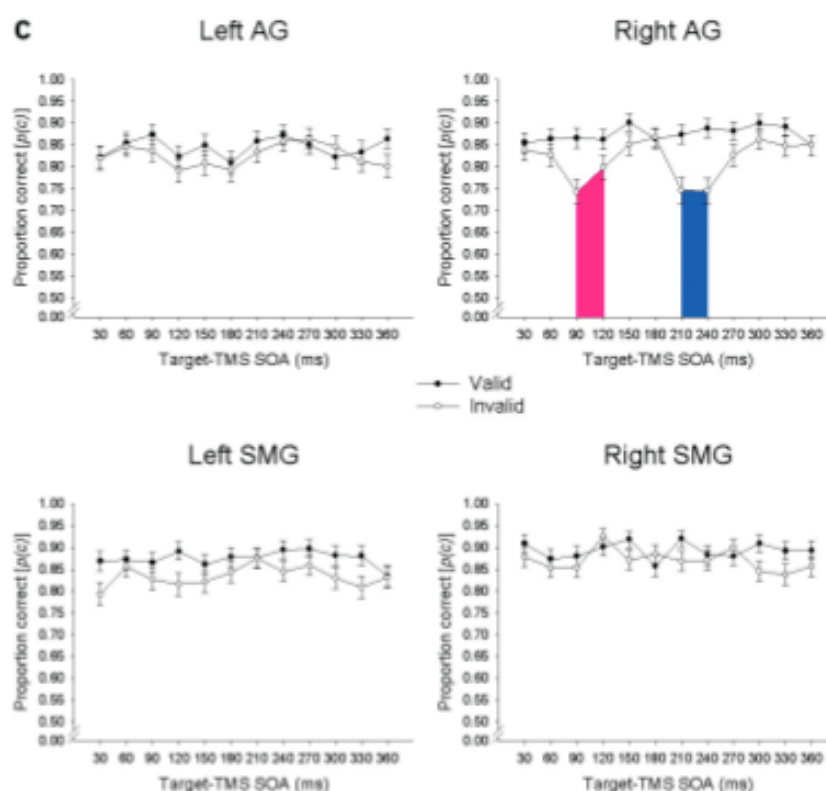


Figure I.3.5

Accuracy as a function of the delay between target onset and TMS pulses for the four stimulated areas, in valid and invalid conditions. The only significant effect was obtained in the condition involving TMS on the right angular gyrus, and with invalid cues. Stimulation in this case was effective during two time windows: either 90-120 ms or 210-240 ms. From (Chambers, Payne, et al., 2004).

Left and right angular gyri seem to play different roles in attentional control. Right angular gyrus disruption affects either both visual hemi-fields (Ashbridge, et al., 1997; Chambers, Payne, et al., 2004; Chambers, Stokes, & Mattingley, 2004; Dambeck, et al., 2006; Rushworth, et al., 2001), or only the left hemi-field (Hilgetag, et al., 2001; Hung, Driver, & Walsh, 2005; Muggleton, et al., 2006; Muri, et al., 2002; Thut, Nietzel, & Pascual-Leone, 2005), and it sometimes induce ipsilateral facilitation (Hilgetag, et al., 2001; Hung, et al., 2005; Thut, et al., 2005). The left angular gyrus inactivation is associated either to an effect on the right visual field only (Hilgetag, et al., 2001; Walsh, Ashbridge, et al., 1998) or to an absence of effect (Chambers, Payne, et al., 2004; Dambeck, et al., 2006; Muggleton, et al., 2006; Muri, et al., 2002; Rushworth, et al., 2001). This difference in the laterality of the effect of TMS on left and right angular gyri is not surprising, given the clear asymmetry observed in the effect of permanent lesions on visual neglect (Siman-Tov, et al., 2007).

In the functional imagery literature, in striking contrast with the TMS literature, angular gyrus is rarely activated during attentional tasks (Corbetta & Shulman, 2002; Leonards, Sunaert, Van Hecke, & Orban, 2000; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Several notable exceptions are described in the following. Culham and colleagues (Culham, et al., 2001) used a visual tracking task in which subjects must track a variable number of targets as they move randomly amongst distractors (Pylyshyn & Storm, 1988). These targets are briefly cued in red but then become visually indistinguishable from the untracked distractors during the whole tracking period. Subjects have to maintain central fixation during the trial. Authors determined, on one hand, the brain regions that are activated during performance of the task versus passive viewing and on the other hand, regions that are activated proportionally to the number of targets to be tracked, or attentional load. They found task-related activation in the FEF, precuneus, superior parietal lobule (that authors erroneously identify as the human homolog of area 7a), and area MT. The load-related activations were found in different parts of the intraparietal sulcus, the superior frontal sulcus, the supplementary motor area, the precentral sulcus, and critically, the angular gyrus. According to authors, these load-related activations would be related to attention control whereas the task-related activations would reflect other mechanisms such as saccadic inhibition. However, the large number of areas activated, including premotor areas, and the lack of clarity about the exact mechanism involved in multiple target tracking makes the interpretation of these results difficult. Indeed, tracking tasks that involve a higher number of targets are more difficult, as revealed by a higher error rate, and the load-related activations could reflect task difficulty instead of attentional control.

Marois and colleagues used an oddball detection paradigm in which subjects were required to signal occurrence of three types of oddball stimuli (Marois, Leung, & Gore, 2000). Following repeated presentation of a constant stimulus at constant location, the task involved presentation of either a different stimulus at the same location (object oddball) or the same stimulus at a different location (location oddball) or a different stimulus at a different location (conjunction oddball). Inferior parietal lobule was activated in all three conditions, together with inferior temporal gyrus ventrally, and intraparietal sulcus dorsally. These results together with similar ones (Clark, Fannon, Lai, Benson, & Bauer, 2000; Linden, et al., 1999), despite their lack

of specificity, given the large number of areas co-activated, are compatible with the role of angular gyrus in the encoding of salient events.

Along the same line, in a study comparing the neural substrate of reflexive and voluntary saccades, Mort and colleagues found that whereas voluntary saccades activated bilateral FEFs, intraparietal sulci and lateral occipital regions, reflexive saccades were associated with angular gyrus, precuneus and posterior cingulate activations (Mort, Perry, et al., 2003). Angular gyri were activated asymmetrically, with greater activation in the right hemisphere. The involvement of right angular gyrus in the control of reflexive saccade is also in agreement with its putative role in the processing of salient events.

Yantis and colleagues also have found evidence for the role of angular gyrus in attentional control. They used a task where subjects had to monitor one among two peripheral streams of letters and detect digits that indicated either to hold attention on the current stream, or to shift attention to the other, contralateral stream of letters (Yantis, et al., 2002). Authors found that the right inferior and right superior parietal lobules were active transiently during each attentional shift, irrespective of the shift direction.

The inconsistencies in neurodisruption and functional imagery studies, with respect to the role of angular gyrus in attention control can be explained by several factors. First, it has been demonstrated that interpreting the BOLD signal measured in fMRI experiments can lead to false negative results (Logothetis, 2003). Second, the concept of the salience map assumes the existence of winner-take-all mechanisms, in which lateral interactions lead to the inhibition of all non-maximal activities. An area in which such a process occurs would have local variations of activity, but constant global activity (Munoz & Fecteau, 2002). This would lead to an absence of BOLD signal increase when considering the average activation of the whole area. Hence, the absence of consistent fMRI activation can be considered as compatible with the salience map hypothesis.

Another potential human homolog of area 7a is the temporo-parietal junction (TPJ) (Shulman, et al., 2003). This area suffers from a lack of clear anatomical definition (Mort, Malhotra, et al., 2003). Mort and colleagues define it as a triangle linking the following points: A, the origin of the ascending posterior segment of the lateral fissure; B, the point of intersection of a vertical line dropped from point A down to the superior temporal sulcus; and C, the origin of the ascending posterior segment of STS (see Fig. 1.3.6). Lesion of this area has also been repeatedly associated with visual neglect (Husain & Rorden, 2003; Vallar, Bottini, & Paulesu, 2003), and TMS to this region induces extinction-like effects (Meister, et al., 2006). In a thorough review, Corbetta and colleagues identified the TPJ, together with inferior frontal gyrus, as part of a 'circuit breaker' network, responsible for re-orientation of attention towards conspicuous events (Corbetta & Shulman, 2002). Indeed, TPJ is activated by target detection (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000), and unexpected stimuli such as rare salient events (Downar, Crawley, Mikulis, & Davis, 2002; Marois, et al., 2000), or invalidly cued targets (Astafiev, Shulman, & Corbetta, 2006; Corbetta, et al., 2000). Kincade and colleagues compared brain activations during exogenous and endogenous orienting in a Posner-like task, and showed that TPJ was activated more strongly following endogenous than exogenous cues (Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). They concluded that activation of TPJ by salient stimuli is contingent on their behavioral relevance: TPJ is activated by salient targets, but not by salient uninformative stimuli.

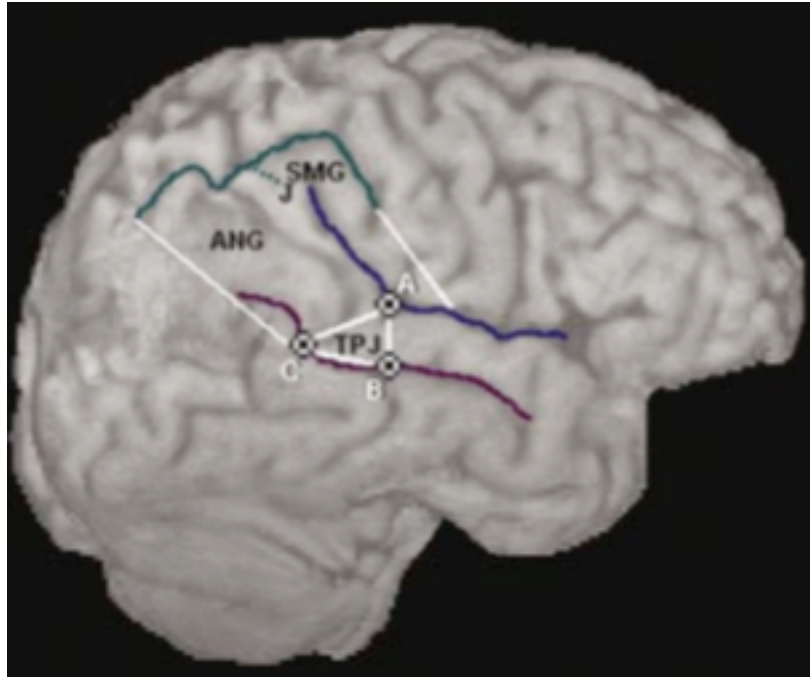


Figure I.3.6

Limits of the TPJ (temporoparietal junction), marked by black and white discs, as illustrated in the Mort et al. paper. ANG = angular gyrus; SMG = supramarginal gyrus; STG = superior temporal gyrus; J = sulcus of Jensen. Bounding sulci are IPS (green), LF (blue) and STS (purple). From (Mort, Malhotra, et al., 2003).

In summary, two potential areas, namely the angular gyrus and temporo-parietal areas, are believed to have a critical role in attentional allocation. However, the variability of, and sometimes contradiction in the results of the human studies presented here do not provide clear arguments either for or against the role of angular gyrus and temporo-parietal junction in the representation of salience.

1.3.1.1.4 Summary

We will try to determine here whether area 7a fulfills the salience map criteria defined above (see section 2.3):

- A. **PROPORTIONALITY.** Several studies showed that area 7a activity is modulated by behavioral relevance (Bushnell, et al., 1981; Constantinidis & Steinmetz, 2001b) and conspicuity (Constantinidis & Steinmetz, 2005). However, none of them assessed whether this modulation reflects a proportional relationship with attentional or saccadic selection probability.
- B. **CAUSALITY.** No study up to now ever used either inactivation or stimulation techniques to investigate the role of area 7a in attentional control. In humans, lesions and transient inactivations of Angular Gyrus, a likely homolog of area 7a, has been shown to lead to attentional deficits.
- C. **SENSORY AND MOTOR ASPECIFICITY.** Some cells in area 7a exhibit specificity for some optic flow features. However, the functional role of this selectivity is unknown.
- D. **TOPOGRAPHY.** Area 7a does not fulfill the D criterion given its large receptive fields and lack of topographical organization.

In summary, area 7a does not fulfill our four salience map criteria. However, this does not mean that this area is not involved in the computation of salience at all. As will be seen below (see section I.3.4), area 7a might interact with a network of areas involved in attentional control, mainly through its connectivity with area LIP and pulvinar.

I.3.1.2 Lateral Intraparietal Area (LIP)

I.3.1.2.1 Anatomy

LIP is located on the lateral wall of the intraparietal sulcus. It is adjacent and medial to area 7a. It is commonly subdivided into two strips (Lewis & Van Essen, 2000b): a ventral part, LIPv, closer to the fundus of the sulcus and a dorsal part, LIPd, closer to the surface. The physiological correlates of this subdivision will be discussed later on. The connectivity of area LIP has been thoroughly studied in two papers: (Blatt, Andersen, & Stoner, 1990; Lewis & Van Essen, 2000a). Area LIP is heavily connected with both ventral and dorsal stream visual areas: V2, V3, V4, TEa/IPa, TF, TEO, and MDP, PO (or V6/V6a), VIP, MIP, 7a, 7b, AIP, MT, MST, DP and also TPO. Grossly speaking, visual inputs from these areas to LIP concern mainly the peripheral portion of the visual field (Baizer, Desimone, & Ungerleider, 1993; Ungerleider, Galkin, Desimone, & Gattass, 2008).

Connections with the frontal cortex are different for the ventral and dorsal parts of area LIP. Whereas LIPd is mainly interconnected with area 46 (dorso-lateral prefrontal cortex), LIPv is heavily connected to FEF. The topography of the connections between LIPv and FEF is also interesting (Bullier, Schall, & Morel, 1996). As it will be discussed later on, FEF is also divided in two parts. The medial FEF is more concerned with long saccades and peripheral vision, whereas lateral FEF is involved in small saccades and central vision. The rostral portion of LIPv is connected to the lateral portion of FEF (central visual field) whereas the caudal part of LIPv is connected to the medial portion of FEF (peripheral visual field) (Stanton, Bruce, & Goldberg, 1995). LIP also sends projection to the parahippocampal gyrus (Suzuki & Amaral, 1994).

Finally, LIP is heavily connected sub-cortically to the intermediate layers of ipsilateral Superior Colliculus (Asanuma, et al., 1985), to the Pulvinar, the pontine nuclei, caudate and putamen (Gioli, et al., 2001; Lynch & Tian, 2005). Interestingly, the populations of cells projecting from LIP to FEF on the one hand and SC on the other hand are clearly distinct, but have very similar functional properties (Ferraina, Pare, & Wurtz, 2002). Regarding connections with the pulvinar, LIP is interconnected with both its lateral and medial parts (Lynch & Tian, 2005), in contrast to area 7a, which is mainly connected to medial pulvinar. The projection from lateral pulvinar to LIP is part of the LIP-SC-pulvinar-LIP circuit (Lynch & Tian, 2005).

Despite the large connectivity of LIP with both ventral and dorsal visual streams, in their study using a mathematical approach to the connectivity of the visual areas, Jouve and colleagues place LIP clearly in the dorsal visual stream and not among relay areas, like FEF and area 7a (see Fig. I.3.1).

I.3.1.2.2 Physiology

Cells in area LIP exhibit both visual and saccadic activities. The delayed saccade task has been extensively used to study separately these two types of response (Gnadt & Andersen, 1988). In a thorough study, Barash and colleagues compared the activity of LIP and 7a cells in the visual, delay, and saccade epochs of a delayed-saccade task (Barash, Bracewell, Fogassi, Gnadt, & Andersen, 1991). The saccade

epoch was further divided in pre-saccadic, saccade-coincident and post-saccadic periods. They found that whereas responses in area 7a were mainly visual and post-saccadic, LIP cells could discharge during any of the task epochs (see Fig. I.3.7). A third of LIP cells responded significantly in the three epochs, and 57% discharged during at least two epochs. Additionally, they calculated the directional selectivity of the cells during these epochs and concluded that visual receptive fields and motor fields in LIP were very well aligned with each other.

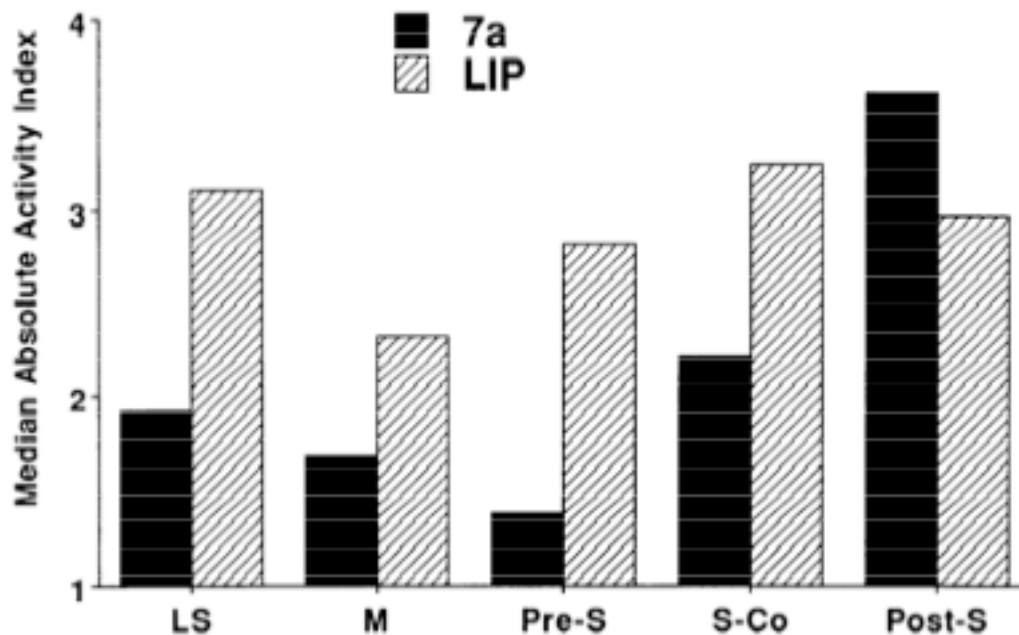


Figure I.3.7

Activity index representing the discharge rate in the different epochs of the delayed-saccade task, normalized by the baseline discharge rate. This index is given for both LIP and area 7a cells. LS: light-sensitive response, corresponding to the visual response 75-275 ms after target onset; M: motor response, 200-400 ms after target onset; Pre-S: pre-saccadic activity, 200-25 ms before saccade onset; S-Co: saccade coincident, 25 ms before to 75 ms after saccade onset; Post-S: post-saccadic, 200-500 ms after saccade onset. From (Barash, et al., 1991).

The spatial properties of LIP neurons differ from area 7a in several aspects. These spatial properties have been studied thoroughly by Ben Hamed and colleagues in different parts of LIP (Ben Hamed, Duhamel, Bremmer, & Graf, 2001). They found that the centers of the receptive fields were mainly contralateral (90-95% of cells), and foveal (75% of cells have their peak of activity in the central 10° of the visual field). Sixty seven percents of the cells had a receptive field width smaller than 15°. Receptive field width was positively correlated with eccentricity. When analyzing the representation of the visual field at the population level, authors found a massive over-representation of the fovea. However, monkeys in this study had to perform a fixation task and the same authors demonstrated in another study that the over-representation of the fovea strongly depends on the task at hand (Ben Hamed, Duhamel, Bremmer, & Graf, 2002). Some rough topography could be extracted from these data: a broad representation of the horizontal meridian runs from the upper anterior border of LIP to the deeper posterior border. The lower field representation lies above, and the upper field representation below this region. This topographical

separation probably corresponds to the dorso-ventral anatomical distinction between LIPd and LIPv.

The visual response in LIP cells is enhanced when the stimulus appearing in the receptive field is the target of an impending saccade, but also when it is behaviorally relevant and that no saccade is explicitly planned towards it (Colby, Duhamel, & Goldberg, 1996; Goldberg, Colby, & Duhamel, 1990). In a very influential study, Gottlieb and colleagues showed that stable, irrelevant stimuli were unable to drive LIP cells response: when the monkey made a saccade that brought a stable stimulus inside the cell receptive field, no or few visual response was evoked (J. P. Gottlieb, et al., 1998; Kusunoki, Gottlieb, & Goldberg, 2000). In contrast, when the stimulus abruptly appeared just before the saccade, or when it was relevant because it was defined as the next saccadic target, the cell strongly responded to the entrance of the stimulus in its receptive field. Similarly, the cells responded to the entrance of the cue in their receptive fields, even when it indicated a saccade outside from the receptive field. However, when a saccade was planned to the cell receptive field, but that no visual stimulus was present at that location, no response was observed. Along the same line, when a saccade is programmed away from a relevant item, such as in antisaccade paradigms, LIP activity represents reliably the location of the visual stimulus and only weakly the direction of the impending saccade (J. Gottlieb & Goldberg, 1999). This strongly suggests that the signal conveyed in LIP does not reflect the intention to move the eyes but instead, the salience of the visual stimuli, induced by its abrupt onset (stimulus-driven), or by its relevance to the task (goal-directed), either because it is a saccadic target or because it relays information (the cue). It is noteworthy that when the item brought inside the cell receptive field is a saccadic target, the cell response begins to rise before the stimulus actually appears in its receptive field. This anticipation effect, known as remapping, shows that the cells in LIP anticipate the retinal consequences of the upcoming saccade and shift their receptive field in advance to the location where it will land after the saccade (Duhamel, Colby, & Goldberg, 1992).

Similarly to area 7a, cells in LIP respond more to stimulus that are outside than inside the focus of attention (Powell & Goldberg, 2000; D. L. Robinson, Bowman, & Kertzman, 1995). This was initially regarded as evidence that activity in LIP drives the re-allocation of attention to new locations. This view has been questioned by the findings of Bisley and Goldberg, which showed in a very important study, that LIP represents continuously the current locus of spatial attention. Authors used a task inducing attention shifts between a saccadic target and a distractor, and measured the contrast threshold for detection of a probe to determine attention allocation at the saccadic target and at the distractor location (Bisley & Goldberg, 2003). They showed that contrast threshold was minimal at the saccadic target location, unveiling attentional allocation to the target, but that 200 ms after distractor appearance, this contrast threshold advantage shifted to the distractor location before shifting back to the saccadic target. This result demonstrates that purely stimulus-driven attentional capture can occur in monkeys (see section 1.2.1.1.3.2). The authors then measured the target- and distractor-related activities in LIP as a function of attentional allocation. When comparing the activities at the target and distractor locations, they found that the greatest activity was systematically found at the location where attention was allocated, irrespective of the magnitude of the difference between both activities (see Fig. 1.3.8). In other words, attention was fully allocated on the location corresponding to the greatest activation, even when the difference with respect to the opposite location was very small. This suggests that the activity from a single LIP cell cannot be used to predict attentional allocation, but that it must be compared to the other cells activity. This result is a very strong evidence for the existence of a salience map in LIP, in which each visual stimulus is represented by its gradual

salience, but only the most salient actually drives attention.

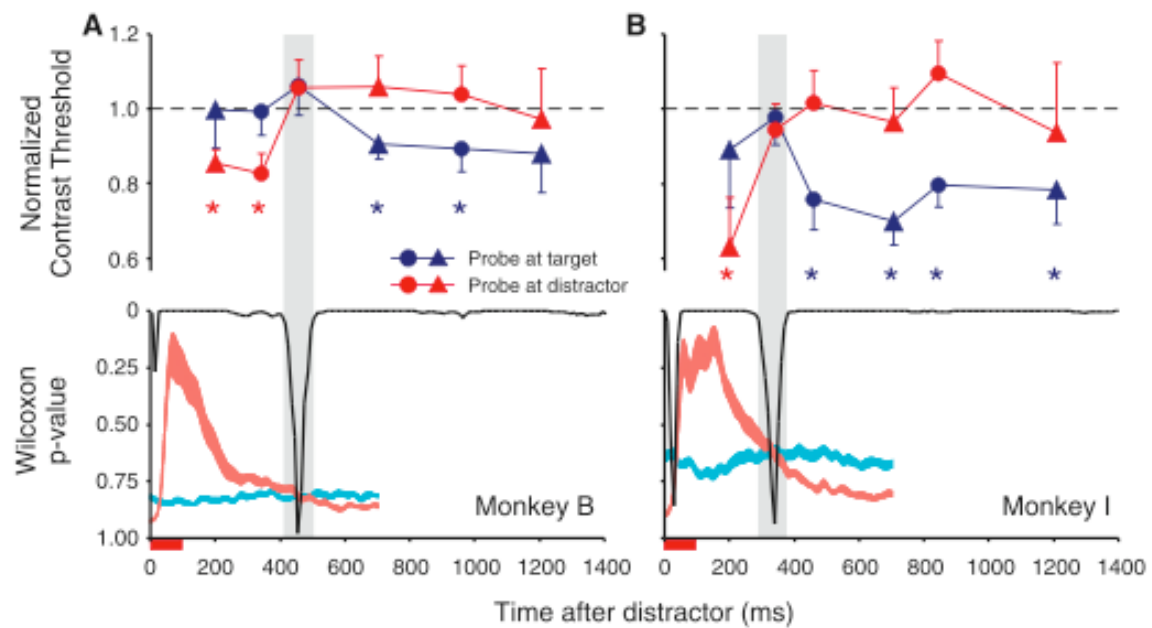


Figure I.3.8

Aligned representations of monkey performance in the task (upper graphs) and neural activity in area LIP (lower graphs) for monkey B (graph A) and monkey I (graph B). Upper graphs: the normalized detection threshold of the probe when displayed at the target (blue) or distractor (red) location is represented as a function of the time after distractor onset. Lower graphs: normalized population activity when the distractor (red trace) or target (blue trace) is in the RF of the cells. The black trace indicates the p value of the wilcoxon comparison between the blue and red traces. From (Bisley & Goldberg, 2003).

The existence of gaze capture by conspicuous distractors in monkeys, and its neural correlate has been studied by Ipata and colleagues (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006). They showed in a free-viewing search task that monkeys were able to ignore a salient distractor when it was never the target. In addition, they showed that LIP activity was lower when the item in the receptive field was the salient distractor than when it was another distractor. Finally, there was a significant inverse correlation between the activity linked to the salient distractor in LIP and the ability of the monkey to ignore it. These results, again, argue for the role of LIP in guiding eye movements. The fact that the conspicuous distractor is under-represented in LIP when it is irrelevant is evidence for the representation of goal-directed salience in this area. Along the same line, cells response to a salient distractor is correlated with the RT increase induced by the distractor (Balan & Gottlieb, 2006).

Several studies investigated the role of LIP in decision making as a function of reward expectancy. An influential study by Platt & Glimcher showed that LIP activity was correlated with the amount and probability of reward expected when making a saccade towards the cell's receptive field (Platt & Glimcher, 1999). In the free-choice condition in this study, when a saccade choice was likely to lead to a high reward, the monkey was more likely to make this choice, and the activity in LIP cells representing this choice was higher. Sugrue & colleagues have further formalized this idea in a study where a trial-by-trial correlation was found between LIP activity and the fractional income, i.e. a temporally local representation of expected value (Sugrue,

Corrado, & Newsome, 2004). They also showed that behaviorally, the probability to make a given choice is directly proportional to its fractional income. Consequently, stating that LIP activity is proportional to fractional income is equivalent to assuming that it represents choice probability, i.e. salience. Along the same line, Roitman and colleagues asked their monkeys to perform a motion discrimination task and to respond by making a saccade towards the target located in the direction of the motion of a random-dot stimulus (Roitman & Shadlen, 2002). Activity in LIP cells increased as evidence accumulated in favor of motion direction that required the monkey to make a saccade towards the RF. Here again, these results can be interpreted equivalently in terms of decision making or in terms of salience computation.

As mentioned above, LIP cells have remarkably stereotyped response during delayed saccade tasks, with visual-, delay-, and saccade-related responses. Janssen & Shadlen studied how the delay-related response can be modulated by the probability of occurrence of the upcoming saccade (Janssen & Shadlen, 2005). They asked monkeys to make an eye movement towards a target displayed in the cells receptive fields, at the time of a Go signal. In addition, they used different temporal probability distribution of the Go signal (either bimodal or unimodal). They found that the RTs of the monkeys in this task reflected a so-called anticipation function, which depended on hazard rate, i.e. the probability that the Go signal occur at a given time, given the fact that it did not occur before. Importantly, they showed that the pattern of activity in LIP during the delay period fitted very well the anticipation function that corresponded to the current temporal probability distribution (see Fig. 1.3.9). When the probability distribution was bimodal, the delay period activity paralleled the bimodal anticipation function, with two peaks of activity separated by a period of lower activity. When the probability distribution was unimodal, the activity fitted the unimodal anticipation function, with a steady discharge rate increase. These patterns of activity occurred only when the saccadic target was inside the receptive field, and not when the cue providing the Go signal was in the receptive field. Authors proposed that LIP cells represent elapsed time, when it is relevant to saccadic behavior. In fact, these results are completely compatible with an extended version of the salience map hypothesis: the probability of occurrence of a saccade towards the target (i.e. target salience) changes overtime and LIP cells activity is a reliable representation of this probability. In this framework, salience does not represent only the probability that a given item will be selected instead of competitor items for the next saccade but also when the saccade will occur.

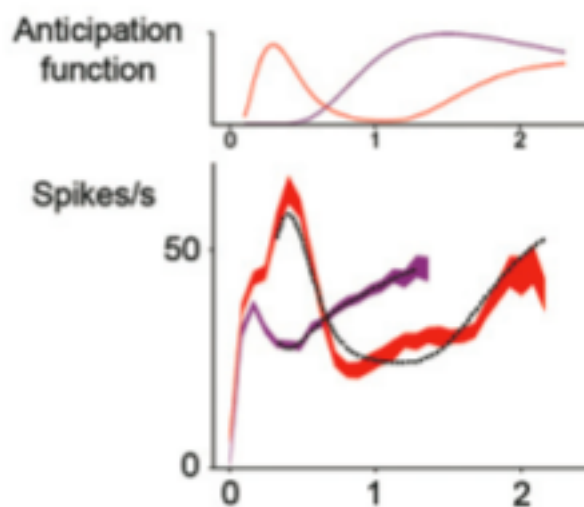


Figure I.3.9

Upper graph: anticipation functions for the unimodal (purple) and the bimodal (red) distributions. The X-axis represents the time elapsed in seconds, after target onset.

Lower graph: example of activity of a single neuron during the delay period under the unimodal (purple) and bimodal (red) time distributions.

From (Janssen & Shadlen, 2005).

Saccades are always preceded by an automatic attentional shift (Deubel & Schneider, 1996), and covert attention shifts are believed to be the consequence of preparatory eye movement commands that are not executed (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). Because of this tight coupling between attention shifts and saccades, it is difficult to determine whether LIP is involved in attentional control only, or whether it has also a role in the execution of eye movements (Goldberg, Bisley, Powell, & Gottlieb, 2006). Electrophysiological recordings provided evidence for both interpretations. Examples of evidence in favor of the role of LIP in saccadic control:

- The signal recorded in LIP is a better predictor of impending eye movements than reaching movements direction (Quiroz Quiroga, Snyder, Batista, Cui, & Andersen, 2006; Snyder, Batista, & Andersen, 1998).
- LIP cell activity accurately predicts the location of impending saccades and is aligned on saccade onset instead of stimulus onset (Ipata, Gee, Goldberg, & Bisley, 2006; Thomas & Pare, 2007).
- In an efficient feature search task, the timing of the discrimination between target and distractors is aligned with saccade onset, with a -30 ms time-lag (Thomas & Pare, 2007).

Examples of evidence in favor of the perceptual level of processing of LIP:

- When a saccade is programmed to a different location than the attentional spotlight, LIP activity represents the attentional locus accurately, but not the saccadic target (Bisley & Goldberg, 2003; J. Gottlieb & Goldberg, 1999; Powell & Goldberg, 2000).
- LIP codes for the saccade direction only when a visual stimulus is present in its receptive field (J. P. Gottlieb, et al., 1998).

Whereas the electrophysiological approach is very useful to study the information relayed and computed inside brain areas, it is not sufficient to reach a conclusion about the actual function of a neural structure. Inactivation and microstimulation studies are more adequate to investigate this question. The ability to evoke saccades by microstimulating LIP cannot be considered as conclusive with respect to the role of LIP in saccade execution control because very high stimulation currents are needed to reach the saccade threshold (Constantin, Wang, Martinez-Trujillo, & Crawford, 2007; Thier & Andersen, 1998). In a more recent study, Hanks and colleagues trained monkeys to make saccades to one out of two targets, depending on the direction of motion they perceive in a random-dot motion stimulus (Hanks, Ditterich, & Shadlen, 2006), and assessed the effect of LIP microstimulation on this task. The discrimination task was arranged so that one of the potential saccadic targets was in the receptive field of the sub-population of neurons located near the stimulating electrode tip. The stimulation biased the choice of the monkey towards the target located inside the receptive fields of the stimulated neurons and decreased the RT for selecting this target. This effect was not observed in a simple delayed saccade task where monkey did not have to make a choice for saccade direction.

Authors proposed that these results demonstrate the role of LIP in the decision about where to look, i.e. in the representation of salience. A potential issue with these results is the size of the effect. Microstimulation biased decision by an amount comparable to adding between 1.0 and 2.1% coherence in the motion. However, stimulation currents were very low (10-20 μ A). Moreover, this very small effect is coherent with the assumption that attentional and saccadic target selection depends on the activity of the whole LIP population. Slightly modifying the discharge rate of a small subpopulation will only have a small effect on the final decision about where to look. Another microstimulation study addressed the effect of electric stimulation of LIP on a Posner task (Cutrell & Marrocco, 2002). They found a non-spatially specific alerting effect of the stimulation on non-cued trials and a spatially specific effects of the microstimulation on invalidly cued trials. The former consisted in a decrease of RT for both contra- and ipsilateral uncued target, and the latter consisted in a decrease of RT for invalidly cued contralateral targets. The stimulation did not affect RT in trials with valid or bilateral cues, but more importantly, no spatially-specific effect was observed during uncued trials, a finding which contradicts the idea that LIP microstimulation would induce a contralateral attentional shift. However, an important problem in this study is the variability of the stimulation-target delay, which is not taken into account in the analysis. Consequently, this negative finding should be interpreted with caution.

Two inactivation studies by Wardak & colleagues give us very valuable insight into the issue of the motor versus perceptual/attentional function of LIP (Wardak, Olivier, & Duhamel, 2002; Wardak, et al., 2004). They injected muscimol, a GABA agonist, to transiently inactivate LIP cells and tested the effect of the inactivation on several tasks involving eye movements (Wardak, et al., 2002) and on covert visual search tasks (Wardak, et al., 2004). They found that neither saccade accuracy, nor latency were affected by the injection during simple tasks, such as visually-guided and memory-guided saccades (in contrast with previous studies (C. S. Li, Mazzone, & Andersen, 1999)). However, they showed that when two potential saccadic targets were present, a strong ipsilesional bias was found, i.e. monkeys preferred to fixate targets located ipsilaterally with respect to the inactivated LIP. Moreover, whereas inactivation had no effect on feature search tasks, conjunction search tasks were slower following inactivation. At least part of this effect was due to a preferential exploration of the ipsilesional visual field. The interaction between set-size and the effect of inactivation was unclear: in one monkey, the effect of the inactivation was found irrespective of the set-size, whereas in the other monkey, only large set-sizes showed inactivation effects. Importantly, no effect of the inactivation was found on the types of distractors visited before target detection. Monkeys visited more often distractors sharing either the color or the shape of the target, in both the control and the inactivation conditions. All these results demonstrate the critical role of LIP in the selection of the saccadic target, when this selection requires complex processing (e.g. conjunction search), and not in the actual implementation of saccade metrics. Finally, when the search tasks were performed covertly, LIP inactivation led to an increase in search time when the target was contralesional. This effect was found in both feature and conjunction tasks, but its magnitude depended on the difficulty of the task. In contrast, the set-size did not significantly affect the importance of the effect. Interestingly, this lack of set-size effect has recently found its electrophysiological equivalent in a study by Balan and colleagues (Balan, Oristaglio, Schneider, & Gottlieb, 2008), in which set-size was shown to have a comparable effect on target and distractor representations, unaffected the discriminability between them. The results from the covert search inactivation study allow extending the conclusion from the overt search study, in showing that LIP is crucial in visual tasks even when no eye movements need to be performed. However, interpreting this finding in terms of attentional allocation is perilous, since the role of attentional

shifts during visual search remains unclear (see section 1.2.1.1.4).

Altogether, the findings described so far provide strong convergent evidence for the role of LIP in the selection of saccadic and attentional targets. However, as will be seen in the following paragraphs, recent findings might ask for reconsideration or at least extension of the current view on LIP function.

In their study, Toth & Assad used color cues that indicated to the monkey which stimulus to fixate after a delay period (Toth & Assad, 2002). The rule that defined the association between the cue (location and color) and the stimulus to fixate changed during each recording session. Authors found that up to 29% of LIP cells exhibited color selectivity when color was the relevant feature for the selection of the stimulus to fixate. Moreover, they showed that this selectivity did not depend on the saccadic direction that was determined by the cue color. This means that these cells actually represented cue color and not the direction of the upcoming saccade that the cue instructed. These findings suggest that stimulus features that become relevant for saccadic behavior can be represented in LIP. Along the same line, Freedman & Assad showed that in a motion direction categorization task, neurons in LIP become direction selective (D. J. Freedman & Assad, 2006). Moreover, they showed that their selectivity was polarized as a function of the category to which the stimulus in the RF belonged. This rule-dependent representation of features in LIP goes beyond the conceptual framework of the salience map. It suggests instead that LIP might be involved in the mapping between visual stimulation and the appropriate motor response. However, it is noteworthy that in these studies, the strategy used by the monkey to solve the task is unclear. In particular, spatial and feature-based attentional allocation was not evaluated. Consequently, it cannot be completely ruled out that the observed effects were in fact attentional. In the Toth & Assad study, for example, the monkey might strategically attend to one of the color and not to the other one (look left when the stimulus is red, right otherwise). This would result in an increased activity when the attended color is displayed in the receptive field of the cell. Similarly, in the Freedman study, monkey might attend to motion around a specific vector, perpendicular to the category boundary, resulting in higher activity when this motion direction is displayed. While unlikely, these alternative interpretations are plausible and make unequivocal the interpretation of these results. A functional evaluation of this category-specific activity in LIP, using either stimulation or inactivation, would be necessary to determine its actual role in the categorization of stimuli.

Still in the same context, Maimon & Assad asked monkeys either to respond to a change in the direction of a moving dot by pressing a lever (reactive condition), or to provoke this direction change by the same lever press (active condition), before the dot reaches a bar (Maimon & Assad, 2006). These conditions were visually equivalent but differed in that in the reactive condition, the monkey had to react to a conspicuous visual event, whereas in the active condition, the monkey had to generate the response internally, at the appropriate time. Whereas all LIP cells reliably responded to the dot motion direction reversal, occurring in their receptive field, a subpopulation of LIP neurons (42%) additionally increased their activity up to a fixed threshold, reached at the moment of the lever press, only in the active condition. Maimon & Assad interpreted this peculiar activity as a proactive action control signal: the action is initiated whenever these cells reach a fixed threshold. In a proactive control condition, the dot turn is delayed by 200 ms with respect to the lever press. In this condition, allowing to dissociate the lever press from the dot turn, neural activity seems to reliably signal the lever press instead of the dot turn. Authors propose that in LIP, a subpopulation of cells, different from the one involved in salience computation (which might be composed of the remaining 48% of cells that do not signal proactive movement initiation), are responsible for the control of the

initiation of proactive actions, i.e. actions that are not triggered by external cues. This role would be independent of the effector involved in the action. However, the fact that these cells have spatial receptive fields comparable to the other cells, and respond equivalently during memory-guided saccades are odd features for cells supposed to be involved in the triggering of actions. Moreover, as discussed briefly by the authors, the connectivity of LIP is not really compatible with a crucial role in action control in general. An alternative explanation could be that, in the proactive condition, when the dot is close to the bar, focused attention is mandatory in order to accurately determine the right time to press the lever. The more the dot close to the bar is, the more salient it becomes, and the more activity in corresponding cells in LIP increases. In summary, these results, while interesting, are not easy to interpret.

Oristaglio and colleagues (Oristaglio, Schneider, Balan, & Gottlieb, 2006) showed, in an orientation discrimination task with non-targeting manual response, that 30% of the cells exhibited limb specificity, responding more strongly to cues implying a right hand response than a left hand response, for instance. The effector specificity of the cells remained unchanged when the cue-response association rule was inverted. This result is an interesting equivalent to the studies described just above. Whereas these studies provided evidence for perceptual feature categorization in LIP, the Oristaglio study suggests the existence of motor categorization. This would be compatible with the idea that LIP is responsible for the acquisition of rules that lead to the association between specific perceptual features and corresponding responses (J. Gottlieb, 2007). It is difficult to explain these results in terms of strategic attentional allocation, like we did for the above studies, because limb specificity exhibited a contralateral bias, the left and right limbs being preferentially represented in the right and left hemispheres respectively. However, the functional significance of this effector specificity in LIP is probably low: LIP inactivation seems to have no observable influence on limb selection during performance of this task (J. Gottlieb, personal communication).

Finally, a recent study by Roitman and colleagues shows that neural signals in LIP convey more information than mere salience. These authors showed that up to 60% of the cells in LIP discharged proportionally (half directly proportionally, half inversely proportionally) to the number of items displayed in their receptive field (see Fig. I.3.10) (Roitman, Brannon, & Platt, 2007). Monkeys had to make a saccade toward a single stable target while a multiple items stimulus was presented in the receptive field of the recorded neuron. The monkey did not have to use this stimulus in order to do the task. However, in a given block, one of the numerosity values displayed was associated to lower reward. The actual processing of this information by the monkey was evidenced by a longer RT when the low reward numerosity value was presented. LIP selectivity for numerosity was totally independent of whether the numerosity displayed in the receptive field was associated to lower reward or not. This shows that numerosity is represented in a stimulus-driven manner in LIP because this representation is not dependent on relevance to the task. The existence of a representation of numerosity in LIP is not predicted by the salience map hypothesis. Authors suggest (along the same line than Walsh (Walsh, 2003)) that LIP neurons might instead code for magnitude, or quantity. Alternatively, it could be proposed, following Hubbard and colleagues (Hubbard, Piazza, Pinel, & Dehaene, 2005), that the representation of space in LIP could be mapped into a representation of numerosity and that, besides shifts of attention in space, LIP might be responsible for the shifts of attention in the mental number line. Finally, a potential confound of this study is that numerosity could be a factor of guidance of attention and that stimuli representing high numerosity values could lead to a higher probability of attentional shifts. In that case, the representation of numerosity in LIP would be explained by its effect on attentional selection probability. This explanation, however, seems unlikely given that the activity of half of the relevant cells were negatively correlated with

numerosity.

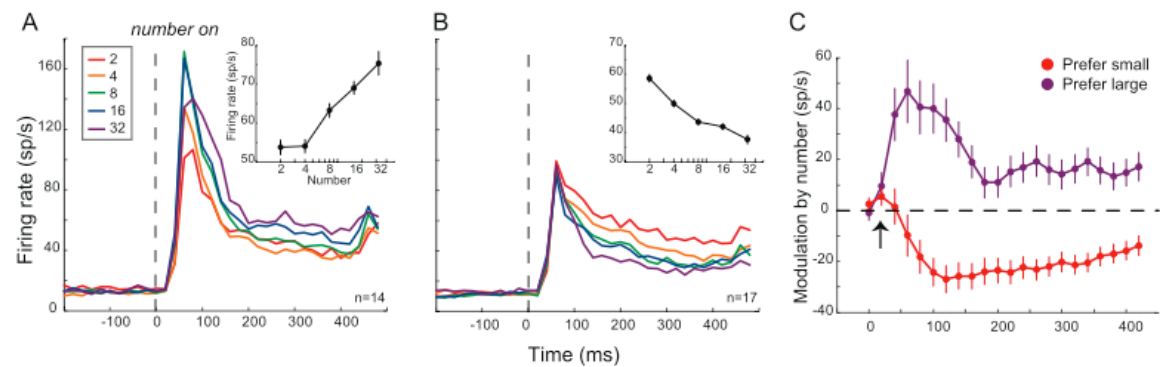


Figure I.3.10

A. Population activity of neurons preferring large numerosity (n=14). The color code indicates stimulus numerosity. Responses are aligned to stimulus onset (dashed vertical line at zero). Inset: correlation between average response during the epoch 50–450 ms following stimulus onset and numerosity.

B. Population activity of neurons preferring small numerosity (n=17). Same conventions as A.

C. Representation of the response modulation for the two groups of neurons shown in A and B. Positive modulation indicates responses that increase with number; negative modulation indicates responses that decrease with increasing number.

From (Roitman, et al., 2007).

In summary, electrophysiological, inactivation and microstimulation studies all lead to the conclusion that LIP is involved in the selection of both saccadic and attentional targets. Additionally, LIP might have other, more complex functions. Evidence for the representation of numerosity (Roitman, et al., 2007) and rule-based feature categorization (D. J. Freedman & Assad, 2006; Maimon & Assad, 2006; Toth & Assad, 2002) appears convincing, but its functional significance needs to be assessed by inactivation studies. Similarly, the observation of a limb specificity in LIP cells (Oristaglio, et al., 2006), suggests a role of LIP in linking visual stimulation to the appropriate effector, but the functional role of this effector specificity seems weak.

I.3.1.2.3 In humans

The human homolog of monkey LIP is believed to be located on the medial wall of the intraparietal sulcus (Grefkes & Fink, 2005; Koyama, et al., 2004; M. I. Sereno, Pitzalis, & Martinez, 2001). Numerous functional imagery studies found bilateral activation of this region during attentional and saccadic tasks (Corbetta & Shulman, 2002; Simon, et al., 2002; Thiel, Zilles, & Fink, 2004). Bilateral intraparietal activation is associated to voluntary attentional shifts (Corbetta, et al., 2000) and voluntary saccades (Mort, Perry, et al., 2003), to endogenous, more than exogenous orienting (Kincade, et al., 2005), and to both spatial-based and feature-based cueing information (Egner, et al., 2008). Surprisingly, these activations are not (Corbetta, et al., 2000), or only weakly (Vandenberghe, et al., 2005) direction selective. Vandenberghe and colleagues used an orientation discrimination task in which subjects had to determine the orientation of a peripheral grating following a 100%

valid cue (Vandenberghe, et al., 2005). In half of the trials, this target grating was displayed together with a contralateral distractor grating. Two foci of activity were found in the intraparietal sulcus (IPS). Interestingly, the side of attention allocation modulated only the left human LIP, which was more strongly activated under conditions of contralateral orienting. Neither left, nor right LIPs were activated by sensory stimulation when the stimuli were irrelevant to the task, but both were strongly modulated by the presence of a distractor. In a study addressing the neural substrate of visual search, Leonards and colleagues compared brain activation during efficient and inefficient feature search tasks, and conjunction tasks (Leonards, et al., 2000). They found that IPS activation was higher during conjunction than feature search, but did not depend on the efficiency of the search, in contrast to findings from inactivation studies in monkeys (Wardak, et al., 2004).

The role of human LIP in neglect is disputed. Patients with chronic parietal lesions involving human LIP show normal latencies in saccades to visual targets (Machado & Rafal, 2004). However, latencies in anti-saccades directed away from contralateral targets are increased (Machado & Rafal, 2004). Moreover, when two potential targets are displayed, patients make more often saccades towards the ipsilesional target (Rafal, 2006). Neglect patients show maximal lesion overlap centered on angular gyrus rather than LIP (Mort, Malhotra, et al., 2003; Vandenberghe, et al., 2005), but LIP lesions might be associated to certain aspects of attentional dysfunction found in the heterogeneous neglect syndrome (Vandenberghe, et al., 2005).

As discussed earlier, TMS studies on parietal cortex targeted angular gyrus instead of LIP. The reason is that early parietal TMS studies used a functional method to locate the stimulation site: the location associated to a significant RT increase in a conjunction search was selected as target site. This site was localized on the brain *a posteriori* and corresponded to the angular gyrus (Rushworth, et al., 2001). Later studies used these coordinates to locate their parietal target site.

1.3.1.2.4 Summary

LIP fulfills all criteria of the salience map as defined above (see section 2.3), except the C criterion (representation of features):

- A. PROPORTIONALITY. Several studies demonstrated that neural activity in area LIP is proportional to selection probability. This proportional relationship appears to be relative instead of absolute: the discharge rate of each cell is interpreted as a function of the discharge rate of other cells, and the cells with maximal activity determine the locus of attentional allocation (Bisley & Goldberg, 2003).
- B. CAUSALITY. Inactivation studies showed that saccadic selection probability was affected by the inactivation of LIP: when there is a competition between several potential saccadic targets, saccades are more often directed to ipsilateral items (Wardak, et al., 2002). Moreover, LIP inactivation also affects covert visual search, even though the exact mechanism involved is less clear (Wardak, et al., 2004).

A stimulation study showed that selection probability could be modified specifically on locations corresponding to the response fields of the microstimulated subpopulation of cells (Hanks, et al., 2006).

- C. SENSORY AND MOTOR ASPECIFICITY. The question of the representation of features in LIP is complex. We discussed above several studies that found some responses specificity in LIP, which are not predicted by the salience map hypothesis, such as a specificity for the limb used to respond to the task

(Oristaglio, et al., 2006), or a specificity for numerosity (Roitman, et al., 2007). However, the functional significance of these signals remains unclear.

- D. TOPOGRAPHY. Receptive fields in LIP are small and they are organized topographically.

I.3.2 FRONTAL EYE FIELDS (FEF)

I.3.2.1 Anatomy

The FEF occupies portions of areas 8a and 45 of Walker, located in the anterior bank of the arcuate sulcus in macaque. Whereas the fundus is associated to the control of pursuit eye movements, the upper, more anterior part is dedicated to saccade control (Lynch & Tian, 2005). Inside the saccade part of FEF, the lateral part is dedicated to small saccades whereas the medial part is concerned with large amplitude saccades control. These two functionally distinct regions exhibit also a different connectivity with visual areas (Stanton, et al., 1995). The lateral part is connected with the foveal regions of retinotopically organized association cortex and with areas that primarily represent central vision, whereas the medial part is connected with peripheral retinal representations in cortical regions (Schall, Morel, King, & Bullier, 1995). The connectivity of FEF with visual and association areas is very similar to LIP. Visual association input arises from areas V2, V3, and V4; from inferior temporal cortex (TE_m, TE_a, TE₃, TE₀); superior temporal sulcus (MT, MST, STP, IP_a); and posterior parietal cortex (PO, LIP, VIP) (see Fig. I.3.11). Additional input comes from the supplementary eye fields (SEF), from area 46 (DLPFC), and from area 23 (posterior cingulate cortex). Much weaker connections exist with MDP, DP and area 7a. Connections with medium-level areas (MST, TE₀, V4) are generally stronger than with lower-level areas (V2, V3) (Schall, et al., 1995). But FEF has no connections with higher-level ventral areas (e.g. rostral inferior temporal cortex), in contrast to area 7a. This pattern of connectivity led Jouve and colleagues, in their study using a mathematical approach of the connectivity between visual areas, to place FEF in a central position amongst relay areas, connecting to most ventral and dorsal areas (Jouve, et al., 1998).

FEF is heavily connected to area LIP and VIP. An interesting feature of this connection is its convergence. A single small injection of retrograde tracer in FEF results in labeled neurons over most of LIP and adjacent VIP (Lynch & Tian, 2005). LIP_v input is much stronger than that of LIP_d (Schall, et al., 1995). Moreover, medial FEF (large saccades) is connected to caudal LIP, whereas lateral FEF (small saccades) is connected to central-rostral LIP (Schall, et al., 1995).

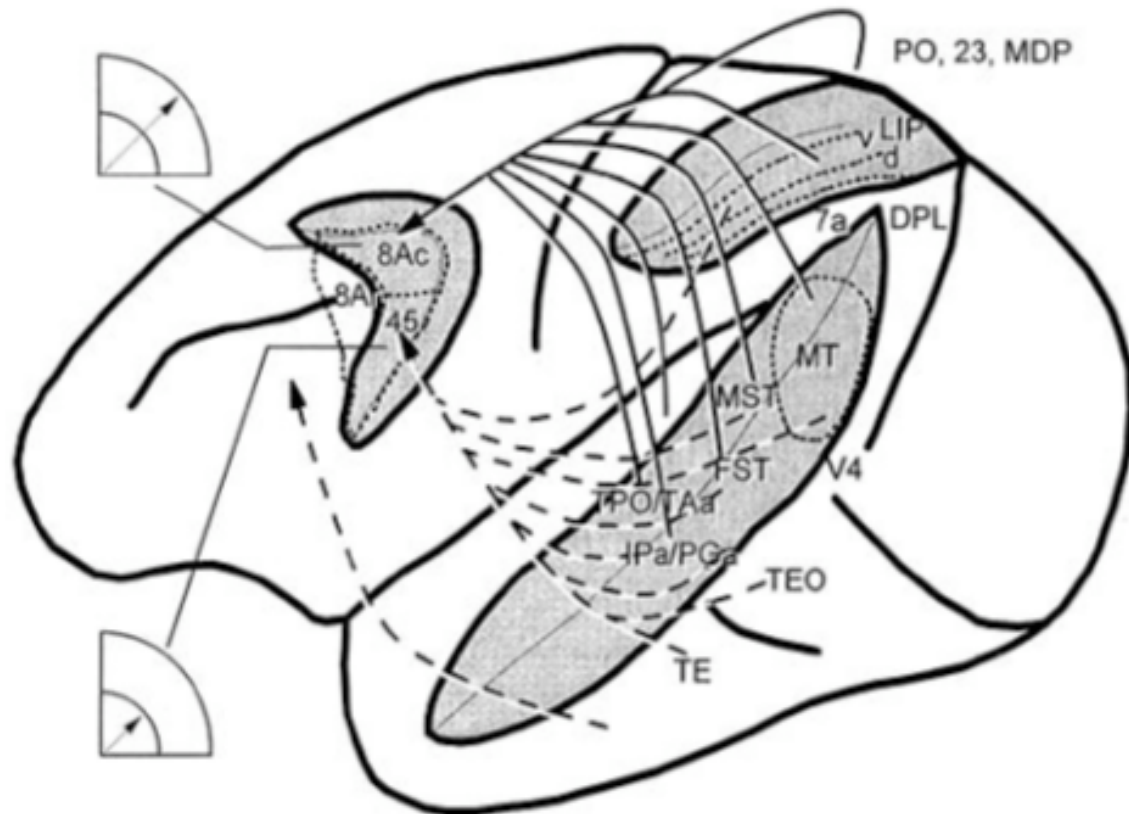


Figure I.3.11

Schematic representation of the connectivity between FEF and other visual areas. Solid lines indicate projections to medial FEF, and dashed lines to lateral FEF. From (Schall, et al., 1995).

The FEF is connected sub-cortically to basal pontine nuclei, superior colliculus (mainly the intermediate layer), basal ganglia (putamen and caudate), thalamus (mediodorsal and ventral anterior nuclei), and in particular, medial pulvinar. An important cortico-subcortico-cortical circuit, which has been extensively studied, connects FEF to SC and then back to FEF (Lynch & Tian, 2005; Sommer & Wurtz, 2000, 2004a, 2004b). The SC-to-FEF connection relays in the medio-dorsal thalamic nucleus, constituting the major thalamic input to FEF. The functional role of this feedback circuit will be discussed later on.

I.3.2.2 Physiology

Cells in FEF have been segregated in different classes, on the basis of their sensory and motor responses. Whereas visual neurons respond only to visual stimulation, movement neurons respond only before and during eye movements and visuo-movement neurons combine both signals (C. J. Bruce & Goldberg, 1985). Roughly half of the cells in FEF have visual response. Their receptive fields are large. They are mainly contralateral but extend often to the ipsilateral space (Schall, 1995).

The role of FEF in saccade control is undisputed. Saccades can be evoked electrically at very low current intensities (typically inferior to 50 μ A (C. J. Bruce, Goldberg, Bushnell, & Stanton, 1985)). Lesion, or inactivation, of FEF leads to transient but strong deficits in simple oculomotor tasks (Dias & Segraves, 1999; Schiller & Tehovnik, 2005; Sommer & Tehovnik, 1997; Wardak, Ibos, Duhamel, &

Olivier, 2006). Activity in movement cells determines the time of saccade onset: saccades are initiated when the discharge rate of these neurons reaches a threshold. The rate of increase of the discharge rate of these neurons hence predicts accurately saccadic latency (Brown, Hanes, Schall, & Stuphorn, 2008; Hanes & Schall, 1995, 1996).

Visual neurons in FEF, like LIP neurons, discriminate visual stimuli on the basis of their relevance with respect to the task. Jeffrey Schall and his colleagues studied extensively the properties of visual cells in FEF by recording their activity during visual search tasks. They showed that, during an overt popout visual search task, the activity of the cells strongly diverged when either a target or distractor was displayed in the receptive field (Schall & Hanes, 1993; Thompson, Hanes, Bichot, & Schall, 1996). This discrimination occurred around 120 ms after stimuli onset, following an early indiscriminative response (mean latency 60 ms). Moreover, target discrimination in visual cells occurred irrespective of whether the monkey had to make a saccade (GO trials) or not (NO-GO trials) towards the target (Thompson, Bichot, & Schall, 1997). This discrimination is not all or nothing: during conjunction search tasks, distractors sharing a target feature induce greater activity than other distractors, but smaller activity than the target (Bichot & Schall, 1999a). Similarly, in singleton search, distractor-related activity is proportional to target-distractor similarity (Sato, Watanabe, Thompson, & Schall, 2003), even in the absence of the target.

Thompson and colleagues recorded FEF neurons during feature search tasks of variable difficulty, and focused mainly on the error trials (Thompson, Bichot, & Sato, 2005). The question that authors first addressed was whether FEF activity selected the saccadic target (which happened to be a distractor in error trials) or the singleton stimulus (the actual target). In a purely stimulus-driven salience map, the singleton target is expected to lead to the highest activity. In contrast, in a salience map integrating both stimulus-driven and goal-directed salience, the location with the highest activity should correspond to the final decision about where to look and, hence, indicate the saccadic target. Authors showed that no neuron whatsoever exhibited selectivity for the singleton stimulus but that a large majority of cells exhibited saccadic target selectivity. This result was found in two conditions involving very different tasks and different types of errors.

Interestingly, the selectivity of the cells for the saccadic goal was always higher in correct than in error trials. Moreover, selectivity depended on the proportion of the error trials. In conditions where error trials were frequent (difficult search), selectivity was lower than in conditions where error trials were rare (easy search). These results are in agreement with the idea that FEF is involved in the process of saccadic target selection. Finally, authors tried to correlate the probability to make a given saccadic choice (either towards the target or the distractors) with the pre-saccadic selectivity for saccade direction in FEF cells. They combined all sessions from all experiments, thus involving different tasks, and different error probabilities. In tasks where the probability of making a saccade to the target was low, because of the high difficulty of the task, the pre-saccadic selectivity was lower than in easier tasks. Likewise, when the probability of making a saccade towards a distractor was high, because of the high difficulty of the task, the pre-saccadic selectivity was higher than in easier tasks. When combining all distractor and target pre-saccadic data, from the easy and the hard visual search tasks, a linear relationship was found between saccadic selection probability and pre-saccadic direction selectivity (see Fig. I.3.12). However, it is important to point out that in this analysis, saccadic selection probability for distractors correspond to the probability of making a saccade to any of the distractors. Therefore, if we have seven distractors, the probability of selecting any given distractor is seven times smaller. Following the salience map hypothesis, we expect activity (or selectivity) to be proportional to the actual probability of selecting a

given location, not a category of items, like in the present study.

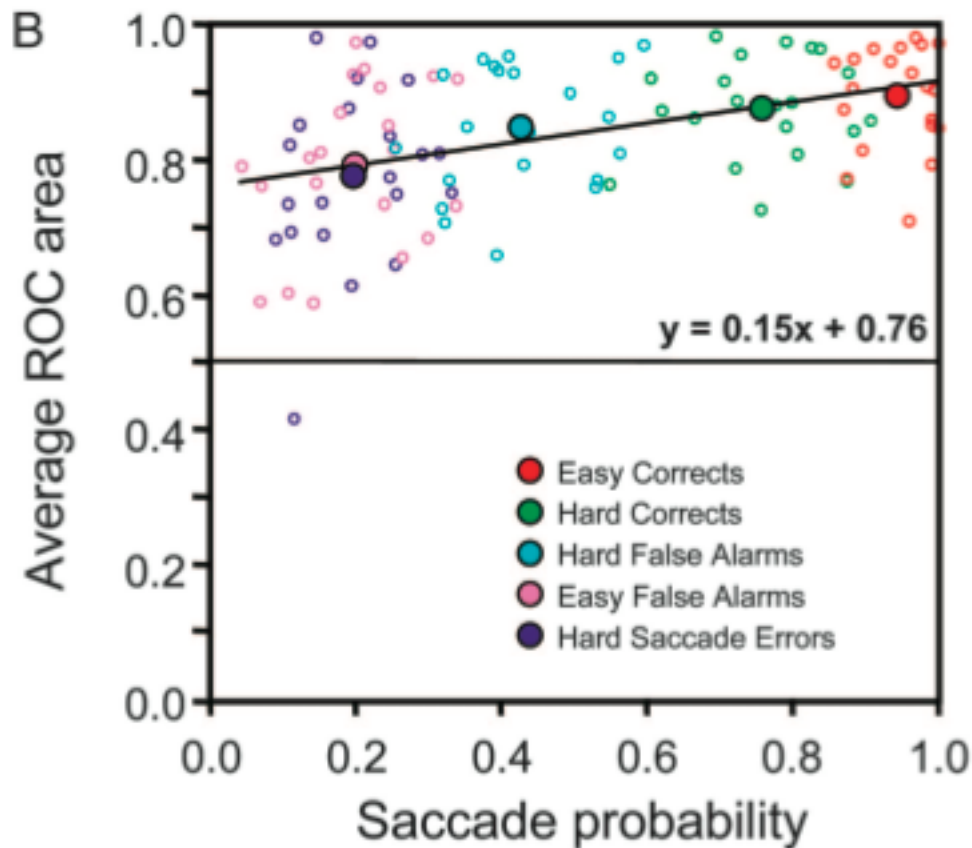


Figure I.3.12

Correlation of presaccadic direction selectivity (ROC area) to probability of behavioral choice. Data from the easy and the hard search tasks are combined. From (Thompson, Bichot, et al., 2005).

In addition to task difficulty, FEF is also modulated by motivational factors. Ding & Hikosaka showed that, in a task where the monkey has to make a saccade to either a left or right target, and the amount of reward for each of these possibilities change block-wise, some FEF neurons (around 20%, mainly visual and visuo-movement cells) discharge differently according to expected reward (similarly to caudate neurons recorded during the same experiment) (Ding & Hikosaka, 2006). From the perspective of the salience map hypothesis, the reward selectivity is expected to show increased activity when the cue instructs a high reward saccade towards the receptive field and a lower activity when the saccade in the receptive field is expected to yield low reward. Accordingly, Ding and colleagues show that preference for high reward in the receptive field was two times more likely than the opposite selectivity in FEF cells. However, surprisingly, strong reward modulation also occurs when the cued location is outside the receptive field (this is the most frequent modulation observed among the recorded cells). In this case, FEF neurons usually prefer when the saccade directed opposite to the receptive field is expected to lead to a low reward. In other words, when a saccade to a given direction has low motivational value, cells corresponding to alternative choices discharge more. This suggests the existence of competition amongst FEF cells to determine the final saccadic goal.

The aforementioned results suggest that visual cells in FEF discharge proportionally to the salience of the visual stimuli in their receptive field. However, because these studies used only overt visual search tasks to investigate visual cells activity in FEF, it is unclear whether the signal recorded depends on saccadic or attentional goal selection. To address this question, Sato and colleagues used an anti-saccade paradigm (Sato & Schall, 2003). Monkeys had to perform a singleton search task and to respond by making a saccade either to the target (pro-saccade condition) or to the stimulus opposite to the target (anti-saccade condition). It is noteworthy that the pro- or anti-saccade condition was instructed by the shape of the singleton target. They isolated two populations of neurons. Type I neurons represented the singleton location first, even in the anti-saccade condition. Their selectivity switched later to represent the saccade direction. The time needed for these neurons to discriminate the singleton from the distractors, and whether it instructed a pro- or an anti-saccade, did not relate to RT. In contrast, type II neurons always indicated saccade direction and not singleton location. The time needed for these neurons to discriminate saccade direction was proportional to the RT and the difference in discrimination delay observed between pro- and anti-saccade trials explained the difference in RT. Whereas type I neurons were more visual than motor, and type II neurons more motor than visual in the memory-saccade task, there was no clear-cut distinction between both categories. Hence, the type I vs. type II cells dichotomy was distinct from the visual vs. movement neurons dichotomy. These results are in striking contrast with the data obtained in an LIP study using a similar paradigm, where the cell activities were found to depend on the cue location and not on the saccade direction (J. Gottlieb & Goldberg, 1999). Thompson and colleagues used a pop-out covert visual search task to investigate the attentional vs. saccadic nature of the visual signal in FEF cells (Thompson, Biscoe, & Sato, 2005). Monkey responded to the task by manually turning a lever. As expected, a great proportion (around 80%) of visual and visuo-movement neurons discriminated the target from the distractors during covert visual search tasks as well. In contrast, movement neurons were completely inhibited throughout the trial duration.

Similarly to LIP, recent studies challenged the common view that FEF is not sensitive to stimulus features. Peng and collaborators showed that a small proportion of FEF cells (12%) were selective to shape in a delayed match to sample task (Peng, Sereno, Silva, Lehky, & Sereno, 2008). Critically, approximately 25% of the recorded cells were also selective to shape during a passive task, in which attentional factors are unlikely to be involved. Here again, whether this selectivity in the cell responses in FEF has a functional role in shape discrimination remains an open question that will have to be addressed by means of stimulation and inactivation techniques.

Microstimulation studies in FEF have brought crucial insight into the role of this area in the control of attention. Moore & Fallah showed that when stimulating FEF with a current intensity below the saccadic threshold, discrimination of visual stimuli located in the motor field of the stimulated sub-population is enhanced (T. Moore & Fallah, 2001). Moreover, when recording V4 cells selective for the corresponding location, they found that their activity increased following sub-threshold FEF electrical stimulation (T. Moore & Armstrong, 2003). These behavioral and electrophysiological effects are comparable to the ones obtained when manipulating covert attention (McAdams & Maunsell, 1999). In a recent study, Armstrong and Moore tested the effect of FEF microstimulation on the response discriminability in V4 (Armstrong & Moore, 2007). They presented stimuli in the receptive fields of V4 cells while monkeys performed a passive fixation task and measured the response discriminability of these cells to different stimuli. Discriminability of a given cell is maximal during the early cell's response but decreases progressively with time, an effect called adaptation. When applying subthreshold microstimulation to a subpopulation of FEF cells with the motor field aligned on the stimulus presented in

the V4 receptive field, response discriminability was enhanced (see Fig. I.3.13). This enhancement was observed in late but not in early cell responses and the magnitude of the enhancement was proportional to the magnitude of the loss of response discriminability with time. In other words, FEF microstimulation restored part of the discriminability lost during cell response adaptation. Importantly, the enhancement in discriminability was observed as soon as it was observable, i.e. within the 40 ms following FEF microstimulation. Finally, in a recent study combining functional imagery with microstimulation techniques, Ekstrom and colleagues found that while stimulation of FEF induced an increase in the BOLD signal, independent of visual stimulation in monosynaptically connected areas (LIP, contralateral FEF, STP, SC), modulation of lower visual areas (V1, V2, V3, V4) was found only when a visual stimulus was displayed (Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008). This modulation was also spatially specific, being bigger when the visual stimulus was located in the motor field of the stimulated FEF region. Intriguingly, however, these authors found that neural activity in the region that was driven by the visual stimulus when presented alone was not increased but decreased, and that in contrast, activity in the portion of visual cortex surrounding this region was increased. The interpretation of this very interesting result remains unclear but challenges most current models of visual attention.

In summary, FEF microstimulation induces electrophysiological and behavioral consequences that are very comparable to the effect of attention. Consequently, these findings were considered as strong evidence that FEF microstimulation actually induces an attentional shift. Therefore, it is assumed that in physiological conditions, in FEF, saccadic commands that do not reach the movement threshold induce attentional shifts. This implies that, whether or not FEF attentional signal relays to another brain structure, such as LIP or SC before affecting visual processing in downstream visual areas, it has a central role in the control of attention.

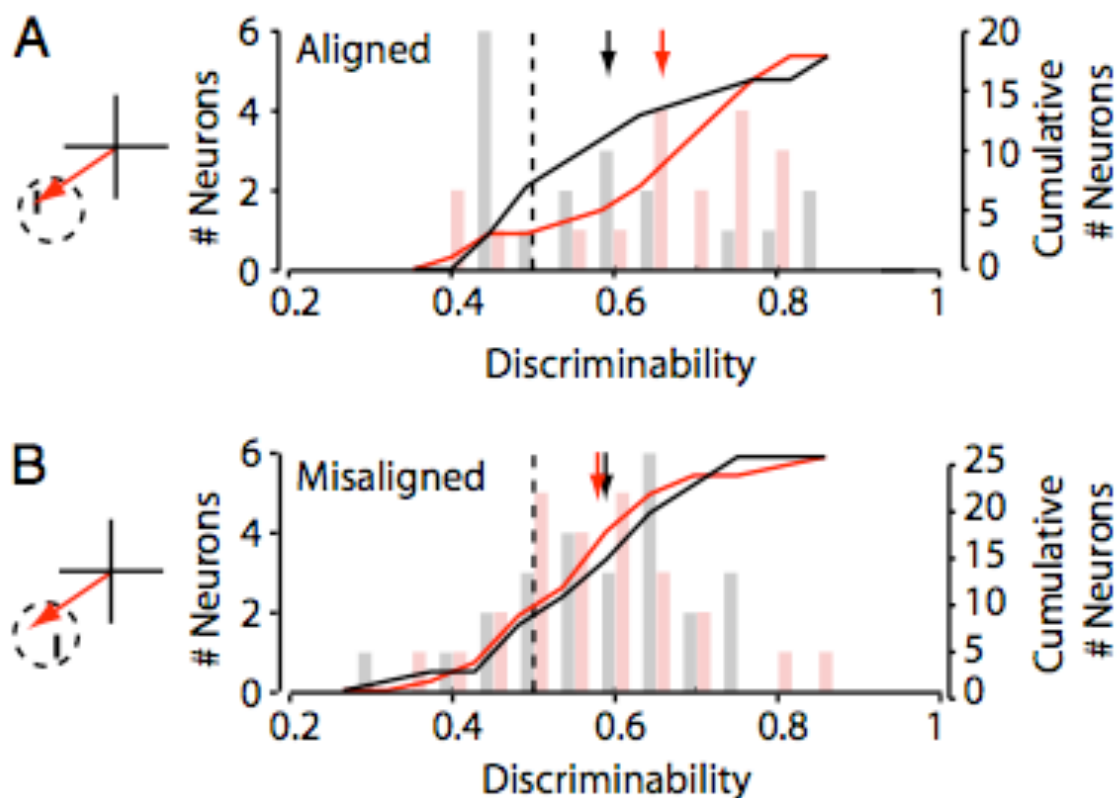


Figure I.3.13

Distribution and cumulative probability of areas under ROC curve for the whole V4 cell population, for stimulation (red) and control (black) conditions. A. The stimulus is aligned with the FEF motor field. B. The stimulus is misaligned with motor field. From (Armstrong & Moore, 2007).

Inactivation studies in FEF are few but they provided valuable insight into the role of FEF in saccade and attentional control as well. Sommer and Tehovnik used lidocaine or muscimol injections to transiently inactivate FEF neurons (Sommer & Tehovnik, 1997). They investigated the effect of this inactivation on several saccadic tasks. When the monkey had to make a delayed saccade to the remembered location of a flashed stimulus, performance was strongly affected by FEF inactivation. When contralateral targets were presented, monkeys either maintained fixation instead of making a saccade to the target, made a premature saccade to an ipsilateral location, or made a saccade to a contralateral location located far from the actual target location (see Fig. I.3.14). Moreover, saccade latency was increased. Interestingly, the results were comparable in the step task - in which monkeys were allowed to make a saccade as soon as the target appeared - as long as the target display was short, so that it was extinguished at the time when the saccade was initiated.

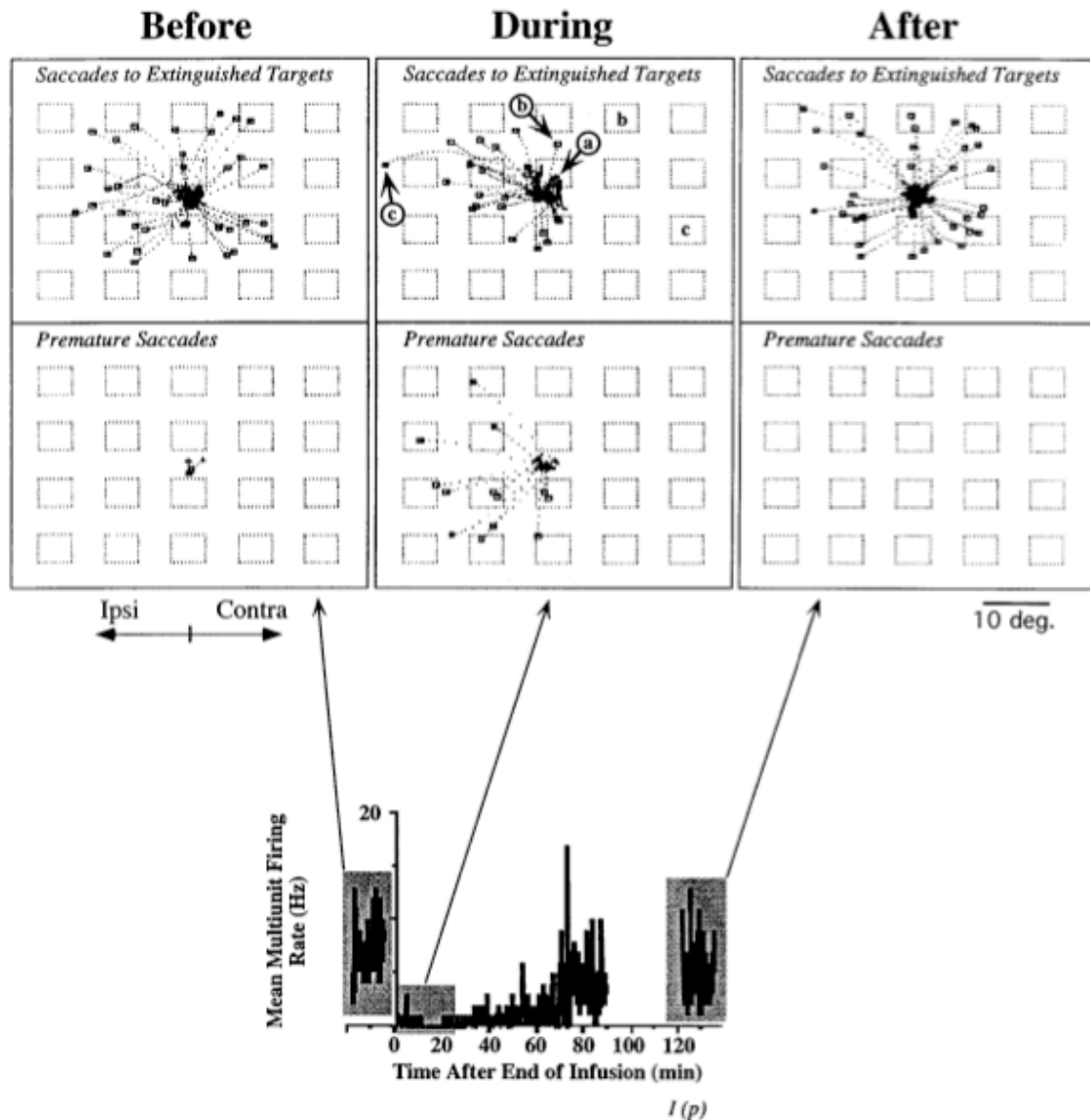


Figure I.3.14

Saccades in the delay task, made before, during and after injection. The effect of the inactivation as a function of time is illustrated in the lower graph, showing multiunit activity aligned on the time of the injection. Data marked with labelled arrows correspond to: “a”, a steady fixation or a drift occurs instead of a saccade; “b”, a saccade is performed in the appropriate hemifield, but it is very inaccurate; “c”, an ipsiversive, instead of contraversive saccade is made. From (Sommer & Tehovnik, 1997).

These dramatic effects of FEF inactivation show that this brain area is crucial for eye movement control. In a more recent study, Wardak and colleagues investigated the effect of FEF inactivation by muscimol on covert visual search tasks (Wardak, et al., 2006). Monkeys performed either a conjunction, an easy feature or a difficult feature search task. These visual search tasks contained two, four or eight items, and the difficult feature and the conjunction search tasks exhibited a small (< 10 ms/item) but significant set-size effect. Authors found that RTs to find contralateral targets were increased following inactivation, but surprisingly, the effect were comparable in all

search conditions, irrespective of the search difficulty, and set-size. Moreover, false alarm rate (only in inefficient searches) and ipsiversive abortive saccade rate were higher following inactivation. This last result is in agreement with previous observations that FEF inactivation leads to an increased rate of premature ipsilesional saccades (Dias & Segraves, 1999; Sommer & Tehovnik, 1997) during simple saccadic tasks. The observation that FEF inactivation, in contrast to LIP inactivation (Wardak, et al., 2002), leads to deficits that are independent of the difficulty of the task, suggests that it is located more downstream than LIP along the process of target selection.

1.3.2.3 In humans

The FEF homolog is located at the crossing between the superior frontal sulcus and the pre-central sulcus (Paus, 1996; Ro, Farne, & Chang, 2002). Acute FEF lesions cause only short-term deficits in initiating visually guided contralateral saccades. The compensation of these lesions depend on the restoration of function through the SC (Schiller & Tehovnik, 2005), which is the only other structure that sends direct projections to the oculomotor nuclei. Chronic frontal lesions (Rafal, 2006), and transient disruption of FEF (Ro, et al., 2002) induce increased latencies in voluntary contralateral saccades. Interestingly, FEF chronic lesions do not affect contralateral reflexive saccades but lead to increased latencies of reflexive *ipsilateral* saccades. This effect could rely on the loss of inhibition of the ipsilateral substantia nigra (SN) pars reticulata (FEF to SN connections are inhibitory), which in turn, leads to inhibition of the opposite superior colliculus (SN to opposite SC are inhibitory) (Rafal, 2006). In an antisaccade task, chronic lesions involving the FEF (Boxer, et al., 2006; Machado & Rafal, 2004) or virtual TMS lesions on FEF (Olk, Chang, Kingstone, & Ro, 2006) lead to impairment of ipsilesional anti-saccades (saccades directed ipsilesionally, away from a contralesional visual target), with an increased rate of reflexive glance towards contralesional visual targets, and/or increased latencies of ipsilesional anti-saccades. So the effects of FEF lesions on saccadic behavior are complex and variable in time, but seem compatible with a role of FEF in the control of voluntary saccade, especially in conditions where reflexive saccades must be inhibited, such as in anti-saccade paradigms.

Lesions of the FEF can lead to visual neglect, but these symptoms are usually transient (Richards, 1998). In addition to its effect on saccade performance, TMS on FEF leads to variable effects, either inhibitory or facilitatory, on attentional control. In a Posner task, right FEF disruption leads to increased RT for the detection of left invalid targets, and decreased RT for both left and right valid or neutral targets. Left FEF disruption induces RT reduction for all right targets (Grosbras & Paus, 2002). In a detection task with backward masking, right FEF stimulation leads to increased detectability of left and right targets, and left FEF stimulation increases right target detectability (Grosbras & Paus, 2003). Left and right FEF stimulation also enhances the detectability of, respectively, contralateral and bilateral TMS-induced phosphenes (Silvanto, Lavie, & Walsh, 2006). But in another study, it was found to decrease the discriminability of contralateral targets (Neggers, et al., 2007). There are several plausible explanations for these apparently contradictory results. First, the technique of stimulation varies from a study to another. Single pulse, double pulses, online repetitive TMS at 10 or 20 Hz, offline repetitive TMS at 1 Hz or in theta burst patterns, lead to different effects on the underlying brain structure (S. Fecteau, Pascual-Leone, & Theoret, 2006). Second, the effect of TMS, and even its facilitatory or inhibitory nature, depends on the sensory stimulation condition and on the task at hand (Ruff, et al., 2007; Silvanto, Cattaneo, Battelli, & Pascual-Leone, 2008). Third, the measured effect of FEF stimulation on the BOLD signal in visual areas depends

on topography. FEF stimulation induces BOLD increase in peripheral, but BOLD decrease in central sectors of V1-V4 (Ruff, et al., 2007). Fourth, like for parietal cortex, the techniques used to localize FEF vary across studies. Localization of the TMS target site was based either on the 10/20 system (Fierro, et al., 2001), on an hunting procedure (Ro, et al., 2002), on co-registration on the basis of anatomical landmarks (Grosbras & Paus, 2003) or on fMRI activities (Neggers, et al., 2007). Consequently, whereas it is clear that human FEF disruption leads to alterations of attentional processes, it is difficult to go further than this simple statement in the interpretation of these results.

The effect of FEF disruption on visual search performance may be more interesting with respect to our topic. Right FEF perturbation decreases performance in conjunction and oddball search tasks (Muggleton, Juan, Cowey, & Walsh, 2003), when applied between 40 and 80 ms after stimuli onset (J. O'Shea, Muggleton, Cowey, & Walsh, 2004). It is noteworthy that this performance decrease is explained by an increase in false alarm rate instead of a decrease in hit rate. This is similar to the reported effects of FEF inactivation in monkeys (Wardak, et al., 2006). It also increases RT for target present but not target absent trials, and this effect is proportional to the set-size (J. O'Shea, Muggleton, Cowey, & Walsh, 2006). This result is, however, different from the effect of FEF transient inactivation in monkeys, which was not affected by set-size change (Wardak, et al., 2006). When compared directly in a same paradigm, the timing of the effect of FEF and parietal disruptions on visual search differs. FEF disruption affects visual search performance when applied during the 40 ms following stimuli onset, whereas the critical parietal disruption timing occurs later, around 150 ms after search items presentation (Kalla, Muggleton, Juan, Cowey, & Walsh, 2008).

Similarly to LIP, both left and right FEFs are almost systematically activated during attentional tasks (Corbetta & Shulman, 2002; Egner, et al., 2008; Hopfinger, Woldorff, Fletcher, & Mangun, 2001; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Simon, et al., 2002). In fact, bilateral LIPs and bilateral FEFs seem to be part of a network of areas that are activated altogether during all attention demanding tasks (Fox, et al., 2005). However, several studies pointed out some differences between the human LIP and FEF activations. In their study on motion tracking, Culham and colleagues found that FEF was activated in the active versus passive condition, but the magnitude of activation was not correlated with the number of targets to track, or attentional load (Culham, et al., 2001), in contrast to parietal areas (see section 3.1.1.3). Authors propose that FEF activations reflect the preparation of eye movements. As only one target can be selected at a time for a saccade, FEF activation is constant, irrespective of the number of items to track. This saccade preparation activity could also be related to covert attention control, but involving a single target at a time. Alternatively, FEF could be involved in saccade suppression, which could be more resource-demanding in active than passive task condition, and hence could induce activation of FEF in the active versus passive contrast.

FEF is also more activated during voluntary than reflexive saccades, similarly to LIP, but in contrast to angular gyrus (Mort, Perry, et al., 2003). Left FEF shows stronger activations for contralateral saccades, but right FEF is activated similarly for saccades in both directions. In a Posner task, FEF, like all other activated areas, responds more strongly to endogenous than exogenous cues (Kincade, et al., 2005). However, FEF is the only area showing stronger activation (even though the effect is marginal) during exogenous than neutral cueing. The response to the target in FEF is enhanced in invalid with respect to valid condition (Kincade, et al., 2005), like in the angular gyrus.

Finally, an interesting difference between LIP and FEF activations is found in the

study of Yantis and colleagues (Yantis, et al., 2002). In their task, where subjects had to shift attention successively between two peripheral rapid serial visual presentation tasks, they found no frontal activation whatsoever. They propose that this lack of activation is explained by the fact that in their task, subjects did not have to disengage attention at fixation, in contrast to most studies having found FEF activations. It would imply that FEF activity would increase when shifting attention from fixation to peripheral targets, but would remain constant when shifting from a peripheral target to another, even when these targets are located in different visual fields.

I.3.2.4 Summary

Regarding FEF, there is evidence in the literature for the fulfillment of three of the salience map criteria defined above (see section 2.3). Given the existence of shape selectivity in FEF, the C criterion is not fulfilled.

- A. **PROPORTIONALITY.** Evidence that activity in FEF is proportional to selection probability is less clear than for LIP. The existence of salience representation in FEF can only be *inferred* from the evidence that activity in this area depends on stimulus relevance (Sato, et al., 2003; Schall, 2002; Thompson, Biscoe, et al., 2005). Only Thompson and colleagues tried to investigate this proportional relationship between cells activity in FEF and selection probability (Thompson, Bichot, et al., 2005). As described above, the analyses they conducted were performed on data gathered from different experiments and used an odd definition of saccadic selection probability (probability of selecting the target or any of the distractors). Therefore, while their results appear to be in line with the salience map hypothesis, they might instead be caused by an effect of the task difficulty, and hence, cannot be considered as conclusive.
- B. **CAUSALITY.** Microstimulation studies have shown very convincingly that FEF is involved in attention control (T. Moore & Armstrong, 2003; T. Moore, Armstrong, & Fallah, 2003; T. Moore & Fallah, 2004), but these results cannot be considered as evidence that this area is involved in salience representation. In order to investigate this question, the efficiency of the stimulation in driving attentional and saccadic allocation should be investigated as a function of current intensity and salience of competitors. The salience map hypothesis predicts that saccadic and attentional shifts should occur towards the motor field of the stimulated subpopulation when the current intensity leads to a cell activation that overrides the activity of the cells representing competitors.

Likewise, inactivation studies showed that FEF inactivation leads to deficits in overt and covert tasks (Wardak, et al., 2006) but the fact that these deficits mainly consist in an increased rate of false alarms and do not depend on difficulty or set-size are not in agreement with the salience map hypothesis.

- C. **SENSORY AND MOTOR ASPECIFICITY.** Recent evidence has shown that some FEF cells exhibit selectivity to the shape of the stimulus presented in their receptive field. In addition, the activity in movement cells is specific for saccadic motor features. Therefore, if FEF contains a salience map, it must be implemented in visual and visuo-movement cells (Thompson, Biscoe, et al., 2005).
- D. **TOPOGRAPHY.** FEF exhibits a topographical organization that is compatible with the salience map hypothesis. However, in contrast to LIP, FEF receptive

fields are large.

I.3.3 SUPERIOR COLLICULUS

I.3.3.1 Anatomy

Superior colliculus (SC) is a small structure located in the dorsal part of the mesencephalon. It is composed of seven cyto- and myeloarchitecturally distinct layers (Viktorov, 1968) which can be classified into two functional groups: superficial, and deep layers. This last group is in fact composed of both the intermediate and deep layers. The superficial, on one side, and the intermediate and deep layers on the other side, exhibit a different connectivity (see Fig. I.3.15). The superficial layer receives direct input from the retina and cortical input from V1, areas 18 and 19. Projections from the superficial layer target mainly lateral geniculate, pulvinar and the lateral posterior nucleus of the thalamus (May, 2005; Sparks, 1988). The intermediate and deep layers receive projections from auditory cortex and auditory brainstem nuclei, somatosensory cortex and somatosensory spinal nuclei, lateral geniculate and visual areas (mainly area 19) and area LIP, FEF and SEF (May, 2005; Sparks & Hartwich-Young, 1989). About half the cells in the intermediate layer are multisensory. The importance of the visual and non visual inputs in the SC varies across species, as a function of the importance of the related sensory information in the animal behavior (May, 2005). Cells in the intermediate and deep layers also receive projections from the substantia nigra pars reticulata and cerebellar nuclei (Sparks & Hartwich-Young, 1989). Their outputs are to oculomotor brainstem nuclei, spinal motor nuclei, cerebellum and to central lateral and mediodorsal thalamic nuclei. This last connection is part of the FEF-SC-thalamus-FEF circuit briefly introduced above.

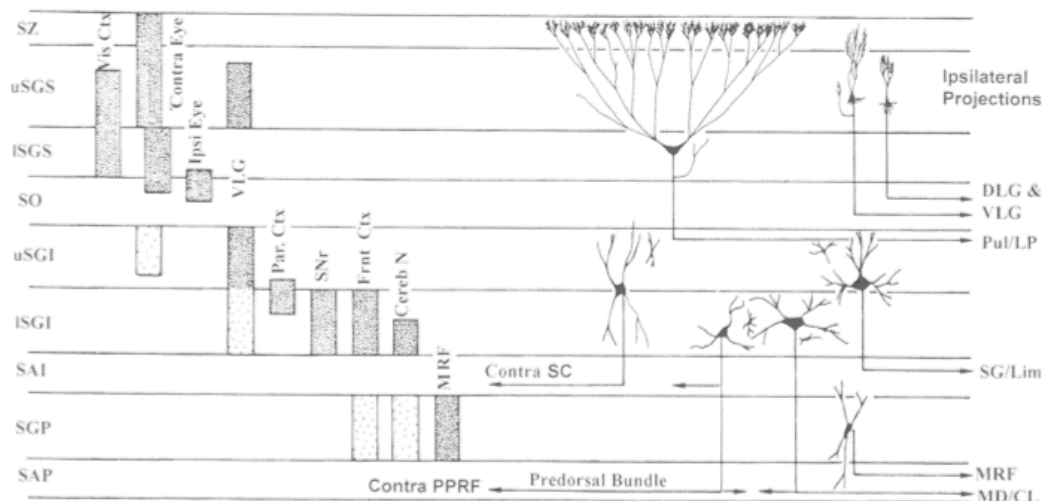


Figure I.3.15

Summary of the inputs and outputs of the different layers of the superior colliculus (abbreviations: SZ: stratum zonale, uSGS: upper stratum griseum superficiale, ISGS: lower stratum griseum superficiale, SO: stratum opticum, uSGI: upper stratum griseum intermediale, ISGI: lower stratum griseum intermediale, SAI: stratum album intermediale, SGP: stratum griseum profundum, SAP: stratum album profundum, VLG: ventral lateral geniculate, DLG: dorsal lateral geniculate, Cereb N: cerebellar nuclei, MRF: mesencephalic reticular formation, PPRF: parapontine reticular formation, Pul: pulvinar, LP: lateral posterior thalamic nucleus, MD: mediodorsal thalamic nucleus, CL: central lateral thalamic nucleus, SG: supragenicolate, Lim: nucleus limitans). From (May, 2005).

I.3.3.2 Physiology

Cells of the intermediate and deep layers are commonly classified in four categories with respect to their visual and saccadic responses:

- fixation cells, located in the rostral SC, discharge during fixation and are inhibited during saccade execution;
- burst neurons generate high frequency bursts of activity just before saccade onset directed to their motor field, and may also respond to visual stimuli;
- build-up neurons begin to discharge earlier before saccade than burst cells, during the delay between target onset and saccade onset, and their discharge rate increases slowly until saccade onset;
- quasi-visual cells exhibit a complex mix of visual and motor responses.

Electrical microstimulation induces saccade at very low current intensities in SC, and this method has been used to map the topography of SC deep layers: small saccades are represented anteriorly and large saccades posteriorly; upward and downward saccades are represented medially and laterally, respectively (Sparks, 1988). Many recording and microstimulation studies have been made with the head of the animal restrained. When microstimulating SC in a head-free animal, a combination of eye and head movements is evoked. Interestingly, SC does not seem to code for either eye or head movement amplitude but for a combination of both, i.e. for the location of the stimulus to foveate (E. G. Freedman, Stanford, & Sparks, 1996). Some cells in intermediate layers also exhibit somatosensory responses, with a strong bias for head and forelimb representation, and auditory responses, with a topographical organization similar to the visual topography (Sparks, 1988). In superficial layers, cells respond only to visual stimuli. The topographical organization of their receptive fields matches the topography of the motor fields found in deeper layers.

There is much evidence in the literature that SC is not merely a motor area coding for the saccade metrics and latency. Basso & Wurtz showed that the activity of build-up neurons was proportional to saccade probability (Basso & Wurtz, 1998). In their task, a variable number of stimuli was first displayed (1, 2, 4 or 8), during a so-called pre-selection phase. After a delay, the saccadic target was indicated by the dim of one of the stimuli. Authors showed that the activity of build-up neurons during the pre-selection phase decreased as the number of potential targets increased (see Fig. I.3.16). As soon as the actual target location was instructed, only the cells that contained the target in their receptive field remained active, and their discharge rate did not vary with the number of stimuli displayed. This suggests that the variation of activity in build-up neurons is related to the uncertainty about the target location, and not to a general effect of the number of stimuli. The more a given location is likely to become the target (few potential targets), the more corresponding build-up neurons discharge during the delay period. In addition, Basso & Wurtz showed a comparable effect on the visual phasic response of burst neurons. Interestingly, the data from Basso & Wurtz have been re-analyzed by Krauzlis and colleagues (Krauzlis, Liston, & Carello, 2004). They showed that the correlation between discharge rate of build-up neurons and the log of the target selection probability was clearly linear ($R=0.99$). This suggests that activity in these neurons might represent the log-likelihood of selection alternatives. Representing this type of value can lead to very efficient computations for decision-making (Krauzlis, et al., 2004).

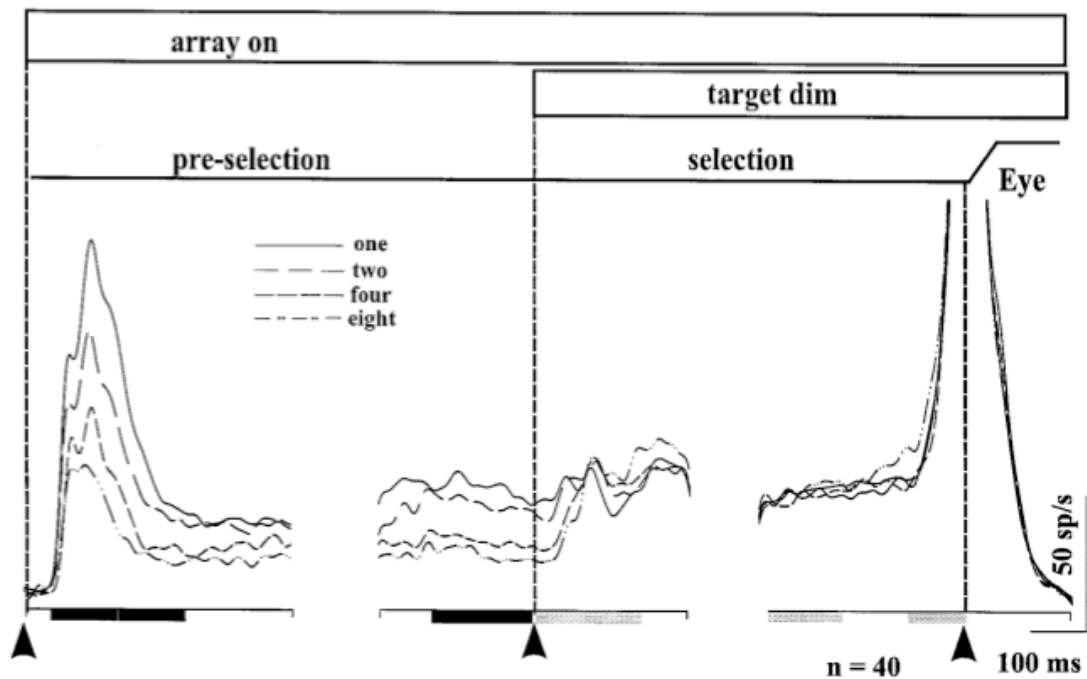


Figure I.3.16

Peri-stimulus time histogram of the population of build-up neurons during the three periods of the task used by Basso & Wurtz, 1998.

Along the same line, Dorris and colleagues manipulated the saccadic goal location probability and recorded build-up neurons activity (Dorris & Munoz, 1998). In a given block of trials, saccadic target occurred always (100% probability), never (0% probability) or in half of the trials (50% probability) inside the cell receptive field. Authors showed that cell activity was directly proportional to the probability of a saccade towards the receptive field, and inversely proportional to the saccadic latency. Similarly, in a random-dot stimulus motion discrimination task, the visual response of some SC cells (30% of the population) is proportional to the coherence of the motion instructing a saccade towards their receptive field (Horwitz & Newsome, 2001). Saccade metrics is poorly predicted by this visual response. In contrast to visual activity, the peri-saccadic activity is better correlated with saccade metrics than with movement coherence (see Fig. I.3.17). This suggests that the early visual response in SC is concerned with target selection, whereas peri-saccadic activity is involved more in the actual implementation of the saccade.

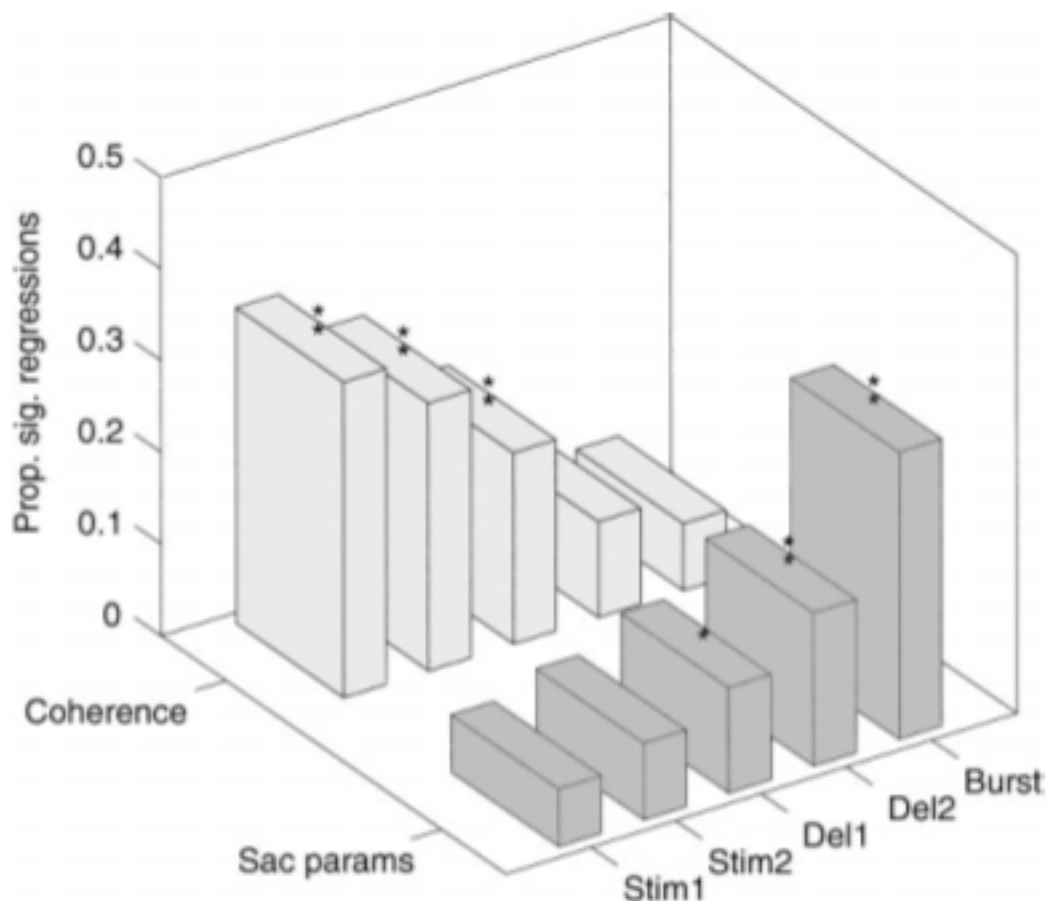


Figure I.3.17

Proportion of cells exhibiting a significant effect of coherence (light grey) and saccade metrics (dark grey) during the different periods of the random-dot motion discrimination task. From (Horwitz & Newsome, 2001).

The aforementioned results suggest that SC is involved in the selection of saccadic targets. Its role in the control of attention, suspected for a long time (Goldberg & Wurtz, 1972), was more recently investigated. In a Posner task, using exogenous cues that could be either informative (75% validity) or non-informative (50% validity), Fecteau and colleagues found that the level of activity in SC cells followed the evolution of RT as a function of the cue target onset asynchrony (CTOA) (J. H. Fecteau, Bell, & Munoz, 2004). For short CTOAs, RT is shorter when the target appears at cue location, irrespective of whether the cue is informative or not. Correspondingly, target-evoked activity in SC cells is higher at the cue location than at the opposite location. For longer CTOAs, when the cue is uninformative, the RT becomes longer at cue location than at the opposite location, an effect called inhibition of return. In this case, the target-evoked activity in SC cells is also stronger at the position opposite to the cue location. In contrast, when the cue is informative, the RT benefit at the location of the cue is maintained in longer CTOAs and SC activity remains higher at cue location. These results strongly suggest that SC activity in intermediate layers parallels attentional allocation in a Posner task. This result is strikingly different from the signal observed in LIP and area 7a, where the response to a visual stimulus is reduced when it appears at the locus of attention.

To study the effect of attention on the delay period activity in SC cells, Ignashchenkova and colleagues also used a cueing task to manipulate attentional allocation (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004). The cue validly

indicated the location of a stimulus (a Landolt 'c') that the monkey had to discriminate. In some trials, the cue was absent, and the performance of the monkey was poorer in these trials, indicating that the animal used the cue to orient its attention to the location of the upcoming stimulus. Authors distinguished three types of cells on the basis of their response in a memory-guided saccade task: visual, motor and visuo-motor cells (this last category includes buildup neurons). When the 'c' target or the cue was displayed in the receptive field, visual and visuo-motor cells exhibited a visual response. Motor cells never responded in these trials because no saccade was ever programmed toward the 'c' target. Similarly to the study by Fecteau and colleagues, the target-evoked activity was greater when following the cue in visual and visuo-motor cells. In addition, Ignashchenkova and colleagues studied the period of activity between the cue and the target, i.e. the period during which attention has to be maintained on the cue location. They found that visuo-motor, but not visual cells, showed maintained activity during this period (see Fig. I.3.18). Moreover, the enhancement of activity during the cue-target delay period in visuo-motor cells was correlated with the acuity benefit induced by the cue. However, surprisingly, the influence of the cue on visuo-motor cells activity completely disappeared when using central instead of peripheral cues. The only remaining modulation in this condition was the increased discharge rate of visual neurons when the target appeared at the cued location. This suggests either that SC is involved in the control of attention following peripheral cueing only, or that the delay period activity observed in visuo-motor cells is explained by maintenance of the visual cue-related activity and not by attentional allocation. The fact that the enhancement of cell activity during the delay period is proportional to the enhancement of acuity induced by the cue is a strong argument against this last hypothesis.

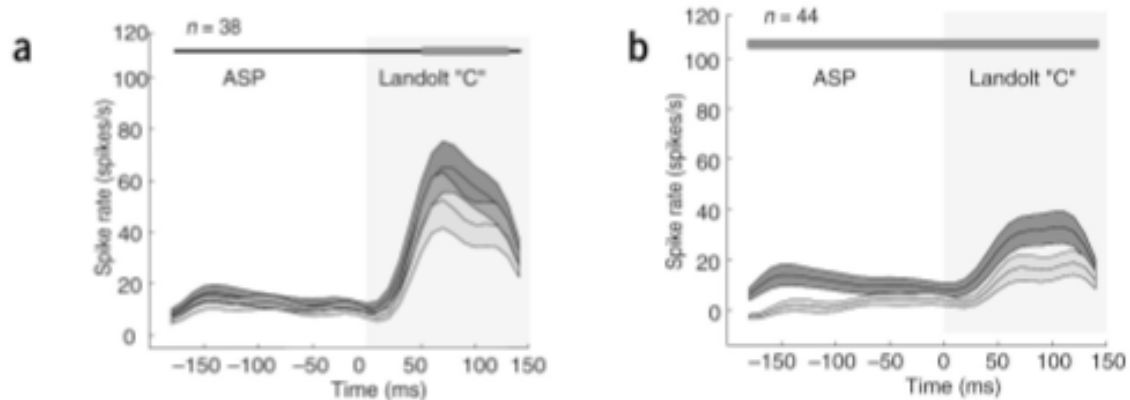


Figure I.3.18

Discharge rate of visual (a.) and visuo-motor (b.) cells, as a function of time, aligned on 'c' target onset. Dark grey and light grey traces represent activity in cued and non-cued trials, respectively. ASP: attention shift period. From (Ignashchenkova, et al., 2004).

Convincing evidence that SC is involved in target selection instead of saccade execution control comes from inactivation studies. McPeck & Keller inactivated portions of SC by injecting lidocaine or muscimol (McPeck & Keller, 2004). They determined the motor field of the inactivated sub-population by microstimulating prior to the injections. The effect of the inactivation on simple visually-guided saccades made to the affected part of the visual field was modest but significant: lower velocity,

lower accuracy, higher latency. Interestingly, when the monkey had to perform a colour singleton search task, and the target of the search was located in the affected part of the visual field, the deficit induced by the inactivation differed from the simple visually-guided saccade tasks. In this case, in addition to the effect of the inactivation on saccade metrics, the inactivation led to an increased error rate. These errors consisted in accurate saccades performed towards the wrong location, selecting a distractor instead of the target. Moreover, this effect was dramatically increased in difficult search conditions.

A much more dramatic effect of SC inactivation has been observed in cats. Fitzmaurice and colleagues conducted 113 experiments with muscimol injections in the SC (Fitzmaurice, Ciaramitaro, Palmer, & Rosenquist, 2003). They found that in 67% of these experiments, the cats were impaired in a simple peripheral detection task, where they had to report with a foot press, the appearance of a supra-threshold target. Cats were specifically impaired in contralesional target detection. The strongest effects were obtained with deep injections, likely to have targeted intermediate and/or deep layers. During these injections, performance for contralateral target detection could drop from around 100% to around 0%.

As stated above, SC microstimulation reliably evokes saccadic movements at low current intensities (D. A. Robinson, 1972). Carello and Krauzlis found that, when applying microstimulation at current intensities below the saccadic threshold, even though no saccade was evoked, the choice of the saccadic target was biased toward the motor field of the stimulated SC region (Carello & Krauzlis, 2004). But even more compelling, in another condition where the monkey had to select the target by following its motion by a pursuit eye movement, designed so that in order to select a right-hand target, the monkey had to make a leftward pursuit, the effect of the microstimulation still biased the target selection towards the motor field, even though the direction of the pursuit eye movement was opposite. This result demonstrates the critical role of SC in target selection, even when this selection does not involve a saccadic movement towards the target.

The role of SC in covert orienting also has received support from microstimulation experiments. Similarly to FEF, microstimulation of SC leads to an enhancement of detection performance of stimuli displayed inside the receptive field of the stimulated population. Cavanaugh and colleagues used a change detection task, where monkeys have to detect the motion direction change of one out of multiple random-dot stimuli (Cavanaugh, Alvarez, & Wurtz, 2006; Cavanaugh & Wurtz, 2004). They showed that SC stimulation enhanced performance in the discrimination of the stimulus located in the motor field of the stimulated subpopulation, mostly by increasing the hit rate, with a marginal reduction of false alarm rate. One possible confound with microstimulation studies is that the behavioural effect can sometimes be explained by internal cueing: the animal uses the sensation associated to microstimulation as a cue to orient attention. In order to demonstrate that the effect of microstimulation on change detection performance involved covert orienting and not internal cueing, authors used several control tasks (Cavanaugh, et al., 2006). They showed that, when displaying a 100% valid visual cue at target location prior to stimuli onset, the performance enhancement was different than with microstimulation: the cue induced an increase in hit rate and an increase in false alarm rate. Moreover, when using microstimulation prior to stimuli onset, at the time the cue was normally displayed, no effect of microstimulation was found. These results (together with other control tasks) demonstrate that the effect of microstimulation does not involve internal cueing and hence, is likely to be explained by covert orienting.

I.3.3.3 In humans

Given their size and location, superior colliculi are difficult to study in humans. Advances in fMRI technology, like the use of 3 tesla magnets, and methods to remove artifacts produced by nearby blood vessels, made possible the study of superior colliculi function by means of functional imagery only very recently (Schneider & Kastner, 2005). Consequently, up to now, fMRI studies investigating SC activation as a function of saccadic or attentional factors are few. In such a recent functional imagery study, superior colliculus was shown to be more active during visual search than simple visually guided saccades, even though the visual stimulation conditions were comparable (Himmelbach, Erb, & Karnath, 2007), a result compatible with the role of SC in the selection of the saccadic target. However, a potential confound is that the number of saccades performed during acquisition was superior in the search than in the visually guided saccade condition. Authors tried to take this into account by adding the number of saccades as a covariate in their analysis, but this method is valid only under the assumption that the number of saccades affects superior colliculi activity linearly. Authors give no reason whatsoever to consider this assumption as valid.

Several case studies addressed the function of superior colliculi in saccade and attention tasks. Patients with collicular lesions showed increased latency for contralateral saccades (Pierrot-Deseilligny, Rosa, Masmoudi, Rivaud, & Gaymard, 1991), mostly reflexive (A. B. Sereno, Briand, Amador, & Szapiel, 2006), and with prolonged (Sapir, Soroker, Berger, & Henik, 1999), transient (A. B. Sereno, et al., 2006) or absence (Pierrot-Deseilligny, et al., 1991) of suppression of the gap effect (i.e. shorter saccade latencies when fixation point disappears prior to target onset). They also show a deficit in the inhibition of reflexive ipsilateral saccades in fixation (Pierrot-Deseilligny, et al., 1991) and in anti-saccade tasks (Pierrot-Deseilligny, et al., 1991; A. B. Sereno, et al., 2006). Finally, inhibition of return is severely disrupted by collicular lesion (Sapir, et al., 1999; A. B. Sereno, et al., 2006), and exogenously cued attention shifts appear slower (A. B. Sereno, et al., 2006).

I.3.3.4 Summary

The superior coliculus fulfills all of the four salience map criteria defined above (see section 2.3):

- A. **PROPORTIONALITY.** Activity in SC has been shown to be proportional to the saccadic selection probability (Basso & Wurtz, 2002). The signal relayed in SC reveals also the locus of covert attention (J. H. Fecteau, et al., 2004; Ignashchenkova, et al., 2004). Moreover, the magnitude of the activation of the cells representing the attentional locus is proportional to the behavioral effect of attention.
- B. **CAUSALITY.** Microstimulation and inactivation studies have shown that SC is involved in saccadic and attentional target selection (Carello & Krauzlis, 2004; Cavanaugh & Wurtz, 2004; McPeck & Keller, 2004) in a way that is compatible with the salience map hypothesis. However, the same remark as the one made for FEF microstimulation studies can be made here: the observation that FEF microstimulation induces a bias in target selection and an attentional shift can be interpreted either in terms of salience representation, or in terms of all-or-nothing attentional allocation.
- C. **SENSORY AND MOTOR ASPECIFICITY.** Like in FEF, eye movement metrics are represented in movement cells in the deep layers of SC. The representation of salience might involve strictly visuomotor cells (Ignashchenkova, et al.,

2004).

D. TOPOGRAPHY. SC exhibits a very robust topographical organization.

I.3.4 THE NETWORK

The striking feature of all the aforementioned results is the similarity between all the described structures. All these structures show visual and saccadic responses, exhibit no visual feature specificity (with the notable, but still disputed, exception of LIP), and are strongly modulated by attentional variables and relevance. The microstimulation of most of them (except area 7a) induces saccades, and affects behavioral performance at spatially specific locations. The inactivation of these structures (except area 7a) leads to deficits in target selection. All these structures are heavily interconnected with each other (Lynch & Tian, 2005), with the exception of area 7a and superior colliculus on the one hand, and area 7a and FEF on the other hand. Finally, the ablation of any of them lead to only mild chronic deficits (Schiller & Tehovnik, 2005). The two fundamental questions that ought to be addressed are how each of the structures involved in the network process incoming signal and what signal do they relay to the other areas. While the former was discussed in the previous chapters, we will try to address the latter in the following.

Amongst the cortical areas involved, the status of the FEF is peculiar. It sends direct projections to the oculomotor centers and, in contrast to parietal cortex, FEF microstimulation induces saccades even after SC lesion (Schiller & Tehovnik, 2005). Moreover, lesioning bilaterally both FEF and SC leads to a permanent inability to perform any visually guided saccadic movement (Schiller & Tehovnik, 2005). This shows that FEF and SC are the only outputs of the visuo-saccadic system. However, the functional significance of the direct FEF-brainstem projections in absence of any chronic lesion has been questioned by the work of Hanes and colleagues. They showed that when the motor field affected by transient inactivation of the SC was aligned with the motor field targeted by FEF microstimulation, saccades could no longer be evoked (Hanes & Wurtz, 2001), suggesting that, in physiological conditions, FEF was involved in saccadic control only by relaying through the SC. Interestingly, they also showed that when SC inactivation and FEF stimulation fields were misaligned, the saccades evoked by FEF microstimulation were deviated away from the inactivated SC motor field, exactly like if SC inactivation removed a component of a vector average. These results are very strong evidence against the role of the connection between FEF and brainstem oculomotor centers in initiating eye movements in physiological conditions. Additionally, it confirms that the projections from FEF to SC respect the topography of each structure (Sommer & Wurtz, 2000), since suppression of evoked saccades occurred only when corresponding motor fields were targeted. Finally, it suggests that the covert orienting effects observed following FEF microstimulation might in fact rely on this indirect fronto-tectal route.

The fronto-tectal and tecto-frontal pathways have been extensively studied by Sommer, Wurtz and colleagues. The FEF cells projecting to SC (identified by means of antidromic SC electrical stimulation) can be of any type: visual, visuo-movement or movement cells. But there exists a bias for cells exhibiting more visual and delay activity and less pre-saccadic activity (Sommer & Wurtz, 2000). Similarly the SC cells projecting to FEF via the mediodorsal thalamic nucleus (MD) (identified by SC orthodromic stimulation), all exhibit visual activity, while only the half of them show pre-saccadic activity (Sommer & Wurtz, 1998). Inactivating MD cells that relay information from SC to FEF induces a contraversive shift in the second saccade of a double step saccade task (in which subjects have to make two successive saccades to remembered locations) (Sommer & Wurtz, 2002), while leaving largely unaffected the first saccade, or single visually guided saccades. Authors interpreted these results as reflecting the disruption of the corollary discharge of the saccadic

command sent from SC to FEF, which permits to calculate the updated location of the second saccadic target, after execution of the first saccade. Hence, the SC to FEF pathway would be critical in the transmission of the corollary discharge signal of the saccade to the visual system. Moreover, following MD inactivation, the monkey was unable to adapt the second saccade amplitude and direction to the error of the first saccade on a trial by trial basis (Sommer & Wurtz, 2004b), suggesting that the corollary discharge of the first saccade is no longer available to correct the endpoint of the second saccade. Finally, inactivating MD relay cells decreases or suppresses remapping in the FEF (Sommer & Wurtz, 2006), which depends critically on corollary discharge. It is noteworthy, however, that MD inactivation led only to partial deviation of the second saccade (19% deviation) in the double step saccade task, and to non complete suppression of FEF cells remapping, suggesting that this route might not be the only one, and maybe not the main one, even though incomplete inactivation of MD cells also could be responsible for these partial effects.

The function of the parieto-tectal pathway is less well understood. Interestingly, SC cells that receive projections from LIP are distinct from cells receiving FEF projections (Wurtz, Sommer, Pare, & Ferraina, 2001). All visual, delay, and saccadic responses are transmitted from LIP to SC cells (Wurtz, et al., 2001). SC cells that receive projections from LIP show a greater independence from visual stimulation and are more modulated by saccade programming than the LIP neurons projecting to the SC (Pare & Wurtz, 2001). Along the same line, LIP cells that project to the FEF are spatially distinct, and exhibit less motor-related activity than cells projecting to the SC (Ferraina, et al., 2002).

Much evidence indicates a gradually increasing role in saccadic control from area 7a to LIP to FEF to SC. Microstimulation in area 7a does not evoke saccades (Thier & Andersen, 1998). Saccades are evoked by microstimulating LIP only with high current intensities (Constantin, et al., 2007). In contrast, microstimulation of FEF (C. J. Bruce, et al., 1985) and SC (E. G. Freedman, et al., 1996) induces saccades at low current intensities. The effect of LIP inactivation on saccade execution is mild or inexistent (Wardak, et al., 2002). FEF inactivation leads to saccadic deficits when the target is not visually available (Dias & Segraves, 1999) whereas SC inactivation induces alteration of the saccade metrics even in simple visually guided saccades (Quaia, Aizawa, Optican, & Wurtz, 1998). The effect of LIP, FEF and SC inactivation during performance of visual search shows some difference as well. FEF inactivation leads to an increased rate of distractor selection even in a very simple visual task (Wardak, et al., 2006) whereas the effect of LIP inactivation critically depends on task difficulty (Wardak, et al., 2004). Similarly to FEF, SC inactivation leads to an increased probability of selecting a distractor in simple visual tasks (Carello & Krauzlis, 2004), but similarly to LIP, this effect is greatly increased in case of more difficult visual search tasks (McPeck & Keller, 2004). Finally, the proportion of cells exhibiting strong, specific and reliable motor responses increases from area 7a to SC (Barash, et al., 1991; Pare & Wurtz, 2001; Sato & Schall, 2003; Wurtz, et al., 2001). All these results suggest that, despite a large qualitative overlap of functions, each of the areas constituting the fronto-parieto-tectal network have a quantitatively different role in saccadic control.

Valuable information on the signal flow occurring in the fronto-parieto-tectal network could be gathered by measuring response latencies. Indeed, if a hierarchy exists in this network, we expect earlier areas in this hierarchy to exhibit earlier discriminability of visual stimuli on the basis of their salience. One study specifically addressed this question by directly comparing latencies of target discrimination in LIP, FEF and dorsolateral prefrontal cortex (DLPFC) cells simultaneously recorded during visual search tasks (Buschman & Miller, 2007). They found that in a pop-out search task, a sub-population of LIP cells (35%, 162 ms before saccade on average) were the first

to discriminate the target, followed by DLPFC (51%, 77 ms before saccade) and FEF (31%, 40 ms before saccade). The rest of the population of these three areas had a common discrimination peak around 100 ms *after* the saccade. In contrast, during inefficient feature search, the order was reversed. An FEF subpopulation (32% of cells) discriminated the target around 50 ms before the target, followed by DLPFC (30%, 40 ms). The number of LIP cells discriminating the target before the saccade was not significantly different than the number expected by chance. This number reached significance only 32 ms after saccade onset. While potentially very interesting, these data suffer from a great disparity with respect to the rest of the literature, and are currently largely disputed (Schall, Pare, & Woodman, 2007). A meta-analysis of the literature shows that discrimination of the target occurs in FEF usually around 150 ms (extremes: 100 to 180 ms) after stimuli onset or 60 ms before saccade onset (-120 to -40 ms) (Schall, et al., 2007). LIP cells show very short response latencies, around 40-50 ms (Bisley, Krishna, & Goldberg, 2004), which might convey stimulus-driven salience information related to the abrupt onset of stimuli (Bisley & Goldberg, 2006). Task related modulation and target discrimination occur later in this area, around 70-100 ms before saccade onset (discrimination between GO and NO-GO probe in the receptive field) (Bisley & Goldberg, 2006), or 100 ms (Balan, et al., 2008) to 150 ms after stimuli onset (Balan & Gottlieb, 2006). Hence discrimination latencies of FEF and LIP cells, albeit measured in different animals during different tasks, are grossly comparable. Finally, a surprising finding has been reported in a recent study by Khayat and colleagues (Khayat, Pooresmaeili, & Roelfsema, 2009). These authors found that the discrimination between distractors and targets appear after similar latencies in area V1 and FEF, in both cases around 150 ms. These results suggest that instead of a progressive propagation of attentional modulation from attentional control areas to visual areas, attentional modulation might appear simultaneously in the tecto-fronto-parietal network and in striate and extra-striate visual cortex.

In addition to the structures described above, an important part of the network, which is often overlooked, is the pulvinar. An important circuit, constituted by a cortico-colliculo-pulvino-cortical loop might be crucial for the coherence of the network (Shipp, 2004). Cortical connections with the pulvinar can be represented by two parallel gradients, involving either the ventral or the dorsal visual streams, respectively occupying ventral and dorsal pulvinar. Connections with these cortical visual areas are reciprocal. Along the whole ventral visual stream gradient in ventral pulvinar, visual activities are well organized in two topographical visual maps (the primary and secondary maps). These visual maps receive projections from the SC. This pattern of connections suggest a central role of the pulvinar in dispatching the feedback attentional signal, possibly relayed through the SC, to the whole ventral visual stream simultaneously (Shipp, 2004). However, the precise function of the pulvinar remains still largely unknown. While some authors argue that it is involved in attentional control, others propose instead that it is important for response selection in situations of competition. Neurons in the dorsomedial part of lateral pulvinar (connected with parietal cortex) exhibit visual and saccadic responses (mostly post-saccadic), and show strong modulations with respect to the behavioral significance of the displayed stimuli, i.e. cells discharge more for stimuli that are targets for the next saccades or that are attended (Petersen, Robinson, & Morris, 1987). The inferior and lateral nuclei show saccadic modulation as well, but this modulation occurs irrespective of whether a saccade toward or away from the stimulus in the receptive field is prepared (D. L. Robinson & Petersen, 1992). Bender and Youakim showed that the level of modulation by attention in pulvinar is comparable to that found in visual cortical areas (Bender & Youakim, 2001). Reversible inactivation of the pulvinar leads to deficits in a Posner task (Petersen, et al., 1987). RTs are longer in all cueing conditions whenever the target is displayed in the contralesional hemifield,

and RTs are shorter when an invalid cue is displayed in the contralesional hemifield, suggesting an inability of attention to shift towards the affected hemifield (see Fig. I.3.19 and I.3.20). However, this deficit does not alter the efficiency of the cue, i.e. contralesional valid cues seem as effective as ipsilesional valid cues (even though this comparison is not addressed by the authors). An equivalent result was found in a single case study of a patient with thalamic lesion. He was generally slow to respond to contralateral targets, but did not exhibit any alteration of the validity effect of the cue (Rafal and Posner 1987). Finally, Desimone and colleagues showed that transiently inactivating the pulvinar leads to inaptitude in filtering out distractors. Whereas monkeys performance was unaffected by pulvinar inactivation in a color and form discrimination task when performed in the absence of distractor, the inactivation led to a dramatic increase of the error rate, when a distractor was displayed in the non affected field (Desimone, Wessinger, Thomas, & Schneider, 1990).

Valid trials, two drug conditions and control

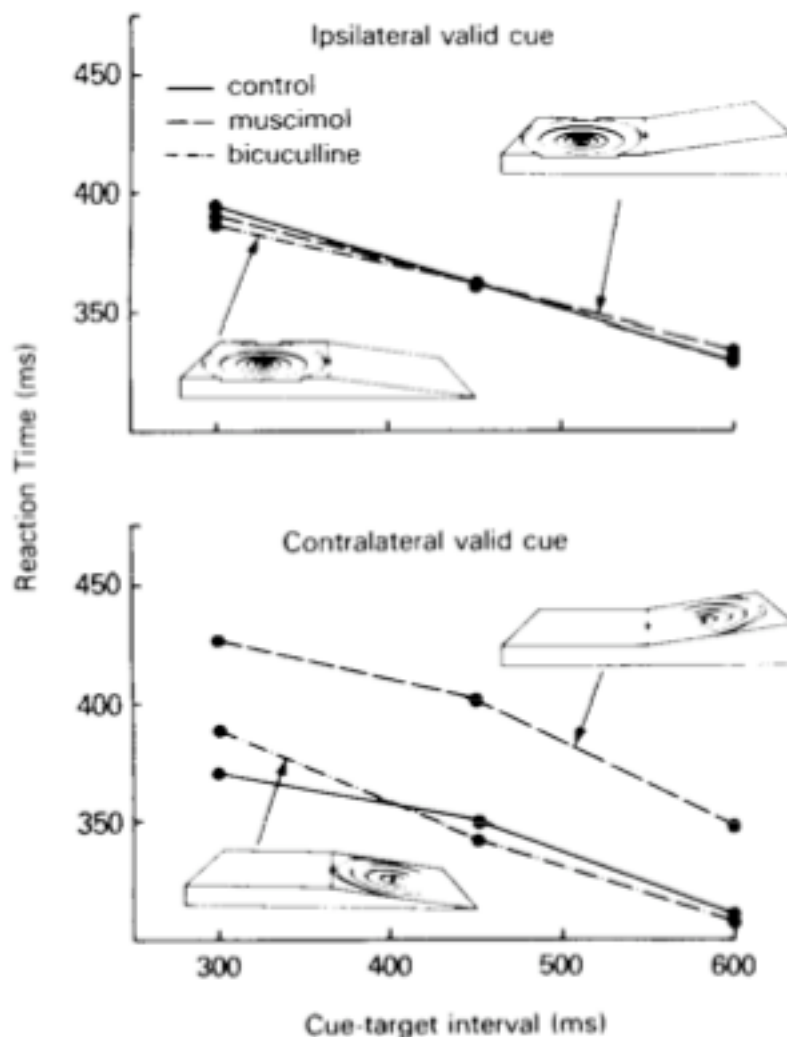


Figure I.3.19

Effect of muscimol or bicuculline injections on the Posner task performance in valid trials. The two cartoons within each graph represent the display. The sculptured pit indicates the location of the cue; the spot represents the location of the target. The

central spot depicts the fixation point. Elevations on the right side of the screen suggest the impeding effect of muscimol on shifts of attention in that direction: depressions on the right side refer to the facilitatory effect of bicuculline on the shift of attention in that direction. From (Petersen, et al., 1987).

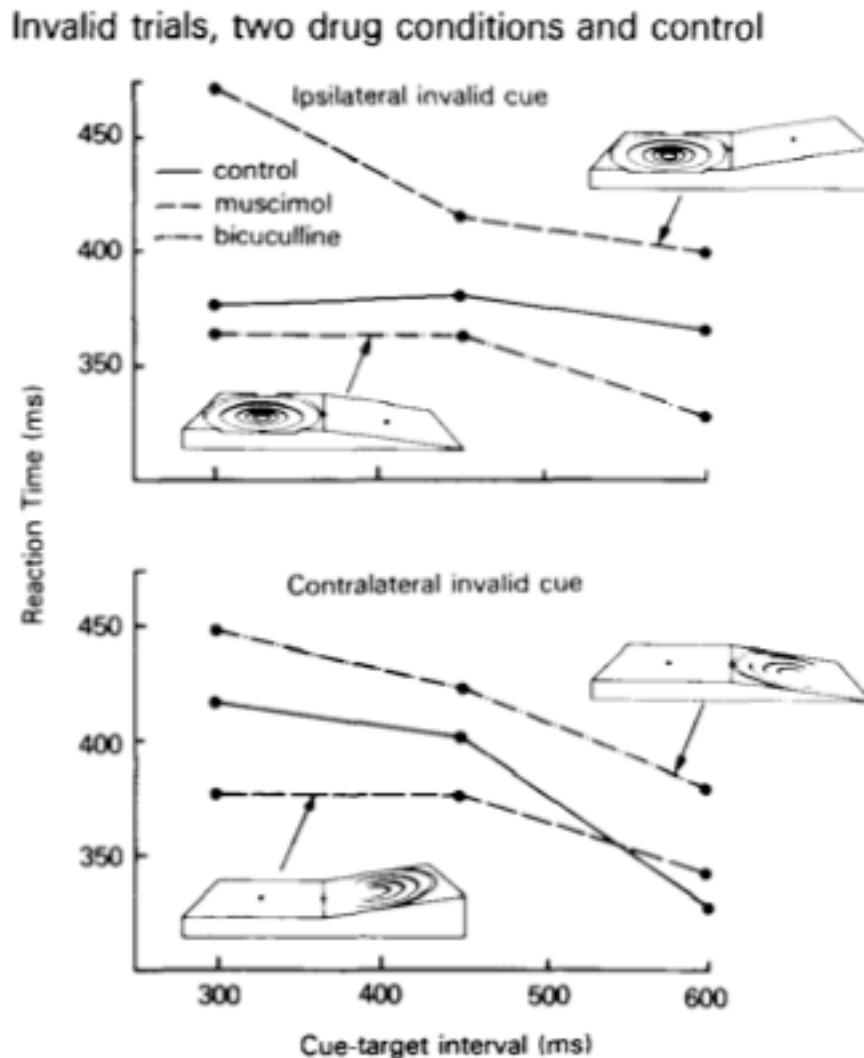


Figure I.3.20

Effect of muscimol or bicuculline injections on the Posner task performance in invalid trials. Same conventions as in I.3.17. From (Petersen, et al., 1987).

The role of human pulvinar in visual neglect is disputed. Some authors reported that lesions encompassing the pulvinar were more often associated to neglect than other thalamic lesions (Karnath, Himmelbach, & Rorden, 2002). Other authors claim that patients with unilateral pulvinar lesions have generally mild deficits and do not exhibit clear oculomotor anomalies or visual neglect (Danziger, Ward, Owen, & Rafal, 2001). In a flanker task, where the target is flanked by either a compatible (indicating the same response as the target) or incompatible distractor (associated to a different response than the target), pulvinar lesions lead to an increased interference from incompatible distractors, when the target is contralesional (Danziger, Ward, Owen, & Rafal, 2004). In contrast, performance is not affected by whether the distractor is

contra- or ipsilesional. For the authors, this pattern of results suggests that human pulvinar is involved in response selection instead of attentional selection, because deficit occurs only when distractors are response incompatible. A potential explanation for the lack of coherence in the aforementioned results is that different sub-parts of the pulvinar might serve different functions (Arend, Rafal, & Ward, 2008).

In summary, the extensive reciprocal connections with the parietal and visual cortex and with the superior colliculus, the existence of strong saccadic and attentional modulation, and the effect of inactivation on target detection suggest an important role of at least some parts of the pulvinar (e.g. mediodorsal nucleus) in attentional control.

Basal ganglia constitute another important node in the network. The two main basal ganglia structures involved are the caudate and the substantia nigra pars reticulata (SNr). SNr sends inhibitory (GABAergic) projections to the SC, mainly in the intermediate layer (Hikosaka & Wurtz, 1983a, 1983b). These cells maintain a tonic inhibition on the SC. Just before saccade execution, the majority of SNr cells contralateral to the saccade direction, and projecting to the ipsilateral SC, receives an inhibitory input from the caudate and stop firing (Basso & Wurtz, 2002; Hikosaka, Nakamura, & Nakahara, 2006). Saccade-related caudate cells projecting to the SNr fire just before a saccade and microstimulation of these cells induces inhibition of the SNr (Hikosaka, et al., 2006). They receive input mainly from the FEF, SEF and DLPFC. These neurons fire anticipatively when a high reward is associated to a contralateral saccade, even in the absence of visual stimulation, and even if the actual direction of the next saccade is unknown (Hikosaka, et al., 2006). This reward specific activity increases ipsilateral SC excitability. The behavioral correlate of this effect is a shorter latency of saccades associated to high reward. This reward-induced latency decrease is attenuated by the injection of dopamine D1 antagonist but increased by dopamine D2 antagonist (Nakamura & Hikosaka, 2006), demonstrating the opposite role of these two dopamine receptors in saccadic control.

In addition to reward selectivity, saccadic caudate cells show also directional specificity. When all saccade directions are equally rewarded, caudate cells respond preferentially to cues instructing contralateral saccades (Kawagoe, Takikawa, & Hikosaka, 1998). When the amount of reward differs as a function of saccadic direction, this spatial response becomes strongly modulated by reward. The spatial tuning of the cell can be suppressed or inverted. This combined spatial and reward selectivity could arise from LTP and LTD modulation of spatially tuned cortical input by reward-tuned dopamine neurons (Hikosaka, et al., 2006). These results indicate that basal ganglia are involved in the modulation of orienting behavior by reward. However, the tasks used in these studies are very artificial in the sense that they associate specific amounts of reward to different saccadic target locations. This situation does not exist in ecological context, where orienting is only a very indirect way to find and gather rewards, such as food. The question remains open as to whether basal ganglia could be involved in the modulation of saccadic target selection probability by more abstract motivational factors. Along this line, humans exhibiting basal ganglia lesions can have visual neglect symptoms (Karnath, et al., 2002).

In humans, other brain areas than the ones described so far are also involved in attentional control. Corbetta and colleagues defined a dorsal and a ventral network of areas, on the basis of multiple fMRI results (Corbetta & Shulman, 2002). The dorsal network, composed of bilateral FEF, posterior and ventral IPS, and area MT, is considered by the authors to be responsible for voluntary attentional orienting, because it responds to the cue in a Posner task (Corbetta & Shulman, 2002). The ventral network, composed of a precentral sulcus region, middle frontal gyrus,

anterior insula, TPJ, and superior temporal sulcus, responds to invalidly cued targets, and is hence presumably affected to re-orienting to conspicuous events. In normal subjects, areas inside these networks exhibit more functional connectivity than areas across these networks (B. J. He, Shulman, Snyder, & Corbetta, 2007), confirming that they constitute distinct functional entities. In two fMRI experiments, Corbetta and colleagues showed that in neglect patients, the severity of visual neglect, and the degree of recovery, were correlated with the imbalance between left and right IPSs (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005), and with the loss of functional connectivity between IPSs (B. J. He, Snyder, et al., 2007), even though these structures were structurally intact. In the dorsal network, the severity of neglect symptoms is correlated to the functional connectivity between both IPSs. In contrast, in the ventral network, left orienting deficit is correlated to the degree of disruption of the connectivity between right medial frontal gyrus (MFG) and STG on the one hand, and right MFG and TPJ on the other hand (B. J. He, Snyder, et al., 2007). A recent intraoperative electrical stimulation study in humans showed that the most effective site to induce rightward deviation in a line bisection task is the superior occipito-frontal fasciculus (Thiebaut de Schotten, et al., 2005). This fronto-parietal pathway, located below the inferior parietal lobule, might be responsible for the functional interactions between MFG and TPJ.

I.3.5 CONCLUSION

In summary, neural correlates of salience are found in a multiplicity of brain structures. Given the current state of the literature, the exact function of each of these structures in the computation of salience and in the control of saccades and attention can only be hypothesized. If we follow the arguments of parsimony and phylogeny, superior colliculus is likely to be the core structure involved in the representation of salience. Indeed, in a great diversity of animals, SC has been shown to be involved in orienting behaviors, either with respect to visual or other sensory information (May, 2005). The level of complexity of orienting behaviors is variable and ranges, with respect to visual modality, from the grasp reflex - foveation of an abrupt visual onset -, to the anticipative displacement of the eyes towards a part of the visual field where a critical event is going to happen (M. F. Land & McLeod, 2000). In submammalian vertebrates, the visual grasp reflex is known to rely on the optic tectum (Rafal, 2006). The homolog of this structure in mammals is the superior colliculus. The connectivity of the superior colliculus, receiving inputs directly from the retina and striate cortex, and sending strong outputs to brainstem oculomotor centers, is compatible with this simple reflexive function. So is the suppression of express saccades observed following SC ablation (Schiller & Tehovnik, 2005). However, it is unlikely that more complex computations, like the anticipative eye movements to the location of an upcoming critical event could take place in the superior colliculus. We could assume instead that all the complex cognitive factors that influence the selection of the next saccadic or attentional target, coming from frontal and parietal cortex, converge in the SC. However, SC cannot be considered as a necessary bottleneck where all the information relative to the orienting of eye movements needs to relay, as eye movements can still be made after chronic lesion of the SC (Schiller & Tehovnik, 2005). Following such lesions, the frontopontine route, from FEF to the pontine oculomotor nuclei, normally not functional in physiological conditions (Hanes & Wurtz, 2001), becomes crucial. In contrast, lesions of both the FEF and SC lead to a total inability to perform any visually-guided eye movement (Schiller & Tehovnik, 2005).

The anatomical connections of area 7a with high-level visual areas and with cingular and para-hippocampal cortex, together with the complexity of the response of its cells, suggest a role in the computation of complex salience factors. Given its quasi absence of connection with either the SC or the FEF, its influence on the selection network should relay through LIP. The results of recording and inactivation studies, suggest that the role of LIP in the selection of the saccadic or attentional target is more critical in difficult tasks, for instance in condition of high target-distractor similarity (Wardak, et al., 2002, 2004). Recent results described above, showing the existence of limb specific activity (Oristaglio, et al., 2006), or of responses specific for task-defined feature categories in LIP (D. J. Freedman & Assad, 2006) have led some authors like Jacqueline Gottlieb, to propose a broader function for LIP than the selection of the saccadic targets (J. Gottlieb, 2007). Following her, LIP would be involved in linking relevant sensory information with behavior not only for saccadic or attentional orienting but also for more abstract, rule-based actions.

The importance of FEF in the computation of salience is less clear. Its inactivation, in contrast to LIP (Wardak, et al., 2006), leads to difficulty-independent deficits in visual search tasks. FEF is a relay area, interconnected with most ventral and dorsal visual areas on one hand, and with oculomotor structures (SC and pontine nuclei) on the other hand. These findings, together with the striking effect of FEF microstimulation on attentional allocation, suggest that instead of being involved in the computation of salience, FEF could be needed to implement the attentional shift in the visual system,

being at the origin of the modulation observed in visual areas.

At the level of the network, two cortico-subcortical loops might be of critical importance in orienting behavior. The first loop, connecting FEF to SC, and then to mediodorsal thalamic nucleus and back to FEF, could be involved in the prediction of the visual consequences of saccadic movements (Sommer & Wurtz, 2008). The second loop links LIP to SC, to pulvinar and back to LIP. Even though the function of this latter loop has never been experimentally assessed, it is probably crucial for salience computation. Finally, basal ganglia might influence the state of the network with respect to motivational factors.

Whereas much energy has been devoted to the exploration of the function of the cortical areas involved in saccadic and attentional control, the results discussed in the present work suggest that the function of each of these structures can be understood only when considered as part of a broad network. In this perspective, studies targeting multiple areas in the same time and using either recording, inactivation or stimulation approaches, or a combination of them will probably proliferate in the future. These studies, aiming at addressing the transfer of information between these areas, will certainly provide critical information on the way our brain decides where to move the eyes and which visual information to select.

I.4 Content of the following chapters

This thesis comprises five original experimental studies. The first set of studies (Chapters II.1, II.2 and II.3) concerns the behavioral investigation of the mechanisms involved in covert visual exploration whereas the second set of studies focuses on the computation of factors of salience in the brain.

The starting point of this first set of studies was the observation that visual search models, and particularly the Guided Search Theory, are based only on indirect evidence, and this evidence can be misleading, as detailed above (chapter 1.2.1.1.4). I used a dual task technique allowing to track attentional allocation over time to investigate three different aspects of covert visual search models that are usually assumed to be accurate, despite lack of direct evidence. In the first study, I investigated whether, and to what extent, attention allocation relies on goal-directed and stimulus-driven features during visual search. In the second study, I addressed the question of whether attentional selection is based on a winner-take-all process, as consensually assumed, or whether attention selects multiple relevant visual items at the same time. Finally, in the third study, I addressed, by means of the same technique, the question of the parallel versus serial processing of visual information during covert visual search.

The second set of studies (Chapters II.4 and II.5) investigated the representation of visual salience in the brain. In the fourth study, I used Transcranial Magnetic Stimulation (TMS) to interfere transiently either with the function of FEF or of the Angular Gyrus in humans during the performance of covert visual search tasks. By analyzing how these transient perturbations affected attentional guidance during search, I was able to gain further insights into the role of the targeted areas in the computation of salience. In the fifth study, I recorded single cells in monkey area 7a, during a task in which the animals were free to explore an array of stimuli. I tried to determine whether cell activity in this area depends on the physical feature contrast of the stimuli or, as predicted by the salience map hypothesis, whether it reflects saccadic preference, i.e. the probability that the monkey would select these stimuli as saccadic targets.

II ARTICLES

II.1 Spatial and temporal dynamics of attentional guidance during inefficient visual search ¹

II.1.1 ABSTRACT

Spotting a prey or a predator is crucial in the natural environment and relies on the ability to extract quickly pertinent visual information. The experimental counterpart of this behavior is visual search (VS) where subjects have to identify a target amongst several distractors. In difficult VS tasks, it has been found that the reaction time (RT) is influenced by salience factors, such as the target-distractor similarity, and this finding is usually regarded as evidence for a guidance of attention by preattentive mechanisms. However, the use of RT measurements, a parameter which depends on multiple factors, allows only very indirect inferences about the underlying attentional mechanisms. The purpose of the present study was to determine the influence of salience factors on attentional guidance during VS, by measuring directly attentional allocation. We studied attention allocation by using a dual covert VS task in subjects who had 1) to detect a target amongst different items and 2) to report letters briefly flashed inside those items at different delays. As predicted, we showed that parallel processes guide attention towards the most relevant item by virtue of both goal-directed and stimulus-driven factors, and we demonstrated that this attentional selection is a prerequisite for target detection. In addition, we show that when the target is characterized by two features (conjunction VS), the goal-directed effects of both features are initially combined into a unique salience value, but at a later stage, grouping phenomena interact with the salience computation, and lead to the selection of a whole group of items. These results, in line with Guided Search Theory, show that efficient and rapid preattentive processes guide attention towards the most salient item, allowing to reduce the number of attentional shifts needed to find the target.

¹ Published paper: Zenon A., Ben Hamed S., Duhamel J. R., Olivier E., PLoS ONE. 2008 May 21;3(5):e2219.

II.1.2 INTRODUCTION

A rapid identification of pertinent stimuli is crucial in the natural environment and this ability relies on a selection mechanism known as spatial attention, which permits the allocation of more neural resources to process behaviorally significant elements. Our understanding of attentional mechanisms mainly comes from studies using covert visual search (CVS) tasks – where subjects have to detect a given target amongst distractors, without performing eye movements. Two types of CVS are classically distinguished: 1) efficient CVS in which the reaction time (RT) remains constant irrespective of the number of items, suggesting that visual information is processed in parallel, and 2) inefficient CVS in which RT increases proportionally to the number of items, a relationship known as the “set-size effect” and classically regarded as evidence for a serial processing of visual information. However, in inefficient CVS, the slope of the regression line between RT and the number of CVS items typically varies from 25 to 60 ms/item, leaving very little time to process each item serially (J. M. Wolfe, 1998b). Moreover, estimates of the attentional dwell time range between 200 and 400 ms, values which are incompatible with the attentional shift time estimated from the set-size slope (Duncan, Ward, & Shapiro, 1994; C. M. Moore, Egeth, H., Berglan, L., & Luck, S. J., 1996). This suggests that, besides serial mechanisms, parallel mechanisms most likely contribute to visual information processing in inefficient CVS (Hubner, 2001; J. M. Wolfe, et al., 1989). The Guided Search Theory (GST) proposed that the role of preattentive parallel mechanisms in visual search is to guide attention on the basis of the salience value assigned to each CVS item (Cave & Wolfe, 1990; J. M. Wolfe, et al., 1989; J. M. Wolfe & Horowitz, 2004); this salience value is supposed to be assessed from both goal-directed (or top-down) and stimulus-driven (or bottom-up) factors.

Importantly, the conclusion of most studies on CVS relied on the interpretation of changes in RT and set-size slope in different experimental conditions. However, because variations in RT may be caused by different sensory, sensori-motor and motor factors, it is always difficult to interpret them in terms of attention allocation. Indeed, several recent studies have shown that it is possible to explain the variation of performance as a function of set-size during CVS without requiring serial attentional mechanisms (e.g. see (Eckstein, et al., 2000; Palmer, et al., 2000; Vergheze, 2001)). Therefore, in order to study thoroughly attentional allocation during CVS, it is necessary to demonstrate a spatially specific perceptual improvement during CVS, revealing the attentional selection of one - or multiple – item(s).

Several studies have already used this approach. For example, Maljkovic and Nakayama (Maljkovic & Nakayama, 1994, 1996), were able to demonstrate, in a pop-out visual search task, that attention systematically shifted onto the target. These results were extended to inefficient CVS by Nothdurft (H. C. Nothdurft, 1999), who used the illusory line motion effect to probe attentional allocation on the target. Kim & Cave (Kim & Cave, 1995), went a step further by studying the attentional allocation during CVS, not only on the target, but also on distractors. These authors probed attentional allocation by using both a dot detection task and a letter detection task. This study showed, notably, that in conjunction CVS, where two features (shape and color) define the target, letters located inside items sharing one feature with the target were detected more often, suggesting the existence of a preferential selection of potentially pertinent items. However, in this study, attentional guidance was affected by strong Gestalt grouping mechanisms (Kim & Cave, 2001) making the interpretation of these results in terms of attentional guidance difficult. Moreover, Kim & Cave did not investigate the role of stimulus-driven salience, known to play a central role in GST. Finally, in order to avoid saccades towards the CVS items, Kim &

Cave used very short presentation times, and, consequently, the search process was most likely conducted in visual memory instead of on visually available stimuli (Sperling, 1960).

The purpose of the present study was to extend the Kim & Cave study in order to 1) determine the magnitude, and the timing of the effect of both goal-directed and stimulus-driven salience factors, 2) determine whether GST and/or grouping phenomena are responsible for the preferential selection of items sharing a feature with the target.

To address these issues, we conducted three experiments using a dual CVS task, in which a letter detection task was used to probe attention allocation during the performance of a difficult CVS where the distractors could have different levels of resemblance with the target. We used long presentation times to allow attention to select visually available items and eye fixation was controlled online during the task performance.

In Experiment 1, we determined the influence of goal-directed, stimulus-driven and spatial factors on attentional allocation during an inefficient feature CVS task in which subjects had to detect a vertically oriented item displayed amongst distractors of various, non-vertical orientations. Letters were also displayed inside these items at different intervals with respect to VS items onset (see Fig. II.1.1). The influence of goal-directed salience factors was determined by analyzing the letter detection probability in each CVS item as a function of similarity with the target. We predicted that letters located either inside the target or inside items resembling the target, should be detected more often. To study the influence of stimulus-driven factors, we also analyzed the effect of orientation contrast, i.e. the difference in orientation between neighboring items, and our prediction was that letter detection should be better for greater orientation differences between adjacent items. Finally, we investigated the potential effect of spatial location of the CVS items on attentional allocation by analyzing letter detection as a function of their position in the display, since it has been suggested that letters located in the inferior hemifield should be detected more often (S. He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001).

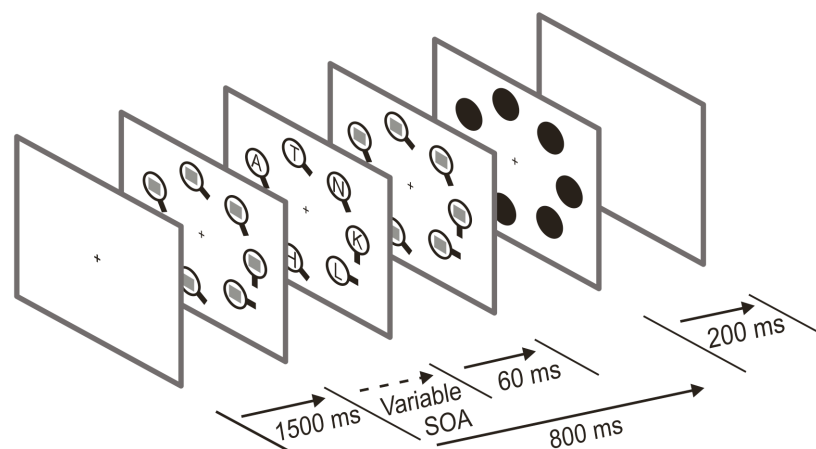


Figure II.1.1

Experimental design of Experiment 1.

A fixation point was displayed for 1500 ms, followed by the presentation of 7 CVS items. The target was the circle with a vertical line. After a variable delay, the mask displayed inside each CVS item was replaced, for 60 ms, by letters. Eight hundred ms after the onset of the CVS item display, CVS items were replaced by black disks flashed for 200 ms.

Whereas Experiment 1 will allow us to investigate attentional allocation during CVS, it cannot help us to determine whether attentional selection of the target is a consequence of, or a prerequisite for, the target detection. To address this issue, in Experiment 2, we used the same dual task as in Experiment 1 but the duration of the CVS item presentation was changed across trials and the letters were always flashed at the end of the trial (see Fig. II.1.2). We predicted that if attention selection is critical to target detection, there should be a tight correlation between letter detection performance in the target and target detection probability. Specifically, we expected to find that target detection should be at chance level in the absence of attentional selection (i.e. 0% letter detection) and that the slope of the target detection function should link minimal and maximal performance levels of both variables.

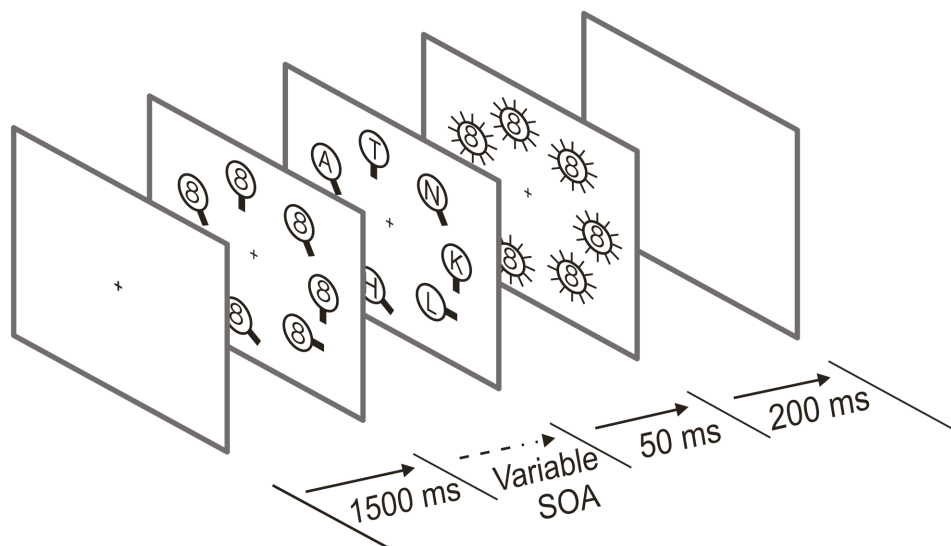


Figure II.1.2

Experimental design of Experiment 2.

Only the case where two targets were displayed simultaneously is illustrated here. Compared to Experiment 1, the CVS items display duration was variable (50%, 75% and 90% correct response in CVS), and letters were always displayed during the last 50 ms of the trial.

Finally, in Experiment 3, we used conjunction search to assess the role of grouping phenomena in the selection of the items sharing a feature with the target. Kim & Cave (Kim & Cave, 1995) showed that, in conjunction search tasks where the target was defined by color and shape, subjects tended to detect more often the letters that were displayed inside items that shared one feature (either color or shape) with the target than in the other distractors. The first interpretation of these results, in line with GST, assumes that each feature (color and shape in this case) is encoded into a separate feature map, where the activity induced by each item depends on its

resemblance with the target with respect to this feature. Then, the two feature maps corresponding to color and shape are added together to lead to a global activation map. The items that do not share any feature with the target will induce the minimum activation in this map, the items sharing one target feature will induce intermediate activation, and the target will generate the maximum activation, resulting from the addition of the maximum activation values in the two feature maps. The second interpretation of the Kim & Cave results is that color and shape, being in this case both very easily discriminable (green versus red and squares versus circles) induce strong gestalt grouping effects (Kim & Cave, 1999a, 2001; A. Treisman, 1982). Therefore, the group of items sharing one target feature would be selected as a whole, and the target would be searched only in this group (Duncan, 1995; Egeth, Virzi, & Garbart, 1984). To distinguish between these two hypotheses, we studied attentional allocation during a conjunction CVS (orientation and color), where three different levels of orientation difference between target and distractors were used (see Fig. II.1.3). Again, a letter detection task was used to probe attention during the CVS task, as in Experiments 1 and 2. In order to induce grouping effects, we used only two easily discriminable color levels. Our predictions were that, if GST is correct, the salience effect of color and orientation should have an independent (or additive) effect on letter detection, whereas if the grouping hypothesis is correct, we should find an interaction between both effects: orientation should affect detection probability of the letters in the items sharing the target color, whereas items with the non-target color should be all excluded from the search process, and hence, their selection probability should not be affected by their orientation (Egeth, et al., 1984).

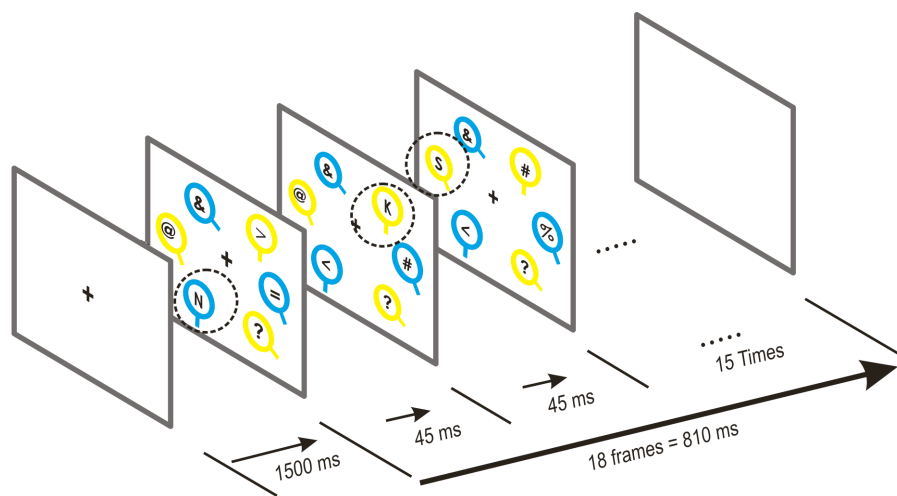


Figure II.1.3

Experimental design of Experiment 3.

The target was the blue circle with a vertical line. Every 45 ms, a different letter was displayed in a different location (surrounded by dotted circles, not shown on actual display). All other items contained irrelevant signs.

Additionally, to have a more precise idea of the timing of these effects, we modified the letter display, allowing us to monitor attentional allocation with a higher temporal resolution. To achieve this increased resolution, instead of displaying a letter inside all VS items at the same time, a single letter was displayed in a given item at a given time, and this letter was moved and changed every 45 ms.

II.1.3 MATERIALS AND METHODS

II.1.3.1 Experiment 1

II.1.3.1.1 Subjects

Twelve healthy subjects (21-25 years old), with normal, or corrected to normal, vision participated in Experiment 1; all subjects were native French speakers. All experimental procedures were approved by the Ethics Committee of the Université catholique de Louvain, and subjects gave their written informed consent.

II.1.3.1.2 Task

In this experiment, we used a probe paradigm (Kim & Cave, 1995) in which subjects had to report the presence, or absence, of a target displayed amongst 7 items arranged in a circle around a central fixation point (see Fig. II.1.1). In addition, subjects had to identify letters flashed for 60 ms inside each CVS item, at different stimulus onset asynchronies (SOAs) with respect to the onset of the CVS item presentation. The rationale behind this paradigm is that the letter detection probability should be higher at positions where attention is located, allowing us to infer a posteriori attentional allocation in both space and time.

Before each experiment, subjects were trained in the CVS task alone, then on the letter identification task alone and finally they practiced the dual task. At the end of the training session, a staircase procedure was used to adjust the contrast of the CVS items against the background in order to make sure that all subjects achieved a performance of 70 % of correct trials in the CVS task. The final contrast obtained was, on average, equal to 70 %. The gray level-luminance function of the screen was obtained with a psychophysical method of gamma correction (Bordier C. & Knoblauch K., personal communication).

At the beginning of each trial, a fixation point was presented at the center of a computer screen situated at a distance of 55 cm, in front of the subjects; the subjects had to fixate this point throughout the task. The eye position was monitored using an electro-oculogram and trials were interrupted, and repeated, whenever subjects broke fixation. After a 1500 ms delay, seven grey circles (1.8 degrees wide) were displayed equidistantly at an eccentricity of 4 deg. These CVS items were filled with a white noise mask and had a small bar attached to them, that could be either vertical (target) or oriented at 30, 60 or 90 degrees from the vertical (distractors). The target was present in 50 % of the trials and at least two distractors of each type were present in each trial. After a variable SOA (50, 300, 500 or 700 ms), the masks displayed inside the circles were replaced by letters (1.1 degree wide) which were flashed for 60 ms and then replaced by a new mask. In a given trial, every letter was different. Eight hundred ms after the onset of CVS item presentation, all items were replaced by black disks displayed for 200 ms.

Subjects were instructed to press, as fast as possible, the « one » key of the numeral pad of a computer keyboard to indicate that the target was present or the « three » key to indicate it was absent; then they had to type on the keyboard, without any time constraint, the letters they identified inside the CVS items. Subjects then triggered the next trial by pressing the space bar. The experiment was divided in 5 blocks of 160 trials each.

II.1.3.1.3 Control task A: letter detection only

In order to determine whether the effects we observed in the main experiment were specific to CVS, and not to the letter detection task, a control experiment was performed under the same experimental conditions as in Experiment 1, except that subjects ($n=10$) were only asked to report as many letters as possible without taking notice of the CVS items.

II.1.3.1.4 Control task B: target detection only

This second control experiment was identical to the main experiment (Experiment 1) except that subjects ($n=7$) only had to report the presence, or absence, of the CVS target, without paying attention to the letters. In this experiment, the number of CVS items was either 4 or 8 in order to allow us to determine the difficulty of the CVS task and to estimate the “set-size effect”.

II.1.3.1.5 Data analysis

A goal-directed salience value, varying from 4 to 1, was assigned to each CVS item depending on its similarity with the target, 4 being attributed to the target and 1 to the most dissimilar distractor. In addition, an orientation contrast index was calculated for each CVS item by computing the sum of the differences between the orientation of the bar attached to the item and its two neighbors. For example, an item with a 30° oriented bar (salience value: 3) surrounded by the target (salience: 4) and by an item with a 90° oriented bar (salience: 1) had an orientation contrast index of 3 ($|3-4| + |3-1|$).

II.1.3.1.6 Statistical analysis

We used ANOVAs on repeated measurements (RM ANOVA) for most statistical analyses. In order to achieve normality, percentages of detection were arcsine-root transformed, a transformation appropriate for data that lie between an upper and lower bound (Zar, 1996). When data distribution of probability differed from normality, a non-parametric ANOVA on ranks test was performed.

II.1.3.2 Experiment 2

Eight subjects (20-29 years old) participated in Experiment 2, which was exactly the same as Experiment 1 except that 1) the duration of the CVS item presentation varied from trials to trials, and 2) we used a different masking stimulus, the digit 8, which has proved to be more efficient as a mask in a letter identification task (see Fig. II.1.2)(Enns, 2004). The duration of the CVS item presentation was determined for each subject at the beginning of the experimental session by means of a staircase procedure adjusted to obtain 50, 75 or 90% of correct responses in the CVS task, while the contrast was kept constant (70%). In this staircase procedure, subjects had to perform the CVS task only, without reporting the letters displayed inside the CVS items. The duration of CVS items presentation was then adjusted to these three values in the main experiment and the three display durations were counterbalanced across trials. In addition, also in contrast to Experiment 1, the letters were always

flashed during the last 50 ms of the CVS item presentation. Then, all stimuli were replaced by a mask: the letters were masked with a figure-eight and the CVS items were masked with circles with 12 bars attached every 30°, from 0° to 330°. One, two or no target could be displayed, these three conditions being equally probable (33% each). In the foregoing analyses, we only considered trials where one or no target was displayed. The response keys used to indicate that the target was present or absent were the same as in Experiment 1. The subjects were not informed that two targets could appear simultaneously in some trials and the response required in these cases was the same as when only one target was detected. As in Experiment 1, subjects had also to type the detected letters, with no temporal constraint and the next trial was triggered by pressing the space bar. In this experiment, eye movements were monitored by using an infrared camera (Thomas Recording).

II.1.3.3 Experiment 3

Eight subjects participated in Experiment 3. The task was, as in Experiments 1 and 2, to detect the presence of the target (50% probability), as quickly as possible, and to report as many letters as possible. Eye position was controlled by means of an infrared eyetracker and trials were interrupted, and repeated, whenever subjects broke fixation. In this task, three blue and three yellow isoluminant circles were displayed on the screen, at fixed eccentricity (4°). The orientation of the bar attached to them was 0°, 20° or 40° from the vertical. The target was defined as the blue circle with a vertically oriented bar. In target present trials, each item of a given color had a different orientation. In target absent trials, two items with the target color had a 20° orientation.

One ASCII sign was displayed inside each VS item but, in only one item, this sign was a letter; in the other VS items, the signs were irrelevant ('&', '%', etc...). At every frame change (i.e. every 45 ms), the relevant letter and two irrelevant signs were changed; the new relevant letter was flashed at another location (see Fig. II.1.3). The duration of the CVS items display was 810 ms, corresponding to 18 frame changes. The letter was displayed in each VS item in a pseudo-randomized order so that, in a given trial, a different relevant sign appeared three times inside each VS item ($n=6$), with a variable delay between each presentation. In the analyses, in order to have a sufficient number of trials in each condition, we grouped adjacent letter onset times by pairs, yielding 9 different letter onset time values (1-45 ms, 90-135 ms, 180-225 ms, ...). An additional control experiment was conducted in which the display was exactly the same, but subjects only had to report the letters.

II.1.4 RESULTS

II.1.4.1 Experiment 1

II.1.4.1.1 General performance

We first found that the CVS task used in the present study was inefficient. The control task B (see Methods) showed that RTs increased as a function of the number of CVS items (2-way ANOVA RM : $F=8.12$, $p=0.029$) and were larger when the target was absent than when present ($F=10.19$, $p=0.019$). The difference between RT in the 8-items CVS task (median $\pm$ interquartile interval (IQI) : 1378 ± 673 ms for target absent and 863 ± 666 ms for target present) and the 4-items CVS task (1172 ± 590 ms for target absent and 805 ± 555 ms for target present) was 97 ± 237 ms (median $\pm$ IQI) for target absent trials and 69 ± 109 ms for target present trials. This corresponds to a

mean increase of 20 ms per item, a value compatible with the magnitude of set-size effects classically reported in the literature for inefficient CVS tasks (J. M. Wolfe, 1998b).

In the main experiment (Experiment 1), we found that the number of detected letters increased with SOA. On average, 0.8, 0.97, 1.18, 1.39 letters were reported for 50, 300, 500 and 700 ms SOAs, respectively. Median RT in the CVS task was 1190 ms (IQR = 282 ms, $n=12$) and longer SOAs for letter display, were associated with longer RTs in the CVS task. This finding can be explained if we assume that the processing of the letters and their storage in memory occurred during the preparation of the motor response of the CVS task, leading to an interference. For the CVS task, when the target was present, we found $75.2 \pm 13.6\%$ of HITS (correct detection of the target) and $24.8 \pm 13.6\%$ of MISSES (failure to detect the target when present); when the target was absent, we observed $81.0 \pm 13.6\%$ of CORRECT REJECTIONS (correct rejection of target presence) and $19.0 \pm 13.6\%$ of FALSE ALARMS (detection of the target while absent).

II.1.4.1.2 Influence of goal-directed salience on attentional allocation

We first investigated the influence of the goal-directed salience factor (similarity with the target) on the probability to detect letters inside CVS items. For all types of responses (HITS, MISSES, CORRECT REJECTIONS and FALSE ALARMS), we found that the target-distractor similarity significantly influenced letter detection probability (main effect: F ranged from 5 to 280, all $p < 0.02$). For HIT responses, the probability to detect a letter was higher when flashed inside the target (post-hoc: all $p < 0.0001$) and, to a lesser extent, inside level 3 distractors, i.e. the most resembling distractors (post-hoc: $p = 0.03$, Fig. II.1.4A). For MISS responses, the letter detection rate was higher in the level 3 distractors than in the target (post-hoc: $p = 0.008$). When the target was absent (CORRECT REJECTION and FALSE ALARM), letters flashed inside the level 3 distractors were more likely to be detected than those flashed inside level 2 and 1 distractors (post-hoc: all $p < 0.0001$, Fig. II.1.4B).

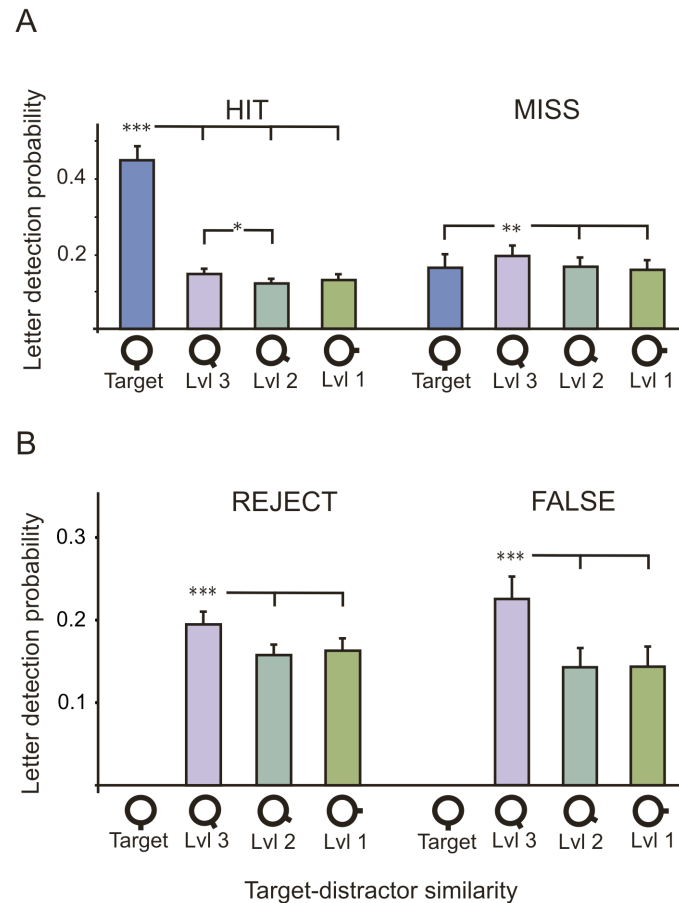


Figure II.1.4

Effect of target-distractor similarity on letter detection performance.

A. Main effect of target-distractor similarity on “target present” trials for HIT (left) and MISS (right) trials. In the HIT trials, letters located inside the target were more likely to be detected than other letters, whereas this effect was reversed in the MISS trials. In both types of trials, letters located in level 3 distractors were more often detected than those located in level 2 and level 1 distractors (*: $p < 0.01$; **: $p < 0.001$; ***: $p < 0.0001$). Y axis: percentage of letter detection. X axis: target-distractor similarity varying from 4 (target) to 1 (most dissimilar distractor). Error bars correspond to standard errors.

B. Main effect of target-distractor similarity on “target absent” trials for REJECT (left) and FALSE ALARM (right) trials. In both types of trials, letters located in level 3 distractors were more likely detected than those located in level 2 and level 1 distractors. Same conventions as in A.

In addition, we investigated the influence of the SOA (delay between the presentation of CVS items and the letter display) on the probability of letter detection. For HIT trials, we found a significant interaction between TARGET-DISTRACTOR SIMILARITY and SOA ($F=49,90$, $p < 0.0001$). This interaction can be explained by the fact that, although the detection rate of letters flashed inside the distractors was not influenced by the SOA, the detection rate of letters flashed inside the target increased with the SOA (post-hoc: all $p < 0.0001$, Fig. II.1.5). It is noteworthy that, even for SOA as short as 50 ms, the detection rate of letters flashed inside the target was already significantly higher than for letters flashed inside distractors.

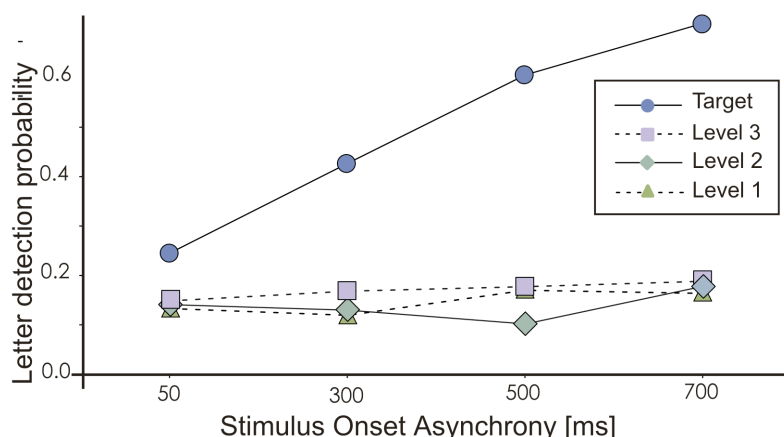


Figure II.1.5

Target-distractor similarity - SOA interaction for HIT trials.

The benefit of letter detection inside the target for HIT trials was already significant for a 50 ms SOA and it increased monotonically with the SOA. The detection probability is represented on the Y-axis, SOAs on the X-axis.

In order to determine whether these effects were actually goal-directed, we conducted a control experiment where subjects only had to detect the letters, without paying attention to the CVS items (control task A, see Methods). In this task, we failed to find an influence of the TARGET-DISTRACTOR SIMILARITY on the letter detection ($F=.03$, $p=.99$).

II.1.4.1.3 Influence of stimulus-driven factors and spatial location on attentional allocation

We then investigated the influence of a stimulus-driven salience factor (the local orientation contrast) on the target and letter detection rates. Orientation contrast was computed for each item by estimating its dissimilarity with its two neighbors (see Methods). As shown in figure II.1.6, the letter detection probability increased proportionally with the local orientation contrast (ANOVA on Ranks, $\chi^2=52.81$, $p<0.001$; post-hoc: all pairwise multiple comparisons significant except contrast 6 vs 5). However, it may be argued that this effect was due to the higher detection rate of letters displayed inside the target because, on average, the target had a higher orientation contrast value than the distractors. In order to rule out this hypothesis, we performed the same analysis after removing all letters detected inside the target and we found identical results i.e. an increased detection probability of letters as a function of the local orientation contrast (ANOVA on ranks, $\chi^2=39.07$, $p<0.001$, Fig. II.1.6). In addition to the effect on letter detection, we found that the local orientation contrast also influenced the target detection probability (RM ANOVA $F=5.26$, $p=0.001$). However, this effect was essentially due to a lower detection rate of the target when surrounded by two distractors very similar to the target (post-hoc: $p<0.001$).

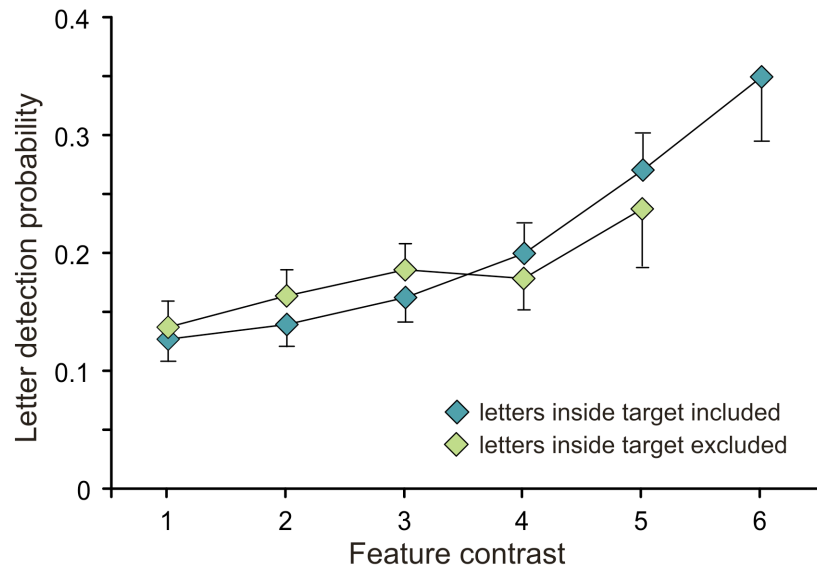


Figure II.1.6

Effect of local orientation contrast on letter detection probability.

The letter detection rate increased proportionally with the orientation contrast. Contrast level is represented on the X-axis and percentage of detection on the Y-axis. Error bars correspond to standard errors.

As far as the effect of spatial location on attentional allocation was concerned, we found a significant effect of the item position in the display on both the target ($F=6.32$, $p<0.0001$) and letter detection ($F=18.3$, $p<0.0001$) rates; namely a higher detection rate was observed for CVS items and letters located near the horizontal meridian (Fig. II.1.7).

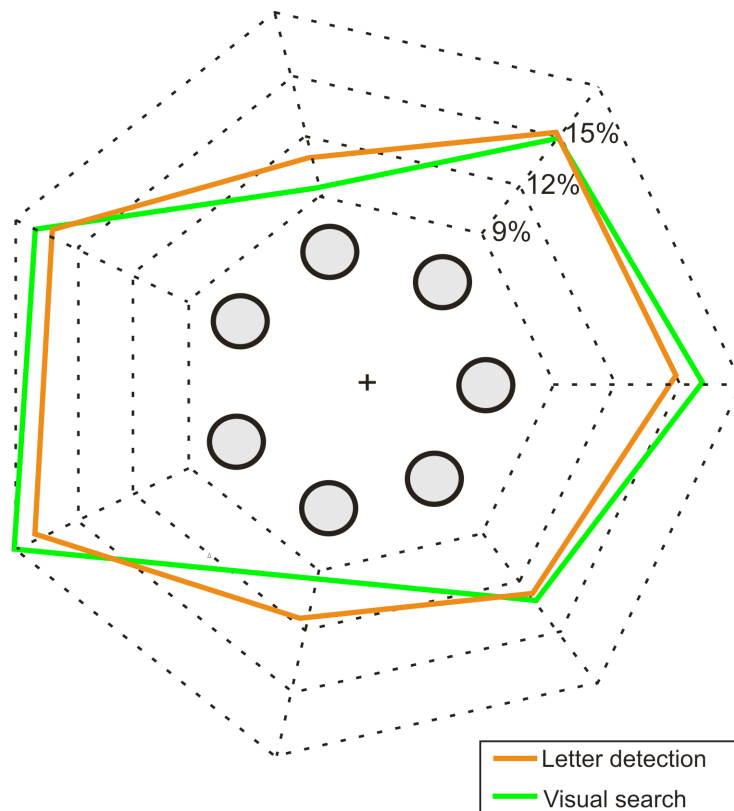


Figure II.1.7

Effect of position.

Radial plot showing the proportion of objects detected in each position on the display for visual search (green) and letter detection (orange) in the dual task. CVS items and letters located on the horizontal meridian were detected more often. Item positions on the graph correspond to the positions in the display as seen by subjects.

In order to determine whether the effect of orientation contrast and spatial location on letter detection probability was specific to CVS, we analyzed letter detection performance in the control task A, where subjects were only asked to report letters without performing the CVS task. We confirmed a significant effect of position ($F=2.36$, $p=.045$) with the same preference for horizontal positions as in Experiment 1, but we failed to find an effect of the orientation contrast ($F=1.04$, $p=.40$). This finding indicates that the CVS items have to be processed in order to induce a local orientation contrast effect, suggesting that the stimulus-driven effect of the orientation contrast is influenced by the task at hand. In contrast, the significant effect of position for the letter detection performed alone was expected since, if attentional allocation probability depends on spatial location, it will affect stimulus detection irrespective of the nature of the stimulus to be detected.

II.1.4.2 Experiment 2

The results of Experiment 2 confirmed those of Experiment 1, i.e. we replicated the effect of target-distractor similarity ($p<0.0001$, $F=17.15$), of position ($p=0.036$,

$F=2.51$) and of orientation contrast ($p=0.012$, $F=4.63$) on letter detection probability.

Relation between attention allocation on the target and target detection

Experiment 2 was designed to allow us to determine the relationship between attention allocation and target detection since in this task, the letter detection can only occur at the very end of the search process. The relationship between the display duration and subject performance is illustrated in Figure II.1.8. For the CVS task, the better performance associated with longer display presentation was mainly due to a decrease in FALSE ALARM rate (RM ANOVA with FALSE ALARM rate in function of CVS items display duration condition: $p<0.0001$, $F=52.74$) rather than to an increase in HIT responses (RM ANOVA: $p=0.35$, $F=1.13$). This indicates that, when the display was presented for a short period of time, the subjects favored the “target-present” responses and that the opposite was true for longer display durations. This bias was estimated by the C value, based on signal detection theory. We found a significant decrease of the C value as the duration of display presentation decreased (C VALUE x DISPLAY DURATION, RM ANOVA: $p<0.0001$, $F=23.81$). Because of this bias, in the following analysis, we used the percentage of correct trials for both “target-present” and “target-absent” trials as a measure of the performance; this measure is almost proportional to d' ($R=0.97$) in the range of values used, and is more appropriate for the present analysis, given the fact that we compute its correlation to another performance value measured in percentage, thus having a more comparable distribution.

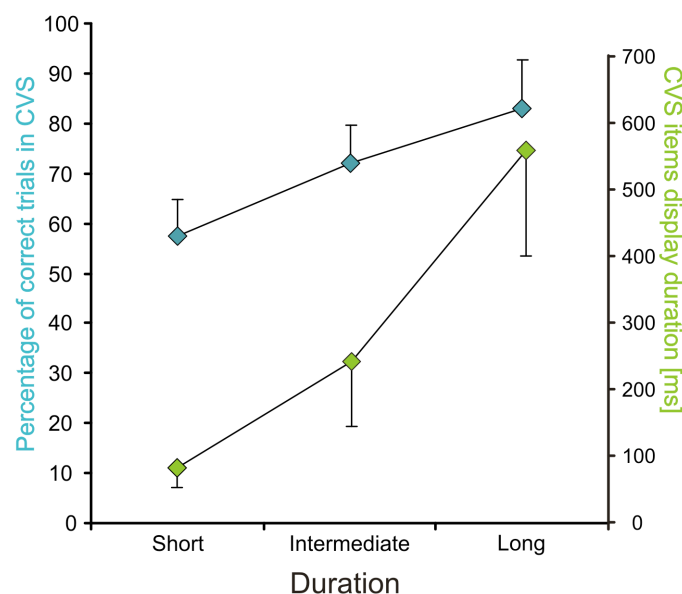


Figure II.1.8

CVS performance as a function of display duration.

Percentage of correct trials in CVS (cyan) and mean CVS items display duration (green) for each of the three duration conditions.

We found a strong correlation between the percentage of correct trials in the CVS (CORR_CVS) and the percentage of detected letters flashed inside the target (TARG_LET) ($R=0.82$, $p<0.0001$; see Figure II.1.9). This suggests that, whatever the display duration, the CVS performance was always proportional to the percentage of letter detected inside the target. Moreover, the regression coefficients (0.49 for the intercept and 0.51 for the slope) indicate that when the CVS task is performed at random (50% of correct trials) the letter detection rate in the target is 0%, and that a

100% performance in the CVS task is accompanied by a 100% of letter detection in the target, confirming our hypothesis. However, we must be cautious while interpreting this correlation because the difference in performance between subjects and the display duration can be considered as hidden variables. To remove the effect of these variables from the regression between CORR_CVS and TARG_LET, we computed a multiple regression with CORR_CVS as dependent variable and TARG_LET and CVS display duration as independent variables with subjects being included as dummy variables. The partial correlation between CORR_CVS and TARG_LET remained highly significant ($R=0.67$, $p=0.0003$). The slope of the regression was still 0.58 ± 0.14 ($b \pm SE$) indicating that a 1% increase in letter detection performance corresponds to a .5% increase in CVS performance, like in the previous analysis. This shows that even when considering only the variations of TARG_LET and CORR_CVS which are not predicted by the display duration or the difference in performance between subjects, a comparable correlation is observed. These results suggest that the detection of the target never occurred if attention was not allocated on the target and that, when attention was allocated on the target, as shown by the letter detection, the target was always detected.

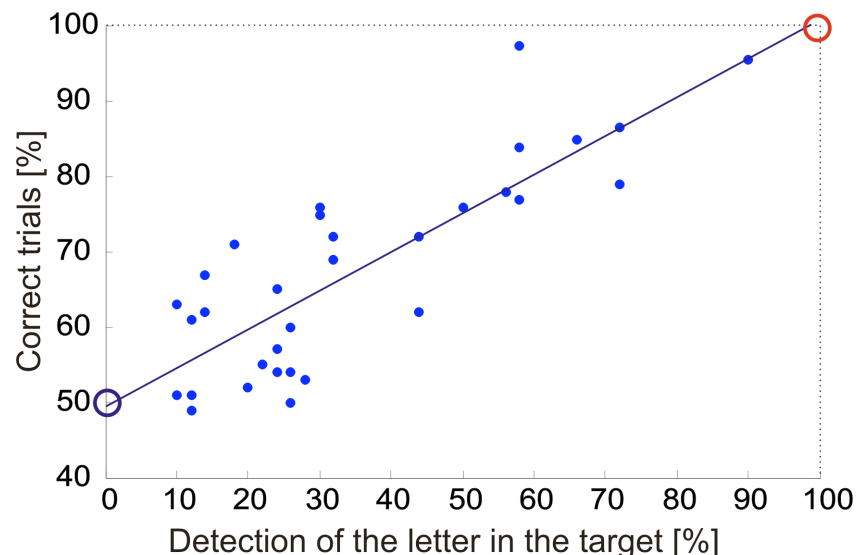


Figure II.1.9

Correlation between the percentage of correct trials and percentage of detection of the letter in the target.

Each dot represents data from one subject for one display duration. Note that the left extremity of the regression line (blue circle) corresponds to 50% correct responses in the CVS task and 0% of letter detection in the target and that the right extremity (red circle) corresponds to 100% correct response in the CVS task and 100% of letter detection in the target.

To corroborate this conclusion, we analyzed trials where the target was not detected (MISS trials). If the above conclusion is correct, in MISS trials, letters should not be detected more often inside the target than inside the distractors. Indeed, we found that in MISS trials, the percentage of detection of letters flashed inside the target was not different from the percentage of detection in distractors (one-way RM ANOVA, $p=0.59$, $F=0.65$; $20.10 \pm 11.01\%$ (mean $\pm$ SD), and $19.83 \pm 9.19\%$, $17.06 \pm 4.94\%$ and $19.35 \pm 7.37\%$ for level 3, 2 and 1 distractors, respectively). Since in Experiment 2, no processing of CVS items could occur after the letter detection, because the letters were always flashed during the last 50 ms of the CVS items display, this finding

indicates that when the target was present but undetected, attention was not located on the target.

II.1.4.3 Experiment 3

On average, subjects reported 1.72 ± 0.64 letters (mean $\pm$ SD, $n=8$) per trial. The median RT was 1332 ms with an IQI of 908 ms for “target present” trials and 1344 ms (IQI : 865 ms) for “target absent” trials. We computed a three-way RM ANOVA with COLOR and ORIENTATION of the circles, and letter onset TIME as independent variables, and letter detection probability as dependent variable (see Fig. II.1.10 A). We found that the letter detection rate increased with the onset TIME ($F = 2.88$, $p = 0.009$), except for the last onset time (765-810 ms), which was associated with a decreased letter detection rate. This last effect can probably be explained by the influence of the masks displayed at the end of each trial. The main effects of ORIENTATION ($F = 44.88$, $p < 0.0001$) and COLOR ($F = 24.58$, $p = 0.002$) were significant, confirming the results from Kim & Cave, and replicating the goal-directed salience effect we found in the feature visual search task (Experiment 1): letters displayed in items with the same color, or the same orientation as the target, were better detected.

The TIME – ORIENTATION and TIME – COLOR interactions were not significant ($p > 0.1$). The ORIENTATION – COLOR interaction ($F = 7.27$, $p = 0.007$) was significant, showing that the orientation affected the letter detection probability for items sharing the target color only, suggesting the existence of grouping phenomena. However, the significant triple interaction ($F = 1.82$, $p = 0.037$, see Fig. II.1.10 A.) indicated that this effect depended on time. While the effect of orientation for items sharing the target color clearly increased with time, the preference for the item sharing the target orientation, but with the non-target color, was only present for early letter onset times and disappeared for onset times beyond 360 ms. These very interesting effects unfortunately did not reach significance in Post-Hoc tests. As a consequence, in order to clarify the effect of early versus late delays, we computed a two-way RM ANOVA with orientation and color as independent variables for letters appearing either early (1-315 ms) or late (360 ms to 675 ms). Longer letter onset times (720-765 ms) were discarded from this analysis, because of the strong decrease in global letter detection performance at these delays. For EARLY delays, the orientation-color interaction was not significant at all ($F = .69$, $p = 0.52$, see Fig. II.1.10 B.), whereas it was significant for LATE delays ($F = 26.72$, $p < 0.0001$, see Fig. II.1.10 C.). This suggests that, at the beginning of the search, both color and orientation affect attentional guidance, and their effect are independent or combined additively, as predicted by GST. However, for longer delays, all items with the non-target color are excluded from the search process, irrespectively of their orientation, whereas the selection probability of the items that share the target color continue to depend strongly on their orientation. This finding can be regarded as evidence for the existence of grouping phenomena. We could not run the same analysis for target absent trials because the design was not balanced. Indeed, the color-orientation combination corresponding to the target never occurred.

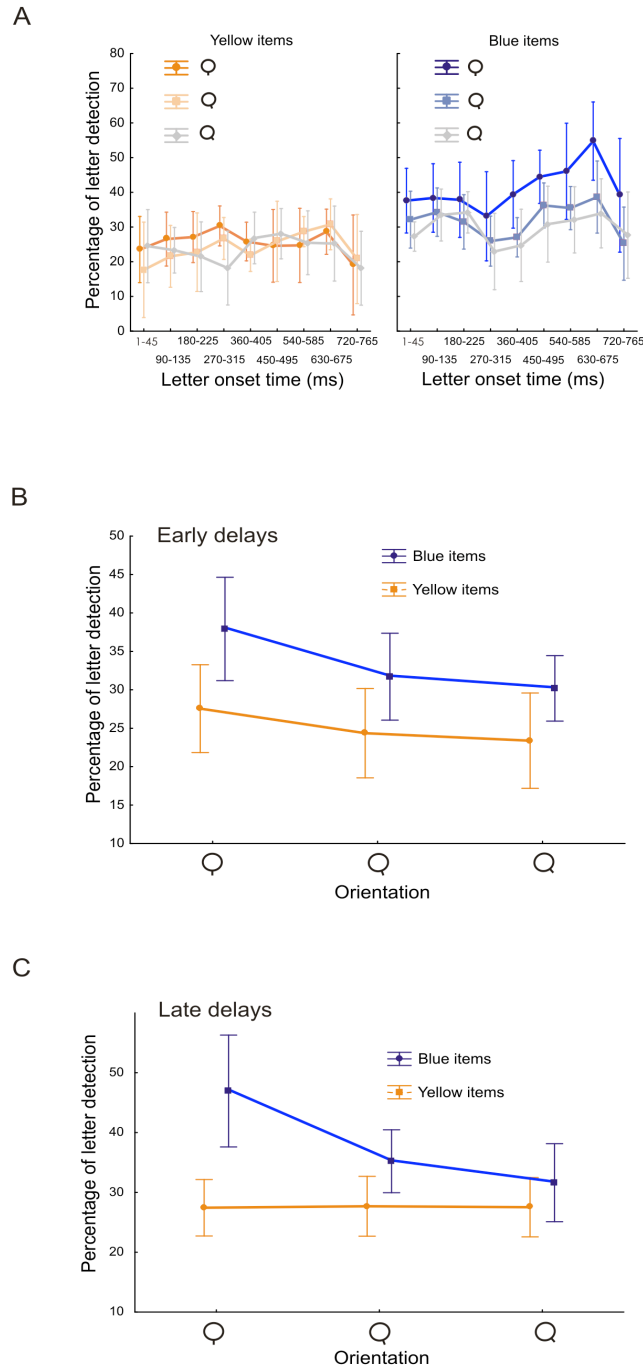


Figure II.1.10

Effect of color and orientation of the CVS items on letter detection performance.

A. Triple interaction ORIENTATION – COLOR – LETTER ONSET TIME with letter detection performance as dependent variable. The Y-axis represents letter detection probability and the X-axis, letter-onset times with 90 ms intervals. The left and right graphs are for yellow (non target color) and blue (target color) items respectively. Color code is for orientation. The more saturated color corresponds to vertical (target orientation), the gray color corresponds to the most dissimilar distractor orientation, and the intermediate color is for the most similar distractor orientation.

B. ORIENTATION – COLOR interaction for early delays. The Y-axis represents letter detection probability, the X-axis the orientation of the items and the color code identifies the color of the item.

II.1.5 DISCUSSION

In the present study, we demonstrate that, during a CVS task, very fast parallel processes guide attention towards the item with the highest saliency, as estimated from goal-directed (target-distractor similarity) and stimulus-driven (orientation contrast) factors, but also from spatial location. We also show that this guidance of attention towards the target is a prerequisite for target detection. Finally, we demonstrate a critical role of grouping phenomena in the later stage of conjunction search processes.

II.1.5.1.1 Influence of goal-directed salience on attentional allocation

The finding that the letter detection probability increased as a function of target-distractor similarity indicates that goal-directed salience factors play a crucial role in attention guidance during inefficient CVS. Indeed, the fact that letters displayed inside the target and in the most resembling distractors were more likely to be detected suggests that a given goal-directed salience value, proportional to target-distractor similarity, was assigned to each CVS item. It is noteworthy that, whereas this goal-directed salience factor was feature-based (dependent on verticality), the effect we measured only relies on spatial attention, namely, the letter was detected because of its inclusion in the spotlight directed on the target location. Our results are in agreement with the existence of a guidance mechanism of spatial attention by features but cannot be interpreted in terms of location-independent global feature-based selection. In addition, we showed that this attention guidance acts very rapidly, since letters in the target were already selected preferentially in the 50 ms SOA condition.

II.1.5.1.2 Role of stimulus-driven salience in attentional allocation

The present study also demonstrates the critical influence of a stimulus-driven salience factor, the local orientation contrast, in the letter detection task. The local orientation contrast was defined as the orientation difference between a given CVS item and its two neighbors and we found that the greater this orientation difference, the higher the letter detection rate. This finding contrasts with previous studies showing that distractors with a high stimulus-driven salience have no effect on CVS performance (Lamy, et al., 2003; Olivers & Humphreys, 2003), a result regarded as evidence for an influence of top-down factors preventing the capture of attention by distractors. However, this discrepancy may be explained if we assume that the stimulus-driven salience factors used in those studies were irrelevant, whereas in the present task, the orientation is a target-defining feature that subjects need to process. This hypothesis about the necessity of relevance, with respect to the task at hand, of the feature defining stimulus-driven salience, is supported by the finding that when subjects were asked to report letters without performing the CVS task (see control task A), this feature-contrast effect was no longer observed.

II.1.5.1.3 Effect of spatial location on attentional allocation

The role of spatial location on attentional allocation in inefficient CVS was also evidenced in the present study. We found a higher detection rate for both the target

and letters when located along the horizontal meridian. Since the stimulus eccentricity was 4°, it could be argued that this preference for stimuli located along the horizontal meridian was due to a higher visual acuity along the horizontal axis and not by an attentional effect (Millidot, 1974; Rovamo, Virsu, Laurinen, & Hyvarinen, 1982). However, current knowledge on visual acuity anisotropies does not support this hypothesis. Indeed, for example, Beirne et al. (Beirne, Zlatkova, & Anderson, 2005), only found very small differences between visual acuity along the horizontal and vertical meridians for an eccentricity of 10° and this difference is probably even smaller at an eccentricity of 4°. Therefore, it is unlikely that the acuity variation could explain the large benefit in detection performance we found for letters located near the horizontal meridian. Finally, whereas Carrasco et al. (Carrasco & McElree, 2001), using a cueing paradigm, failed to find evidence that cued attention can affect the shape of the performance fields, suggesting instead an influence of visual constraints on the performance field, another study (Mackeben, 1999) has reported a performance anisotropy comparable to the one found in the present study, supporting an attentional origin for this effect. Altogether, those results suggest that the influence of spatial location that we observed in the present study is most likely due to a higher probability of allocating attention along the horizontal meridian. This bias could either be related to the probabilistic structure of the natural environment and/or correspond to a consequence of our reading and writing expertise. Finally, it is noteworthy that, in contrast to previous studies showing a better attentional resolution in the lower than in the upper visual hemifield (S. He, et al., 1996; Intriligator & Cavanagh, 2001), we failed to find such a vertical asymmetry. However, a vertical asymmetry has been exclusively observed in crowding and tracking paradigms, suggesting that it may not be an invariant feature of attention which can be generalized to all CVS tasks.

Although the influence of both spatial location and orientation contrast on CVS performance is unquestionable in the present study, the behavioral benefit of these factors remains puzzling. Indeed, whereas goal-directed salience factors are directly related to the cognitive context of the task at hand, local orientation contrast and spatial location are ineffective to help locating the target. In Guided Search Theory, Wolfe and colleagues (J. M. Wolfe, et al., 1989) suggested that stimulus-driven factors are automatically included into the activation map, and hence, influence attention guidance irrespective of the task at hand. The behavioral significance of these salience factors could be revealed in more ecological situations where it may be pertinent to pay attention to high-contrast objects and to objects located along the horizontal meridian. The role of these factors in the construction of the salience map could thus be deeply rooted into the probabilistic structure of the visual world.

II.1.5.1.4 Relationship between attentional selection and target detection

Regarding the question as to whether target selection follows or precedes target detection, we showed in Experiment 2, that the correlation between target detection rate and letter detection rate in the target was perfectly linear. Moreover, the regression showed that minimal (chance level) and maximal (100%) performance in target detection corresponded to 0% and 100% performance in letter detection rate in the target. This suggests that attentional selection is a prerequisite for target detection. Indeed, if target selection followed target detection, and that a better detection of the letter in the target was a consequence of a post-detection shift of attention on the target, we should have found instances, for short display duration, where the target was detected but the display ended before the attentional shift could

occur. In this case, the subjects would have failed to detect the letter flashed inside the target and the regression line represented in Figure II.1.9 should have been shifted upward. In addition, the finding that the goal-directed salience exerted a strong effect on attention allocation in trials where the target was missed and, in Experiment 1, when no target was present, is also in contradiction with the hypothesis that attention selection only follows target detection.

II.1.5.1.5 Grouping phenomena

In Experiment 3, we found that the goal-directed effects of orientation and color are initially combined in a global activation map but that later on, during the CVS processing, the interaction becomes more complex: non-target color items are excluded from the search process, irrespectively of their orientation. We interpret these results as supporting the existence of a two-stage process: first, salience is initially computed from the addition of feature maps, as predicted by Guided Search Theory, and then grouping effects are involved at a later stage, after a 360 ms delay in our Experiment.

This long delay could appear surprising, given the fact that perceptual grouping has been reported for very short display durations (Razpurker-Apfeld & Kimchi, 2007). However, it has been shown that different mechanisms of perceptual grouping occur at different stages of visual processing: while early grouping depends on retinal color similarity, surface color similarity would be involved for grouping at long durations (Schulz & Sanocki, 2003). It is likely that this latter mechanism could be responsible for the grouping effect we observed in our task. Several previous studies argued for a central role of grouping processes in conjunction CVS (Duncan, 1995; Egeth, et al., 1984; Kim & Cave, 1999a, 2001; A. Treisman, 1982). In the present study, we showed for the first time that such grouping phenomena are involved at a late stage in the visual search process.

II.1.5.1.6 Conclusions

The present results are consistent with the existence of a neuronal salience map (L. Itti & Koch, 2001) where different hills of activity, one for each stimulus position, are weighted by both goal-directed (Navalpakkam & Itti, 2005) and stimulus-driven salience factors, and by spatial location. This salience map is used subsequently to guide attention. The existence of parallel mechanisms of attentional guidance in CVS could explain the apparent discrepancy between the slope values of the regression line between RT and item number ("set-size effect"), and the minimum time required to shift attention (J. M. Wolfe, 2003). Indeed, this preattentive salience computation could make CVS more efficient by reducing the number of attentional shifts needed to find the target, leading therefore to a shorter processing time for each additional item. Other phenomena, like perceptual grouping, are also involved later, to increase further the efficiency of the search process, by selecting a whole group of pertinent items at once.

Additionally, the present results show that target detection always follows attentional selection. Consequently, this suggests that target detection never occurs in the absence of attentional selection. An interesting study has already addressed this question in dual tasks involving a central and a peripheral concurrent discrimination tasks (F. F. Li, et al., 2002). Performance in the peripheral discrimination task was compared when performed together with the central discrimination task and when performed alone. In the dual task condition, attention was supposed to be focused on the central discrimination task, whereas in the single task condition, attention was

able to select the peripheral target. This study showed that the detection performance in the peripheral task when attention was focused on the central task depended on the nature of the stimuli used: some discrimination tasks, even very complex, were left almost unaltered by the retrieval of attention, while other tasks, seemingly simple, were much impaired in the absence of attention. Along the same line, Joseph et al. (Joseph, et al., 1997) asked their subjects to perform a pop-out task and were able to demonstrate that a concurrent attention-demanding task (rapid serial visual presentation task) strongly altered performance in the CVS task, suggesting that even pop-out CVS tasks depend on the availability of attention. However, Van Rullen et al. (VanRullen, et al., 2004) showed that targets that do not trigger pop-out could be discriminated from distractors with attention occupied elsewhere and that, conversely, certain pop out CVS tasks need undivided attention to be performed. Altogether, these different studies suggest that the dichotomy between attention-demanding and not attention-demanding CVS tasks might differ from the classic efficient (pop-out) versus inefficient CVS tasks and this question would require further experiments.

II.1.6 ACKNOWLEDGMENTS

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II.2 Attentional guidance relies on a winner-take-all mechanism.²

II.2.1 ABSTRACT

The finding that attention can encompass several non-contiguous items at once challenges the current models of visual search based on a winner-take-all mechanism assuming the selection of a single object. It has been proposed instead that attentional guidance involves mechanisms selecting all relevant items simultaneously. In order to test this hypothesis, we studied attentional allocation during various visual search tasks. We confirmed that attention can indeed select several items concurrently but on the basis of their spatial relation, not relevance. This finding corroborates the view that during visual search, attentional guidance is based on a winner-take-all mechanism.

Keywords: attention; psychophysics; visual search

List of abbreviations: GST Guided Search Theory; WTA, Winner-take-all; DISTRIBUTED, Distributed selection mechanism; ITS item-target similarity; SOA, stimulus onset asynchrony; GOF, Goodness of Fit ratio; IQI, interquartile interval; FEF, Frontal Eye Field; SC, Superior Colliculus

² Published paper: Zenon A., Ben Hamed S., Duhamel J. R., Olivier E., Vision Res. 2009 Mar 18. [Epub ahead of print]

II.2.2 INTRODUCTION

In ecological conditions, the exploration of a visual scene is performed by displacing sequentially the gaze to different locations, so that relevant items can be processed by the visual system. Several factors may influence the selection of the next object to look at, namely goal-directed factors, depending on the task at hand, and stimulus-driven factors, related to the object conspicuity (J. M. Wolfe & Horowitz, 2004). Theoretical models (J. H. Fecteau & Munoz, 2006; L. Itti & Koch, 2001; Koch & Ullman, 1985; J. M. Wolfe, et al., 1989) have suggested that, during visual exploration, both goal-directed and stimulus-driven factors are integrated into a single map, used to guide eye movements; this topographical map is known either as salience (L. Itti & Koch, 2001), priority (J. H. Fecteau & Munoz, 2006) or activation map (J. M. Wolfe, et al., 1989). Because in most conditions, only one spatial location can be selected for the next saccade (see however (Liversedge, White, Findlay, & Rayner, 2006) for an exception), these models are based on a winner-take-all (WTA) competition mechanism (Cave, 1999; L. Itti, Koch C., Niebur E., 1998; Koch & Ullman, 1985; J. M. Wolfe, et al., 1989), leading to the selection of the item located at the peak activation on this map, potentially representing the most relevant item.

Besides eye movements, the exploration of a visual scene also relies on another important selection mechanism, called spatial attention, which permits to concentrate more resources to process selected items (Posner, et al., 1980). So-called covert attentional shifts are performed without eye displacements and have been shown to increase the effective contrast of the selected stimuli (Carrasco, 2006). The same models as those used to describe saccade target selection processes, relying on WTA mechanisms, have been proposed for covert attentional target selection. However, whereas WTA models assume the selection of only one item, several experimental studies have shown that attention, in contrast to eye movements, is able to select simultaneously several non-contiguous objects (Awh & Pashler, 2000; Bichot, Cave, & Pashler, 1999; Gobell, Tseng, & Sperling, 2004; Scharlau, 2004; Sears & Pylyshyn, 2000). These results are in apparent contradiction with the WTA hypothesis and although various solutions have been proposed to resolve this controversy (Cave, 1999), whether attentional allocation actually relies on an WTA mechanism similar to that underlying saccadic selection remains unknown. Indeed, although WTA mechanisms are widely used in visual search models (L. Itti & Koch, 2000; Koch & Ullman, 1985; A. M. Treisman & Gelade, 1980; J. M. Wolfe, et al., 1989), to our knowledge, their existence for attentional selection has never been established experimentally.

It is important to note that, in the present study, we refer to WTA as a mechanism for attentional selection as opposed to stimulus detection (L. Itti & Koch, 2000). Indeed, the contribution of WTA mechanisms to stimulus detection has already been investigated in many theoretical and experimental studies; in these studies, the stimuli are processed by sets of noisy visual filters and a WTA mechanism, sometimes referred to as max-of-output rule, is used to read the activity inside these different filters to decide whether the target is present or not (Baldassi & Verghese, 2002; Eckstein, et al., 2000; Lee, Itti, Koch, & Braun, 1999; Verghese, 2001). Obviously, attention and decision processes interact with each other in such tasks, attention being more likely allocated on the item identified as the target (H. C. Nothdurft, 2002; Zenon, Ben Hamed, Duhamel, & Olivier, 2008), and the target detection performance being enhanced by attentional allocation (Posner, et al., 1980). However, it is sensible to assume that the mechanisms involved in the target selection for attentional shifts and those involved in decision making are distinct, and should be addressed separately. Evidence for the involvement of a WTA mechanism in the decision process related to the target presence does not allow us to infer the

existence of such a mechanism for attentional guidance.

As an alternative to WTA models for attention allocation, DISTRIBUTED models have suggested that multiple items can be selected simultaneously, and that the efficiency of this selection is proportional to the activity generated by each item on the salience map (distributed selection mechanism). For example, Hamker proposed a model of attentional allocation control that assumes a continuous feedback from higher to lower level visual areas (Hamker, 2003, 2005); in this model, attentional feedback influences the processing of visual stimuli gradually with a strength proportional to the relevance of each item (Hamker, 2004a). Based on the signal enhancement theory, Carrasco et al. (2000) proposed a model in which the signal induced by every object on the visual maps is enhanced proportionally to its relevance (Carrasco, Penpeci-Talgar, & Eckstein, 2000). As a result of the gradual attentional effect, the signal-to-noise ratio, and hence, the discriminability of each visual item is modulated by its relevance with respect to the task at hand. It is noteworthy that this model does not integrate the stimulus-driven factors. Similarly, in the present study, we will only address the ability of attention to select multiple items on the basis of their relevance to the task, i.e. a goal-directed factor of guidance, without considering the influence of stimulus-driven factors.

In order to distinguish between WTA and DISTRIBUTED models, we need to determine how attention is allocated when multiple items with different levels of relevance are displayed. Indeed, whereas WTA models assume that only the most relevant item will be selected, DISTRIBUTED models predict that the processing of each item will be enhanced proportionally to its relevance. In order to differentiate between WTA and DISTRIBUTED models experimentally, we investigated the distribution of attention during a covert visual search task, i.e. a task that consisted in detecting a target amongst distractors, and in which no eye movement was allowed. To probe attention allocation during the performance of the task, we used a concurrent letter detection task (Kim & Cave, 1995; Shih & Sperling, 2002), in which the probability of attentional selection of a given search item has been shown to depend on the item-target similarity (ITS), i.e. an estimate of relevance (Zenon, et al., 2008). The use of this dual task allows us to measure attentional allocation independently of the target detection. The goal of the present study was to determine whether ITS influences the detection of multiple items at the same time, as predicted by the DISTRIBUTED models, or of a single one, as predicted by the WTA hypothesis. Results presented here are from two experiments which have already been published (Zenon, et al., 2008), but these data have been entirely re-analyzed to address the distinct issue of the attentional distribution.

II.2.3 EXPERIMENT 1

In Experiment 1, we used a search task in which subjects had to detect a vertically oriented item displayed amongst distractors of various other orientations. In addition, letters were displayed inside those items at different intervals with respect to search item presentation, and subjects had to report as many letters as possible (see Figure). The rationale behind this task is that the detected letter(s) can be used to infer attention allocation (Kim & Cave, 1995; Shih & Sperling, 2002; Zenon, et al., 2008) and trials in which subjects detect more than one letter should allow us to investigate attentional distribution and to identify the factors influencing multiple detections. Therefore, only trials in which subjects detected several letters have been incorporated in the following analyses. WTA models allow us to formulate two hypotheses: 1) the “single focus WTA” hypothesis (WTA1) predicts that attention can select only one location at a time, with a probability proportional to its relevance, or ITS; 2) the “extended spotlight WTA” hypothesis (WTA2) states that attention is

centered on the item with the highest ITS but extending onto neighboring items, because of the spatial properties of the attention spotlight in terms of size and shape (Cave & Bichot, 1999). In contrast, the DISTRIBUTED models predict that several items located at remote and independent locations will be selected concomitantly; that selection should depend on their respective ITS and not on their spatial relationship.

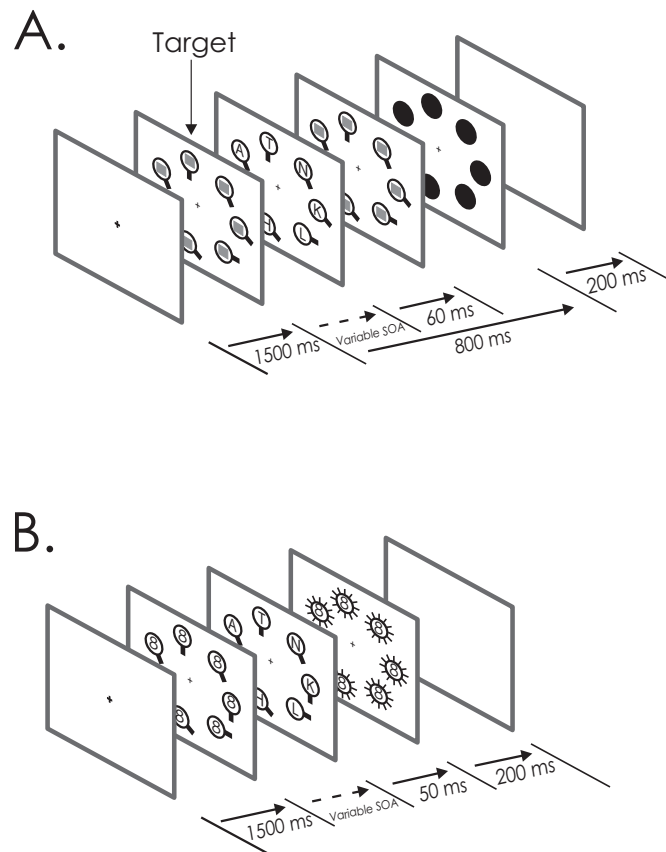


Figure II.2.1.

A. Experimental design of Experiment 1. A central fixation point was displayed for 1500 ms, followed by the presentation of 7 search items containing a mask. The target was the circle with a vertical line. After a variable delay, the mask displayed inside each search item was replaced, for 60 ms, by letters. Eight hundred ms after the onset of the search item display, search items were replaced by black disks displayed for 200 ms.

B. Experimental design of Experiment 2. Only the case where two targets were displayed simultaneously is illustrated here. Compared to Experiment 1, the search items display duration was variable (50%, 75% and 90% correct response in the visual search task), and letters were always flashed during the last 50 ms of the search display presentation.

II.2.3.1 Methods

II.2.3.1.1 Subjects

Twelve healthy subjects (21-25 years old), with normal, or corrected to normal, vision participated in this experiment; all subjects were native French speakers. All

experimental procedures were approved by the Ethics Committee of the Université catholique de Louvain, and all subjects gave their written informed consent.

II.2.3.1.2 Task

In Experiment #1, we used a probe paradigm (Kim & Cave, 1995) in which subjects had to report the presence, or the absence, of a target displayed amongst 7 items arranged in a circle around a central fixation point (see Figure A.). In addition, subjects had to identify letters flashed for 60 ms inside each search item, at different stimulus onset asynchronies (SOAs) with respect to the search item presentation. The rationale behind this paradigm is that the letter detection probability should be higher at the spatial locations where attention is allocated, allowing us to infer, *a posteriori*, attentional allocation in both space and time.

Before each experiment, subjects were trained on the search task alone, then on the letter identification task alone and finally, they practiced the dual task. At the end of the training session, a staircase procedure was applied to adjust the contrast of the search items against the background in order to make sure that all subjects reached a performance level of 70 % of correct trials in the search task. After this adaptive procedure, the contrast of the search items against the background was, on average, equal to 70 %. The gray level-luminance function of the screen was obtained with a psychophysical method of gamma correction (Bordier C. & Knoblauch K., personal communication). Briefly, the subjects were asked, by pressing either the up or down arrow key, to adjust the grey level of uniform patches displayed on the screen to match the luminance of patches made of mixed black and white pixels in different proportions; the function relating the grey levels of the uniform patches obtained after subject-controlled adjustments to the proportion of white pixels in the mixed patches provided an estimate of the gamma function of the screen. At the beginning of each trial, a central fixation point was displayed on a computer screen placed 55 cm in front of the subjects. The subjects had to fixate this point throughout the task. Eye position was controlled by means of an electro-oculogram and trials were interrupted, and repeated, whenever subjects broke fixation. After 1500 ms, seven grey circles (1.8 degrees wide) were displayed equidistantly at an eccentricity of 4 deg. These circles were the search items and had a small bar attached to them (0.2 degree long), that could be either vertical (target) or oriented at 30, 60 and 90 degrees from the vertical (distractors); they were filled with a white noise mask. The target was present in 50 % of the trials and at least two distractors of each type were displayed in each trial. After a variable SOA (50, 300, 500 or 700 ms), the masks displayed inside the circles were replaced by letters (1.1 degree wide), flashed for 60 ms; all the letters displayed in a given trials were different. Then the letters were replaced by a new mask. Different SOA values were used to study the temporal characteristic of attentional allocation and these results have already been published elsewhere (Zenon, et al., 2008); in the present study, all SOAs were grouped together as a unique variable and not further investigated. Eight hundred ms after the display onset of the search items, all items were replaced by black disks displayed for 200 ms (see Figure).

Subjects were instructed to press, as fast as possible, the « one » key of the numeral pad of a computer keyboard to indicate that the target was present or the « three » key to indicate it was absent; then, they had to type, without any time constraint, the different letters they identified inside the search items. Subjects triggered the next trial by pressing the space bar. The experiment was divided into 5 blocks of 160 trials each.

II.2.3.1.3 Control task: target detection only

This control experiment was identical to Experiment #1 except that subjects ($n=7$) only had to report the presence, or absence, of the target, without paying attention to the letters. In this experiment, the number of search items was either 4 or 8 to allow us to estimate the “set-size effect” and therefore to evaluate the task difficulty. We found that this search task was inefficient. Indeed, the difference between median RTs of each subject in the 8-items search task (mean $\pm$ SD: 1231 $\pm$ 386 ms for target absent and 1052 $\pm$ 419 ms for target present) and in the 4-items search task (1114 $\pm$ 359 ms for target absent and 951 $\pm$ 336 ms for target present) was 117 $\pm$ 49ms (mean $\pm$ SD) for target absent and 101 $\pm$ 39ms for target present trials (2-way ANOVA RM with number of items – 4 or 8 – and presence or absence of the target as independent variables: main effect of item number, $F=8.1156$, $p=0.0292$). This corresponds to a mean increase of 25 ms per item, a value compatible with the magnitude of set-size effects described in the literature for inefficient search tasks (J. M. Wolfe, 1998b). There was no difference in accuracy between set size 4 and set size 8 (78 $\pm$ 15% and 75 $\pm$ 7% respectively; one way RM ANOVA, $F=0.91$, $p=0.38$).

II.2.3.1.4 Data analysis

In order to determine the degree to which attentional distribution depends on relevance as predicted by the DISTRIBUTED models, we compared actual data on letter detection rates to the results generated by a model assuming different degrees of attentional distribution as a function of relevance. To predict the letter detection rates, we used a bootstrap procedure that generated 20000 fake trials for each subject. In all these trials, we postulated that two letters were detected and that the probability to detect a letter flashed inside a given search item was influenced by its ITS. To estimate this probability we used a probability distribution OP1, i.e. the “real” detection probability gathered in trials where only one letter was detected. We predicted that, if attention is distributed over multiple relevant locations, the detection of additional letters should be influenced by the ITS of the search items in which they were flashed, whereas, if attention is focused on a single relevant item, ITS should affect the detection of only one letter, any additional letters being detected as a result of other factors than relevance. In the fake trials, the expected detection probability (EP2) of the additional letter as a function of ITS depended on a factor S that could range from chance ($S=0$; same probability for all letters) to OP1 ($S=1$). Thus, S represents the degree to which ITS influences the detection of the additional letter and hence, the degree of distribution of attention: $S=0$ simulates WTA whereas $S=1$ simulates DISTRIBUTED. We calculated the predicted percentage of letters detected in these fake trials, as a function of ITS, for every S value (from 0 to 1, with steps of 0.1). These detection rates were compared with the actual data by using a chi-square analysis, yielding a chi-square value for each S value. We also compared the detection probabilities obtained in actual data to another model in which all letters were chosen randomly. We finally divided the chi-square values obtained with the attentional distribution model, representing the continuum between WTA and DISTRIBUTED, for each S values, by the chi-square values provided by the random model. This yielded a ratio regarded as an estimate of the goodness of fit (GOF) of the model, a ratio smaller than 1 indicating a better fit of the attentional distribution model than of the random model.

II.2.3.1.5 Statistical analysis

In order to achieve normality, percentages of detection of letters were arcsine-root transformed, a transformation appropriate for data that lie between an upper and

lower bound (Zar, 1996). We used ANOVAs on repeated measurements for most statistical analyses and Tukey correction for Post-Hoc comparisons.

II.2.3.2 Results

In the search task, subjects made $75.2 \pm 13.6\%$ of HIT (correct detection of the target) in target present trials, and $81.0 \pm 13.6\%$ of CORRECT REJECTION when the target was absent. On average, the subjects typed 2.14 ± 1.14 letters per trial but only 1.20 ± 0.45 letters per trial were correct (see Fig. II.2.2A for an illustration of the distribution of the number of reported letters). When only one letter was reported, the rate of correct response was $78 \pm 34\%$, whereas the chance level to report a correct letter was 27% (7/26). When two letters were typed, the probability of reporting one letter accurately was $49 \pm 14\%$ and that of giving two correct responses was $44 \pm 19\%$. These results allow us to rule out the possibility that when reporting two letters, subjects identified only one letter and guessed the second one. Indeed, if subjects were using this strategy, even if the first letter was accurately identified in 100% of the cases, the probability of reporting two letters correctly would be only around 24% (6/25). These results clearly indicate that subjects did not guess the letters they reported.

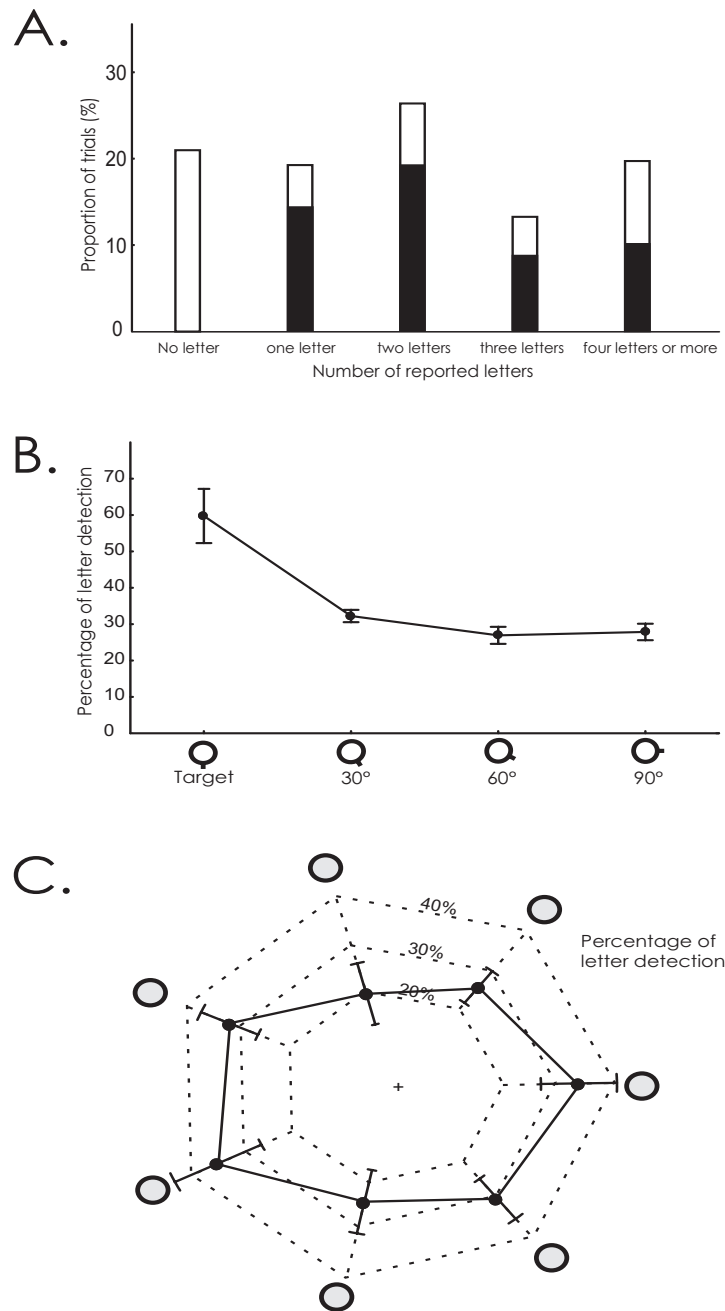


Figure II.2.2.

A. Distribution of the number of reported letters per trial. Unfilled bars indicate the proportion (in percentage) of trials in which a given number of letters were reported. Black-filled bars indicate the proportion of correctly reported letters in these trials. **B.** Effect of item-target similarity (X-axis) on letter detection probability (Y-axis). **C.** Radial plot showing the proportion of letters detected in each position on the display. Letters located on the horizontal meridian were detected more often. Item positions on the graph correspond to their positions in the display as seen by subjects. Error bars indicate the standard error.

Since, in the present study, the letter presentation duration was too short (60 ms) to permit several attentional displacements, the finding that, in $35 \pm 21\%$ of trials,

subjects reported more than one correct letter allowed us to formulate very different predictions based on each of the three aforementioned models: 1) the WTA1 model predicts that attention will be guided exclusively towards the most relevant search item, favoring the detection of the letter flashed inside that item; the detection of any “additional” letters being fortuitous and unrelated to ITS; 2) the WTA2 model states that the spotlight of attention is somewhat “unfocused” and could therefore encompass neighboring search items, predicting that only the detection of one letter should be influenced by the ITS of its search item whereas the others letters should be reported because of their particular spatial relationship with this “central” search item; 3) the DISTRIBUTED model predicts that several search items should be detected because of their high ITS value, the reported letters being therefore located in those highly relevant search items. Because of the very distinct prediction made by each model, a careful analysis of the trials in which multiple letters were detected should allow us to pinpoint the most pertinent model. Consequently, we focused the remaining analyses on those trials in which more than one correct letter was reported. We first confirmed that the orientation (or ITS) of the search item in which the letters were displayed influenced the probability of letter detection in these trials (see Fig. II.2.2 B). Indeed, letters displayed in the target, and in the most resembling distractor, were detected at a higher rate than letters displayed in other distractors (one-way RM ANOVA, $F_{3,11} = 60.57$, $p < 0.0001$, Post-Hoc analyses: $p < 0.0001$ and $p = 0.05$, respectively). Therefore, ITS can be regarded as a “relevance factor” influencing attention allocation. Spatial location was also found to influence letter detection (see Fig. II.2.2 C) since a higher detection rate was found for letters located near the horizontal meridian ($F_{6,11} = 3.55$, $p = 0.004$). Location of the search items in the display will thus be regarded in the following analyses as a “spatial factor” affecting attentional allocation.

II.2.3.2.1 The influence of ITS on attention allocation

The predicted data associated to each model were computed for each subject, by means of a bootstrap procedure (see Methods for a detailed description of the procedure), in which we used a S parameter representing the influence of ITS on attention distribution: S varied from 0 (no influence of ITS, as predicted by WTA) to 1 (identical influence of ITS on all letters, as predicted by DISTRIBUTED). We compared the distributions associated to these predictions with the actual data by means of a chi-square analysis: the smaller the chi-square values, the better the model predictions. The smallest chi-square values were obtained for value of S near 0 and the largest ones for values of S close to 1.

However, the chi-square values obtained with this method are somewhat abstract and do not tell us much about the ability of each model to account for the experimental data. In order to estimate the goodness of fit (GOF) of each model with respect to the actual data, we compared chi-square values gathered for each model to a baseline corresponding to a random model, where the ITS of search items do not influence the probability of detection of any letter. The chi-square values corresponding to each S value was divided by the chi-square value corresponding to the random model, yielding a GOF ratio (see Methods): a GOF ratio smaller than 1 indicates a better fit than the random model. We found that the best fit between experimental data and model predictions was obtained for S values close to 0 (median GOF ratio = 0.54, significantly different from 1: Wilcoxon signed rank test: $p = 0.027$, see Fig. II.2.3), clearly supporting the WTA models in which the detection of only one item is influenced by ITS.

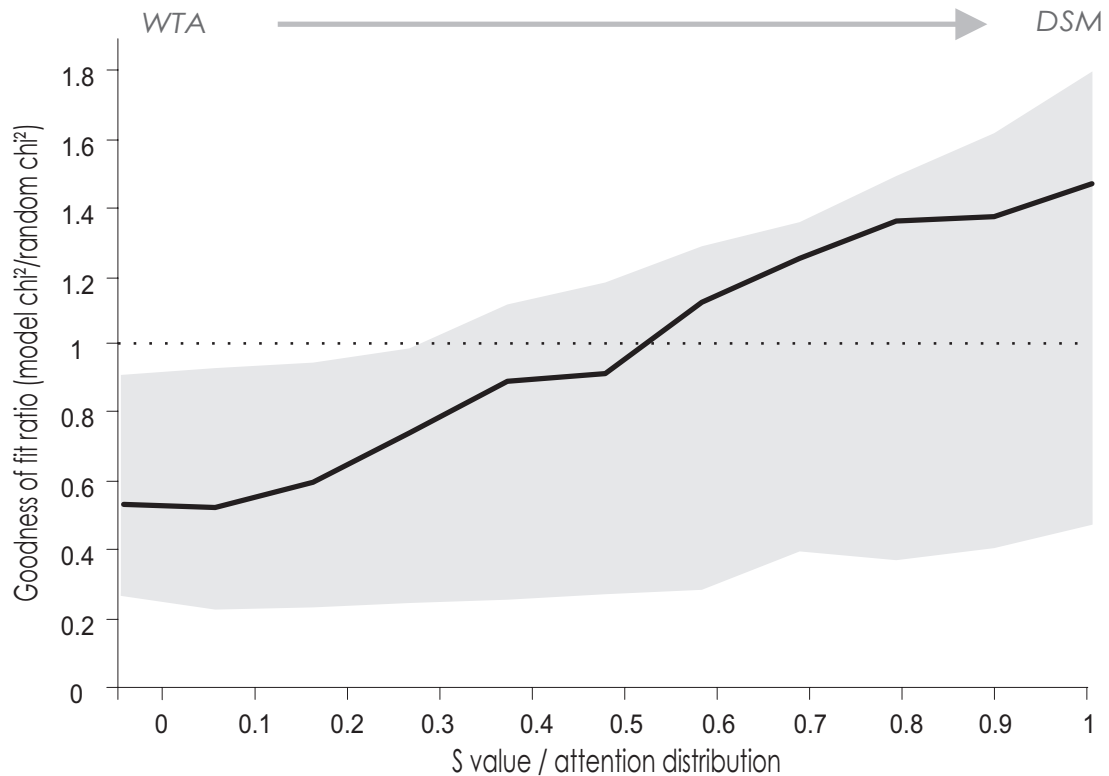


Figure II.2.3.

Comparison between models prediction and experimental data. An S value of 0 corresponds to the WTA model, whereas an S value of 1 corresponds to the DISTRIBUTED model. S value, an estimate of the degree of distribution of attention, is represented on the X-axis. The GOF ratio (see Methods) is represented on the Y-axis. The black line represents the median and the grey surface represents the IQI interval.

II.2.3.2.2 The influence of spatial configuration on attention allocation

The above result indicates that when two letters were reported, the detection of only one letter depended on the ITS of the search item in which it was flashed and the question arises as to which factor influences the detection of the additional letter: WTA1 predicts that this is a random process whereas WTA2 predicts that spatial constraints on the attentional spotlight should influence multiple letter detection. To address this issue we wanted to determine whether spatial location biased the letter detection performance for all locations independently or whether it affected preferentially the co-detection of letters in a specific spatial configuration, for example neighboring letters. We computed the co-detection probability ratio of letters flashed inside all possible pairs of search items ($n=21$). For example, the co-detection probability ratio for the pair of letter positions [P1, P2] was computed as follows: $p(P2 | P1)$ the probability of detecting a letter in position P2, assuming a letter is detected in position P1 was computed and divided by $p(P2 | \sim P1)$ the probability of detecting a letter in position P2 when no letter has been detected in position P1. If the result is larger than 1, it means that letters flashed at location P2 were detected more often concomitantly with letters at location P1, whereas a value smaller than 1 indicates that letters at location P2 were detected more often when no letter was detected at location P1. A one-way RM ANOVA revealed that 5 out of 7 locations had a significant co-detection effect (all $p < 0.01$). These results indicate that when two

letters were co-detected, this was not made randomly but was influenced by their spatial relationships.

We further analyzed these data by comparing the co-detection probability ratio of all pairs of letters as a function of the angle ($n=14$) and distance ($n=3$) between the two letters of the pair (see Fig. II.2.4). The angle between two locations was measured relative to an axis passing through one of the locations and parallel to the horizontal meridian. Hence, angles near 0 or 180 correspond to horizontally aligned positions and angles near 90 and 270 to vertically-aligned locations. A two-way RM ANOVA showed a significant effect of the angle on probability ratio ($F_{13,11}=4.82$, $p<0.0001$), unveiling a preference for angles close to 0° or 180° (Post-Hoc tests: $p<0.05$), and a significant effect of the distance ($F_{2,11}=7.65$, $p=0.003$), indicating a preference for adjacent letters (Post-Hoc tests: $p<0.05$). There was no significant interaction between angle and distance ($F_{26,11}=0.831$, $p=0.7$), suggesting that even letters separated by a long distance could be selected together provided they were located along the horizontal axis (see Fig. II.2.4).

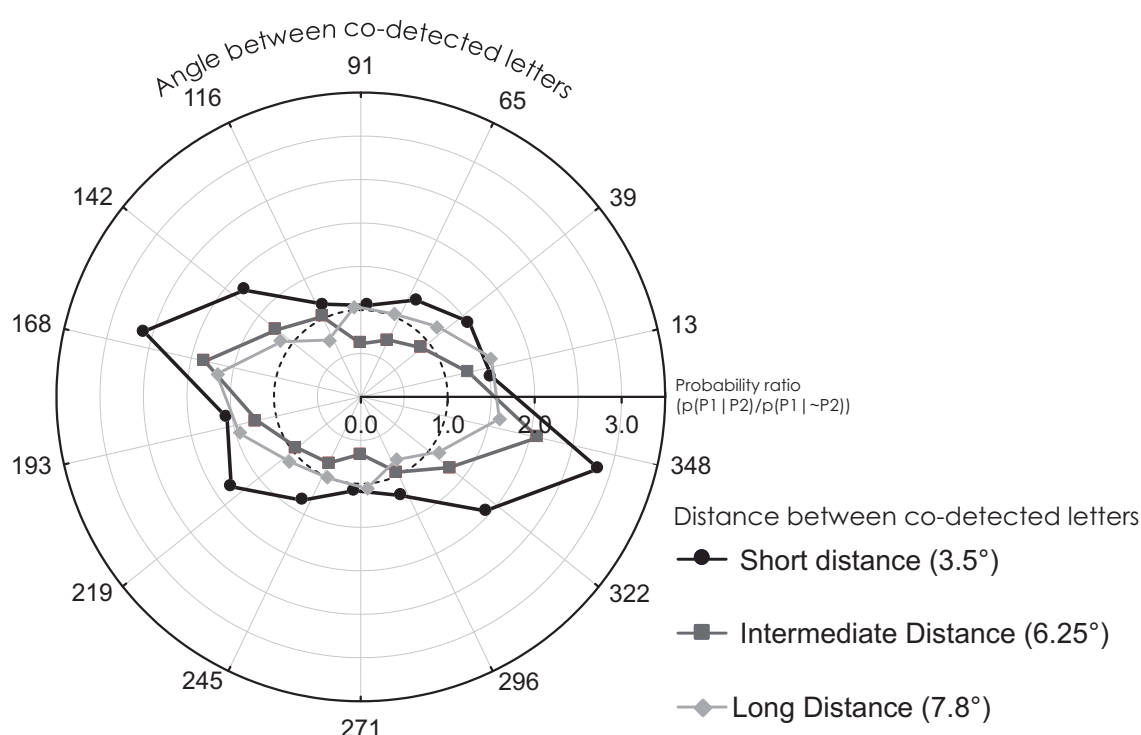


Figure II.2.4.

Radial plot of the co-detection probability ratios as a function of the angle (location on the polar axis) and distance (color code) between the co-detected letters. The black dashed circle represents a co-detection probability ratio of 1.

II.2.3.3 Discussion

The aim of Experiment #1 was to determine whether attention is able to select multiple items during covert visual search, and which factor (relevance or spatial configuration) influences multiple selections. In order to establish the role of relevance, we reasoned as follows: according to the DISTRIBUTED hypothesis, the relevance (estimated here by ITS) should influence the detection of all letters, whereas according to WTA, attention should only select one item at a time, and if

several letters are detected, these “additional” letters should be detected accidentally, irrespectively of the relevance of the search item in which they are displayed. The present results provide support to the WTA models, suggesting that attention is unable to select multiple items because of their high relevance.

Yet, subjects reported several letters in a large number of trials and we found that these additional letters were not selected at random since letter co-detection was constrained by proximity and spatial alignment. Indeed, we showed that letters aligned horizontally, and located in neighboring search items, were preferentially co-detected, in agreement with the WTA2 model. This finding suggests that the spotlight of attention is horizontally elongated. Interestingly, even letters located far apart, in different hemifields, were often co-detected when aligned horizontally, an observation compatible with recent results (Kraft, et al., 2007; Panagopoulos, Von Grunau, & Galera, 2004; Tse, Sheinberg, & Logothetis, 2003). It is noteworthy, however, that in the present study, because of the odd number of stimuli, the locations were never strictly opposed across the vertical meridian and were always slightly offset vertically with respect to each other. It might be argued that this long-distance effect results from a lower perceptual and/or memory interference between letters processed in both hemispheres. However, if it holds true, a similar biased association of letters should be observed for every possible combination of left and right locations whereas our results show such a preferential association only between letters located on a same virtual horizontal line. Another possible explanation for this peculiar pattern of attention distribution is that the representations of the corresponding locations in the two visual hemifields could be co-activated in the visual cortex because of their reciprocal connections. According to this hypothesis, the selection of a stimulus in a given location in one hemifield would automatically activate the corresponding representation in the other hemisphere. However, neuroanatomical and neurophysiological evidence from the literature fails to corroborate this view. Indeed, the transcallosal connections between visual areas are known to involve only positions located on a narrow vertical stripe centered on the midline (Clarke & Miklossy, 1990; Rochefort, Buzas, Kisvarday, Eysel, & Milleret, 2007). Furthermore, although a recent fMRI experiment has demonstrated interhemispheric activations - i.e. a modulation of activity in a cortical area of one hemisphere consequent to the activation of the corresponding area in the opposite hemisphere - in the human visual cortex (Ban, et al., 2006), the co-activated locations did not exhibit a symmetry across the vertical midline similar to that reported in the present study. Rather they reported a symmetry across the central fixation point i.e. stimuli in the upper left visual quadrant interacted with stimuli in the lower right quadrant. In conclusion, no available data in the literature support the view that the effects on co-detection probabilities reported in the present study could result from interhemispheric interactions. Finally, it is important to keep in mind that in this study, stimuli to be reported were letters and, therefore, we cannot rule out the possibility that the horizontal extension of spatial attention spotlight we found is contingent on the utilization of the particular stimuli involved in reading. A replication of these results with non-linguistic stimuli would be necessary to allow us to generalize this conclusion.

Moreover, it is worth mentioning that, because detected letters have to be maintained in memory during the delay between their detections and reports, letter report probability did not depend only on factors affecting detection but also on memory factors. However, memory constraints do not question our conclusion about the crucial influence of attention on letter report probability. Indeed, several studies have shown that letter detection depends on attentional allocation (Egley & Homa, 1984; Kleiss & Lane, 1986; Shaw & Shaw, 1977; Talgar, Pelli, & Carrasco, 2004) and multiple letter report tasks have been used successfully before as a mean to probe attention allocation (Bichot, et al., 1999; Kim & Cave, 1995; Shih & Sperling, 2002).

Therefore, despite the influence of memory factors, the use of a concurrent letter detection task is relevant to monitor attentional allocation.

In summary, Experiment #1 suggests that WTA2, the “extended spotlight” hypothesis, is the most appropriate model to explain our results. However, it could be argued that, in this experiment, because the difference in relevance between the target and distractors was too high, attention was preempted by the target. Consequently, even if attention is able to select multiple relevant items as predicted by the DISTRIBUTED hypothesis, the distribution of attention on the distractors exhibiting the highest ITS would be too weak to be evidenced by our analysis. We tried to overcome this possible flaw in Experiment #2 by adding a significant number of trials in which two targets were present.

II.2.4 EXPERIMENT 2

Experiment #2 was conducted in order to determine whether attention is able to select two search items concurrently when both of them have a high relevance. We used the same dual task as in Experiment #1 except that, in some trials, two targets were displayed simultaneously. Subjects were not informed that two targets could appear simultaneously and they received the same instructions as in Experiment #1, i.e. to report the presence or absence of target. As in Experiment #1, the interval between search display onset and letter onset varied across trials, but here the search display was masked at the same time as the letters, so that the exposure time to the search items also varied. This provided us with a measure of the visual search performance that could be related to letter detection performance and thus to attentional allocation at different delays. Investigating the time-course of letter detection performance in the target during different stages of the visual search performance was used to isolate attentional factors influencing letter detection from other non-attentional factors (see below). This allowed us to compare quantitatively attentional allocation in trials where one or two targets were displayed.

II.2.4.1 Methods

Eight subjects (20-29 years old) participated in Experiment #2 (see Fig. II.2.1B). At the beginning of the experimental session, a staircase procedure was run, during which participants had to perform the same visual search task as in the main Experiment, without reporting the letters displayed inside the search items, and with variable stimulus presentation durations. The duration of the search item presentation was adjusted in order to yield either 50, 75 or 90% of correct responses in the search task, whereas the contrast was kept constant (70%). The duration of search items presentation in the main experiment was then adjusted to these three values and the three possible display durations were counterbalanced across trials. In addition, in contrast to Experiment #1, letters were always flashed during the last 50 ms of the search item presentation. Then, all stimuli were replaced by a mask: the letters were masked with a figure-eight and the search items were masked with circles with 12 bars attached every 30 °, from 0° to 330°. The figure-eight was preferred to white noise since it has proved to be more efficient as a mask in another letter identification task (Enns, 2004). Finally, as already mentioned, in Experiment #2, the number of targets was 0, 1 or 2, these three conditions being equally probable (33% each). The response keys used to indicate that the target was present or absent were the same as in Experiment 1; the subjects were not informed that two

targets could appear simultaneously in some trials and the response required in this case was the same as when only one target was detected. Only two out of eight subjects noticed that two targets were sometimes displayed, although they largely underestimated the proportion of such trials. As in Experiment #1, subjects had to type the detected letters, with no temporal constraint and they triggered the next trial by pressing the space bar. In Experiment #2, eye movements were monitored by means of an infrared camera (Thomas Recording).

II.2.4.2 Results

The results of Experiment #2 confirmed those gathered in Experiment #1 concerning the influence of ITS and of spatial factors on the letter detection probability. Reported letters were mostly those located inside the search target ($p < 0.0001$, $F_{3,7} = 17.15$; target : $30 \pm 13\%$, 30° distractor : $15 \pm 2\%$, 60° distractor : $13 \pm 1\%$, 90° distractor : $13 \pm 2\%$) or in search items near the horizontal meridian ($p = 0.036$, $F_{6,7} = 2.51$; in counterclockwise order from the right-hand horizontal location : $25 \pm 10\%$, $28 \pm 16\%$, $17 \pm 10\%$, $21 \pm 9\%$, $20 \pm 13\%$, $12 \pm 5\%$, $19 \pm 8\%$). The relationship between the display duration and visual search performance is illustrated in Figure II.2.5. The percentage of correct trials in the search task increased with the display duration (see Fig. II.2.5a, blue symbols, $p < 0.0001$, $F_{2,14} = 59.98$) but was slightly different than the one targeted during the staircase procedure (50, 75 and 90%) because of the addition of the letter detection task in the main experiment. Although the mean number of detected letters was identical irrespective of the display duration (see Fig. II.2.5a, green symbols, $p = .40$, $F_{2,14} = .99$), the distribution of detected letters among the different search items varied systematically with display duration. To investigate this effect, we computed a “spatial effect index” defined as the percentage of letters detected on locations close to the horizontal meridian ($n = 3$) divided by the percentage of letters detected on locations close to the vertical meridian ($n = 4$), and a “relevance effect index”, defined as the percentage of letters detected in the target ($n = 1$ or 2), divided by the percentage of letters detected in distractors ($n = 6$ or 5). These indexes were significantly affected by the search display duration (spatial index: $F_{2,14} = 4.13$, $p = .04$, see Fig. II.2.6B, blue symbols; relevance index: $F_{2,14} = 22.08$, $p < 0.0001$, see Fig. II.2.5B red symbols), but while the “relevance effect index” increased with the display duration, the opposite effect was found for the “spatial effect index”. This opposite trend found for the effect of spatial location and relevance further indicates the relative prevalence of ITS as a determinant of attentional allocation with the gradual accumulation of information about relevance.

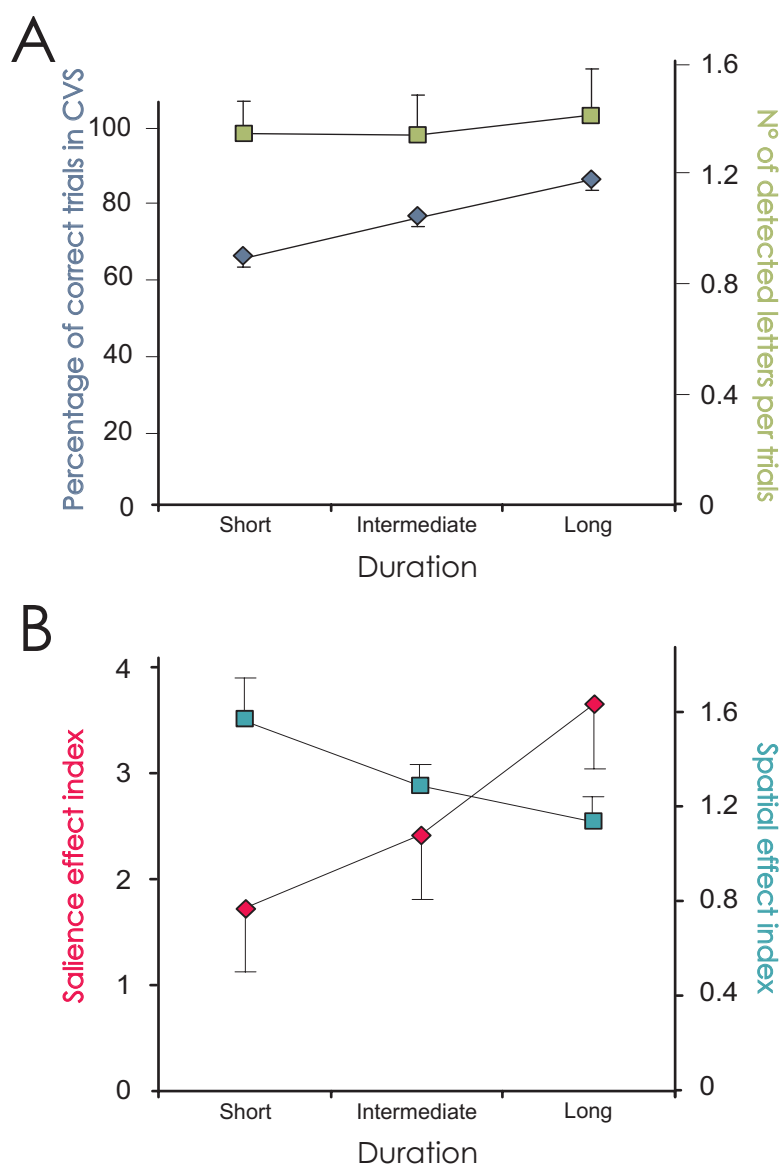


Figure II.2.5.

A. Percentage of correct trials in the visual search task (blue diamonds) and number of letters detected (green squares) for each of the three duration conditions (short : 71 ± 25 ms, intermediate : 218 ± 99 ms, long : 515 ± 159 ms. B. Relevance effect index (red diamonds) and spatial effect index (blue squares) as a function of display duration conditions. Error bars correspond to standard error.

In the following analyses, the predictions of the DISTRIBUTED and WTA models regarding attentional allocation were contrasted by considering only trials in which two letters were detected and by separating trials in which the display contained two targets (TWO TARGETS) versus one target (ONE TARGET). In TWO TARGETS trials, we calculated the rate of double detection for each of the 9 possible pairs of ITS values, varying from 0 (target) to 3 (the most different distractor) (see Methods, Experiment #1). We then compared the double detection rates for the four pairs in which at least one letter flashed inside the target was detected (pairs 0-0, 0-1, 0-2 and 0-3). According to the DISTRIBUTED model, if attention is distributed on several

relevant search items simultaneously, we should observe a higher detection rate for the two letters flashed inside the two targets (pairs 0-0). However, as anticipated from the results of Experiment #1, this was clearly not the case and there was no significant difference between detection rates among the four different pairs ($F_{3,21}=0.12$, $p=0.95$, median detection rate of 6.4% (IQI = 10.1) for pair 0-0 versus 6.4% (IQI = 5.3), 5.7% (IQI = 2.5), 5.3% (IQI = 4.3) for pairs 0-1, 0-2, 0-3, respectively), providing further support to the single-focus hypothesis of the WTA model.

Then we compared the letter report performance in ONE TARGET and TWO TARGETS trials. We defined the letter detection rate per target in search target items as the ratio between the number of letters detected in the target and the number of targets (1 or 2) present in the display; we then compared these values in the two conditions as a function of search display duration. We predicted that if attention is only able to select one target, the letter detection rate per target should be smaller in the TWO TARGETS than in the ONE TARGET condition. A two-way RM ANOVA with display duration and target number as independent factors, and letter detection rate per target as dependent factor showed, in line with our hypothesis, a significantly lower detection rate in the TWO TARGETS condition ($F_{1,7}=10.52$, $p=0.014$), irrespective of the display duration (interaction: $F_{2,7}=1.15$, $p=0.35$). The next analysis is an attempt to quantify this effect even further.

If only relevance affected the distribution of attention, and according to the WTA model, we might expect the letter detection rate per target in the TWO TARGETS condition to be half the detection rate per target in the ONE TARGET condition. However, other factors contribute to the guidance of attention. For instance, the location of the target in the previous trial has a strong impact on letter detection probability (Maljkovic & Nakayama, 1996) and, indeed, we found a significant difference between the detection rate at the location where the target was detected in the previous trial and other locations ($27\pm7\%$ and $19\pm6\%$ respectively, RM ANOVA, $F = 56.7$, $p=0.0001$). Other factors, such as the spatial factors, letter discriminability, memory constraints, etc... are also likely to influence the performance in our search task. In order to disentangle these factors from the specific effect of ITS on attentional guidance, we computed, for each subject, the correlation between the letter detection rate per target and the performance (percentage of correct response) in the visual search task. Our hypothesis was that, when the visual search task is performed at chance level (for very short display durations), the letter detection rate per target should not be affected by relevance. In contrast, the slope of the regression line of letter detection rate per target as a function of search performance should reflect the increase in attentional selection probability of the target, with increasing performance in the search tasks. Hence, if attention is not distributed on both targets, the slope of the regression line for TWO TARGETS trials should be half that of the regression line for ONE TARGET trials. We found that the slope of the regression line for trials in the ONE TARGET condition (partial correlation from a multiple correlation with dummy variables representing subjects: $R=.61$, $p=.0013$, $b=.97\pm.26$) was twice as steep as the slope of the regression line computed for the TWO TARGETS condition (same analysis: $R=.63$, $p=.0006$, $b=.49\pm.12$, see Fig. II.2.6). This indicates that, in the ONE TARGET condition, the letter detection rate per target increased as a function of search task performance, twice as quickly as the letter detection rate per target in the TWO TARGETS condition, because in this latter condition only one of the two targets was selected. This further confirms that attention can select only one target at a time, irrespective of the search items display duration, and that, even in the presence of two targets, attention cannot be distributed simultaneously over several items by virtue of their high level of relevance.

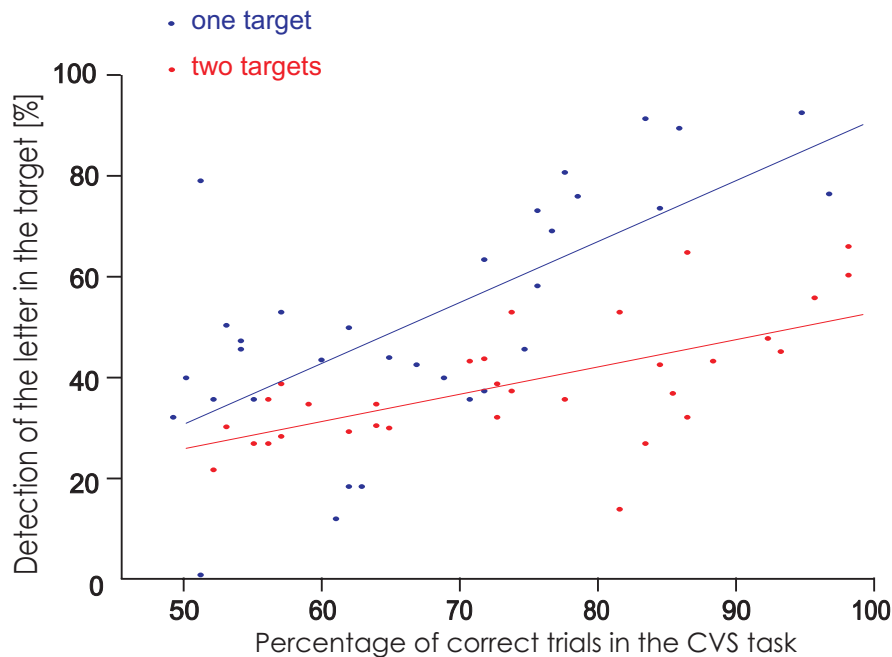


Figure II.2.6.

Correlation between the percentage of correct trials and the percentage of detection of letters in targets for ONE TARGET (blue) and TWO TARGETS (red) trials.

II.2.4.3 Discussion

In Experiment #2, we extended the results of Experiment #1 by showing that, when two items have a high level of relevance with respect to the task, attention cannot select both of them simultaneously, indicating that attention is able to select only one item by virtue of its relevance. It must be stressed that, in this experiment, subjects had no incentive to select both targets, since their response did not vary when one or two targets were displayed. However, these results allow us to rule out the DISTRIBUTED hypothesis, which predict a simultaneous selection of all relevant items, irrespective of the task.

The finding that attentional allocation on the target increases with time, although it corroborates earlier results, may appear in contradiction with the conclusions of a recent study (Donk & van Zoest, 2008). These authors have shown that in a task in which participants have to localize the most conspicuous item in an array, the performance decreases with the presentation duration and this finding is presented as evidence that the visual system can only transiently access information about item conspicuity. This conclusion however, does not contradict the present findings since, in contrast to the Donk and van Zoest study, our target was defined by orientation, not conspicuity and the transient availability of conspicuity information should not lead to a decreased allocation of attention to such targets.

II.2.5 GENERAL DISCUSSION

In the present study, we demonstrated that, in a covert visual search task, attention is able to select only a single locus, potentially the most relevant one. Moreover, we showed that some neighboring locations, mainly those aligned horizontally, are preferentially co-detected. These results are compatible with a WTA mechanism of selection, which postulates a competition for attentional allocation between the different items present in the visual field. While implemented in most theoretical models of attentional allocation, the WTA mechanism has never received, to our knowledge, behavioral experimental support. Only indirect evidence can be found in neurophysiological studies. For example, in the Frontal Eye Field (FEF), a cortical area known to be involved in attentional control and/or representation of relevance (Thompson & Bichot, 2005; Wardak, et al., 2006), (Schlag, Dassonville, & Schlag-Rey, 1998), showed that the pattern of connectivity is compatible with the implementation of a WTA mechanism, namely neurons coding for the same location have excitatory connections between each other, whereas neurons tuned to different directions inhibit each other. Moreover, (Bichot, Thompson, Chenchal Rao, & Schall, 2001)), have used a WTA model to predict the locus of attention allocation from the activity of FEF neurons, demonstrating its efficacy for decoding the neural activity in this area.

However the existence of WTA mechanisms, assuming the selection of a single salient location, is somewhat in contradiction with the ability of attention to split, as demonstrated by several studies (Awh & Pashler, 2000; Bichot, et al., 1999; Castiello & Umiltà, 1990; Gobell, et al., 2004; Hahn, 1998; Scharlau, 2004; Sears & Pylyshyn, 2000; Shaw & Shaw, 1977), for a review see (Gobell, et al., 2004). For example, Bichot and colleagues (Bichot, et al., 1999) trained subjects to detect two uniquely colored targets amongst eight items and to determine whether their shapes were identical or not; letters were displayed inside the eight items (targets and distractors) and subjects had to report as many letters as possible. These authors found that when subjects detected a letter in one of the target, the other detected letters were more often located in the other target, suggesting that attention was distributed over the two targets. Moreover, when the targets were non-contiguous, the distractors in-between were not preferentially selected, indicating that attention was split into two distinct foci. However, in this study, a strong perceptual grouping effect was induced because the two targets had the same color and a feature-based selection of the target group might be involved instead of a spatial selection of noncontiguous locations. In a more recent study, Scharlau (Scharlau, 2004) used a task based on perceptual latency priming and was able to confirm attentional split on multiple non-contiguous items, in a condition providing no strong cues for perceptual grouping. Along the same line, (Sears & Pylyshyn, 2000) demonstrated that attention was able to track multiple moving objects simultaneously, in a task where no cues for perceptual grouping were provided, and that attention was restricted to these selected items and not to distractor locations. Finally, neurophysiological correlates of multiple attentional foci have also been reported in the literature (McMains & Somers, 2004; M. M. Muller, Malinowski, Gruber, & Hillyard, 2003) and single neuron recordings in superior colliculus (SC) (McPeck & Keller, 2002) have shown that two potential saccadic goals can be simultaneously represented in SC, and that while one saccade is performed, the activity corresponding to the other relevant location is maintained, a result compatible with split attention. These results are, however, surprising since SC is thought to be downstream of FEF in saccadic and attentional control (Hanes & Wurtz, 2001), and hence, it is expected that if a single location is selected in FEF, only this location should be implemented in downstream structures.

It is important to stress that these results from the literature are not incompatible with

our finding that, during visual search, attention selects only a single item on the basis of its relevance. Indeed the question addressed in the present study is different from that investigated in aforementioned works. The present study aims at determining how relevance affects attention allocation: relevance can either determine which item will be selected in an all-or-nothing manner, or it can influence the visual processing of all items simultaneously, and proportionally to their ITS. To distinguish between these two hypotheses, we therefore used a task in which subjects were not explicitly asked to split their attention and found that, in agreement with the WTA hypothesis, the relevance was actually unable to affect the detection of all stimuli simultaneously. In contrast, the goal of the aforementioned studies was to determine whether attention is able to split and used, therefore, paradigms which were possible to perform only by dividing attention; their conclusion was that, when required, attention is actually able to select multiple items at the same time. Altogether, these results and ours suggest that, during visual search, attention selects only the most relevant item, but that this winner-take-all selection is not imperative since attention is able to split on multiple items when necessary. In this particular context, it would be of interest to investigate the attentional distribution in a task in which participants have to indicate how many targets are displayed, instead of reporting solely target presence or absence.

A first explanation for the finding that WTA mechanisms are compatible with the ability of attention to split has been proposed by Cave in his Feature Gate model (Cave, 1999): whereas WTA mechanisms would be involved in most cases, they can be relaxed when the selection of multiple locations is required to perform the task (Bichot, et al., 1999; Scharlau, 2004; Sears & Pylyshyn, 2000). Along the same line, Deco and colleagues (Deco, et al., 2002; Standage, et al., 2005) have proposed a model based on attractor networks that can spontaneously implement WTA or DISTRIBUTED mechanisms, depending on the task at hand. Another possible explanation for this apparent contradiction between the existence of WTA mechanisms and the ability of attention to select multiple items relies on object-based attention and grouping. Despite the fact that attention is able to split on several items even when their visual properties do not induce exogenous perceptual grouping, it might be hypothesized that these items can nevertheless be grouped together “endogenously” and processed as a single object. In this case, a WTA mechanism operating on an object-based representation of relevance (Deneve & Pouget, 2003) could help to reconcile the apparently conflicting results found in literature. Further experiments are required to distinguish between these two hypotheses. For example, the difficulty of grouping could be increased by making the to-be-attended stimuli different from each other, but similar to some distractors. In this case, endogenous grouping would be more difficult, and attention split might not be possible.

The idea that the processes underlying both target selection for eye movements and for attention displacements are identical is in agreement with the pre-motor theory of attention, which assumes that covert attention shifts result from the motor preparation of eye movements whose actual execution is impeded (Rizzolatti, et al., 1987). Along the same line, a recent study by Eckstein and colleagues (Eckstein, Beutter, Pham, Shimozaki, & Stone, 2007) has shown that the selection of the first saccadic target during an overt visual search, and the perceptual decision in a comparable covert visual search rely on common visual filters, i.e. on a similar weighting of visual information across space. Many other studies have concurred to establish the functional link between attention and saccades (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corneil, Munoz, Chapman, Admans, & Cushing, 2008; Deubel & Schneider, 1996; Kustov & Robinson, 1996; T. Moore & Fallah, 2004; Sheliga, Riggio, & Rizzolatti, 1994) and some authors have even questioned the ecological importance of performing attentional shifts in the absence of eye movements (J. Findlay & Gilchrist, 2003; Liversedge & Findlay, 2000). Indeed, recent

experimental evidence suggests that no attentional shift occurs between saccades (Motter & Holsapple, 2007), and hence, that shifts of attention in ecological situations would always be accompanied by eye movements. However, the functional link between attention and saccades – and therefore the validity of the pre-motor theory of attention – remains debated since recent studies have reported that, in some instances, attentional shifts and saccades can be dissociated (Juan, et al., 2008; Juan, Shorter-Jacobi, & Schall, 2004; Montagnini & Castet, 2007; Wardak, et al., 2004). Nevertheless, the present finding that attention only selects one item – the most relevant one – at a time and, hence, that attention and saccades rely on the same target selection mechanism rather supports this view that saccades and attentional shifts are tightly coupled.

II.3 Visual search without attentional displacement ³

II.3.1 ABSTRACT

The time needed to search for an object in a complex environment increases with the number of distracting stimuli, a phenomenon known as the “set-size effect”. This observation has led to the view that, during visual search, several attentional shifts are performed, implying a serial processing of visual information. In an attempt to find direct evidence for these attentional shifts, we implemented several dual tasks combining either a covert visual search (CVS) task or a cued target detection task and, concomitantly, a letter reporting task which allowed us to determine, a posteriori, the attentional allocation. We found that, in the cueing task, subjects preferentially reported letters displayed at different locations, indicating clearly that the attention spotlight actually shifted in this condition. In contrast, in either feature or conjunction CVS, subjects predominantly reported letters flashed at the same location, whatever the delay between their presentations, indicating that, despite an obvious “set-size effect”, attention remained static. These results demonstrate that CVS can be performed without shifting attention and that the “set-size effect” does not attest that visual information is processed serially. The present study therefore supports the hypothesis that parallel mechanisms are involved in visual information processing during visual search in agreement with previous theoretical studies.

³ Currently submitted to Journal of Vision, with Suliann Ben Hamed, Jean-René Duhamel and Etienne Olivier as co-authors.

II.3.2 INTRODUCTION

Our everyday life is full of situations in which we have to find a particular object in a complex visual environment: a key on our desk, a signpost along the road or a person in a crowd. The experimental counterpart of such a behavior is visual search, a task in which subjects have to detect the presence of a “target”, amongst a series of averting items, named “distractors”. In order to dissociate attention allocation mechanisms from orienting eye movements, visual search tasks are usually performed covertly, i.e. without any gaze displacement.

Visual search tasks have been widely used to infer mechanisms underlying attentional allocation. Indeed, in easy (or efficient) covert visual search (CVS), the reaction time (RT) is constant, whatever the number of distractors. In contrast, in difficult (or inefficient) CVS, the RT increases proportionally to the number of distractors; this so-called “set-size effect” has been regarded as evidence for a serial processing of visual information, constrained by a step by step displacement of attention (A. M. Treisman & Gelade, 1980). However, theoretical studies have shown that strictly parallel models of attention allocation, based on signal detection theory, can replicate the set-size effect (Eckstein, et al., 2000; Vergheze, 2001), suggesting that the role of parallel mechanisms, or “preattentive processes”, may have been underestimated in inefficient CVS (J. M. Wolfe, 2003). However, experimental evidence supporting this view is still lacking. Indeed, behavioral (Bricolo, et al., 2002; Carrasco & Yeshurun, 1998; Doshier, et al., 2004; McElree & Carrasco, 1999; J. T. Townsend & Fific, 2004), neurophysiological (Bichot, et al., 2005; Woodman & Luck, 2003) and functional neuroimaging studies (Corbetta, Shulman, Miezin, & Petersen, 1995; Donner, et al., 2002; Leonards, Palix, Michel, & Ibanez, 2003; Woodman & Luck, 2003) which have attempted to determine the respective contribution of serial and parallel processes to CVS have led to contradictory conclusions. Indeed, previous behavioral studies were based on indirect methods, relying on the comparison between the observed data and the predictions associated to either parallel or serial models. A more direct approach, consisting in measuring the occurrence of attentional shifts during the performance of CVS tasks could allow us to clarify this issue.

In the present study, we have used three variants of a dual task paradigm to determine the spatio-temporal characteristics of attentional allocation. This dual task consisted of 1) detecting the presence of a target in an array of visual stimuli and 2) reporting letters briefly flashed inside these visual items (see Fig. II.3.1, Fig. II.3.5 and Fig. II.3.6). Importantly, the reporting of the letters flashed inside a CVS item has already been shown as an efficient way to track the spatial location of the attentional spotlight (Bichot, et al., 1999; Egly & Homa, 1984; Gegenfurtner & Sperling, 1993; Kim & Cave, 1995; Kleiss & Lane, 1986; Shaw & Shaw, 1977; Shih & Sperling, 2002; Talgar, et al., 2004; Zenon, et al., 2008). In the present task, several letters were used, but any letter was presented only once during a trial, both at a known timing and location. Therefore, the letters reported by the subjects allowed us to determine a posteriori the deployment of attention during CVS in both space and time (Shih & Sperling, 2002) and to unveil attentional shifts.

In Experiments #1 and #2, the main task was, respectively, a difficult feature (see Fig. II.3.1) and conjunction CVS (see Fig. 5). Experiment #3 was a cueing task (see Fig. II.3.6) designed to determine whether the letter-reporting subtask was an appropriate method to detect attentional shifts when they are known to occur.

II.3.3 EXPERIMENT #1: COVERT FEATURE SEARCH

In Experiment #1, we aimed at determining whether, in inefficient CVS, the set-size effect is due to an increased number of attentional shifts, as predicted by serial models, or to an increased difficulty in the signal detection process because of a lower signal to noise ratio, as proposed by the parallel models. To distinguish between these two hypotheses, we used an inefficient feature visual search task, which, according to serial models, should both necessitate multiple attentional shifts; the performance of subjects in the concurrent letter-reporting task was used as a marker of attentional allocation during CVS. More specifically, we focused on trials in which several letters were reported and we determined whether subjects were more likely to detect letters flashed successively at the same or at different locations. Reporting several letters flashed at the same location would indicate that the attentional spotlight remained stationary on that location during the time interval between the presentation of the detected letters. In contrast, we predicted that the occurrence of attentional shifts would induce a progressive decrease in the probability of reporting letters flashed at the same location, as the delay between the presentation of these letters increases. Hence, comparing the probability of reporting several letters presented at the same location vs different locations as a function of the delay between the letter presentations should allow us to unveil attentional shifts.

II.3.3.1 Methods

II.3.3.1.1 Participants

Ten healthy volunteers (21-30 years old), with normal, or corrected to normal, vision, gave written informed consent to participate in this study. One of them was left-handed. The present protocol was approved by the Ethics committee of the Université catholique de Louvain.

II.3.3.1.2 Behavioral procedure

The task consisted, first, in detecting the presence, or the absence, of a target among six visual items and, second, in reporting letters that were flashed inside these CVS items (see Fig. II.3.1). Subjects were instructed to focus mainly on the CVS task and to consider the letter reporting task as secondary.

Each trial started with the presentation of a fixation point on the center of the computer screen placed at a distance of 55 cm from the subjects. The subjects had to fixate this point throughout the experiment. Eye position was controlled by means of an electro-oculogram and trials were interrupted and repeated, whenever subjects broke fixation. After 1500 ms, the CVS items, namely six grey circles (1.8 degrees wide, 4 degrees eccentricity) were displayed on the screen. These circles had a small bar attached to them, which was either vertical (target) or oriented at 20, 40, 60, 80 or 100 degrees from the vertical (distractors). One ASCII sign was displayed inside each VS item but, in only one item, this sign was a relevant alpha-numeric sign (either a letter, excluding the last letters from « w » to « z », or a digit from 1 to 9) that the subjects had to report. In the other VS items, the signs were irrelevant ('&', '%', etc...). At every frame change (i.e. every 45 ms), the relevant alpha-numeric sign and two irrelevant ones were changed, the new relevant alpha-numeric sign being presented in another location. In each trial, eighteen frame changes occurred; the duration of a trial was therefore 810 ms (18x45 ms). The relevant sign was displayed in each VS item in a pseudo-randomized order so that, in a given trial, a different

relevant sign appeared three times inside each VS item ($n=6$), with a variable delay between each presentation. At the end of each trial, subjects had, firstly, to press as fast as possible the « one » or the “three” key of the numeral pad to indicate that the target was present or absent, respectively. Secondly, they had to type on the keyboard, without any time constraint, the different letters/digits identified inside the VS items. Subjects then triggered the next trial by pressing the space bar.

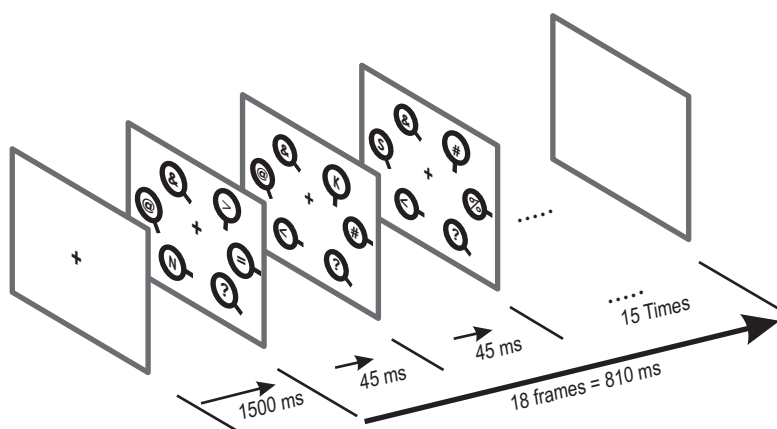


Figure II.3.1

Experimental procedure of Experiment #1. After the fixation point was displayed for 1500 ms, VS items appeared. The target was the circle with an attached vertical line. Every 45 ms, a single letter was displayed in a different location. All other items contained irrelevant symbols. Subjects had to detect whether a target was present or not and to report as many letters as possible.

The experiment was divided into two sessions, performed on two different days. The first session started with a training session during which the subject performed the VS task alone, then the letter identification task, and finally, the dual task; it was followed by a first block of 200 trials. The second session consisted in 3 blocks of 200 trials each.

II.3.3.1.3 Control Experiment A

Control Experiment A was conducted at the end of Experiment #1; in this experiment subjects ($n=6$, 25-29 years old) performed the same dual task (DUAL VS), a single VS task (SINGLE VS) where subjects were not asked to report the letters, a single letter reporting task (SINGLE LETTER) and a dual task with the emphasis placed on the letter reporting task (DUAL LETTER). In the SINGLE VS and DUAL VS conditions, the number of VS items was set either to 4 or 6, in order to estimate the set-size slope of the task.

II.3.3.1.4 Data analysis

Most statistical analyses performed were ANOVA for repeated measurements. Post-hoc tests were Bonferroni corrected. Percentages of detection were corrected by means of an arcsine-root transformation, in order to obtain a distribution close to normal (Zar, 1996).

Analysis on letter report was carried out for nine different delays between letter presentations (from 1 to 9 frames, corresponding to 45 to 405 ms). We did not analyze trials in which delays between two detected letters were larger than 405 ms because they were very scarce (less than 20 trials per subject for all intervals longer than 405 ms).

For reaction times analyses, we first took the median of the reaction times for each subject and then computed means and standard deviations across subjects.

II.3.3.2 Results

The inefficiency of the CVS task was assessed in a control experiment in which either four or six items were displayed (control Experiment A, see Methods); the CVS task was performed alone (SINGLE VS) or in association with the letter reporting task (DUAL VS). We found that these two tasks were inefficient, as shown by the result of a three-way RM ANOVA (TARGET (present vs. absent) x SET SIZE (four or six) x TASK (single or dual)). Indeed, we found a main effect of SET SIZE ($F_{1,5}=36.38$, $p=.002$) on RT but no significant interaction (SET SIZE x TASK: $F_{1,5}=0.26$, $p=.630$; or TARGET x SET SIZE x TASK: $F_{1,5}=0.04$, $p=0.846$). The set-size slope in the SINGLE VS was 31 ms/item for target present trials (RT: mean $\pm$ SD: four items: 955 $\pm$ 242ms, six items: 1016 $\pm$ 188ms) and 39 ms/item for target absent trials (RT: four items: 1119 $\pm$ 164ms, six items: 1197 $\pm$ 313ms); in the DUAL VS, the set-size slope was 20 ms/item (RT: mean $\pm$ SD: four items: 1156 $\pm$ 285ms, six items: 1196 $\pm$ 197ms) and 47 ms/item (RT: mean $\pm$ SD: four items: 1322 $\pm$ 227ms, six items: 1416 $\pm$ 357ms) for present and absent trials respectively. These values are comparable to those reported in the literature for inefficient CVS (J. M. Wolfe, 1998b).

In dual task Experiment #1, the average RT in the CVS task was 1013 $\pm$ 375ms for “target present” trials and 1046 $\pm$ 322ms for “target absent” trials. On average, subjects reported 1.60 $\pm$ 0.99 letters (mean $\pm$ SD, $n=10$) per trial. The probability to detect a letter was influenced 1) by the similarity between the target and the VS item containing that letter (Target present: $F_{5,45}=25.54$, $p<0.0001$, Target absent: $F_{4,36}=2.20$, $p=0.08$; see Fig. II.3.2A), and II.3.2) by the position of the letters in the display (RM ANOVA : $F_{5,45}=3.49$, $p<0.05$, see Fig. II.3.2B). The effect of item-target similarity, in agreement with previous results (Zenon, et al., 2008), indicates that letter report critically depends on visual search features and, therefore, that this dual task paradigm is appropriate to track attention displacements during CVS (see Experiment #3 for further confirmation).

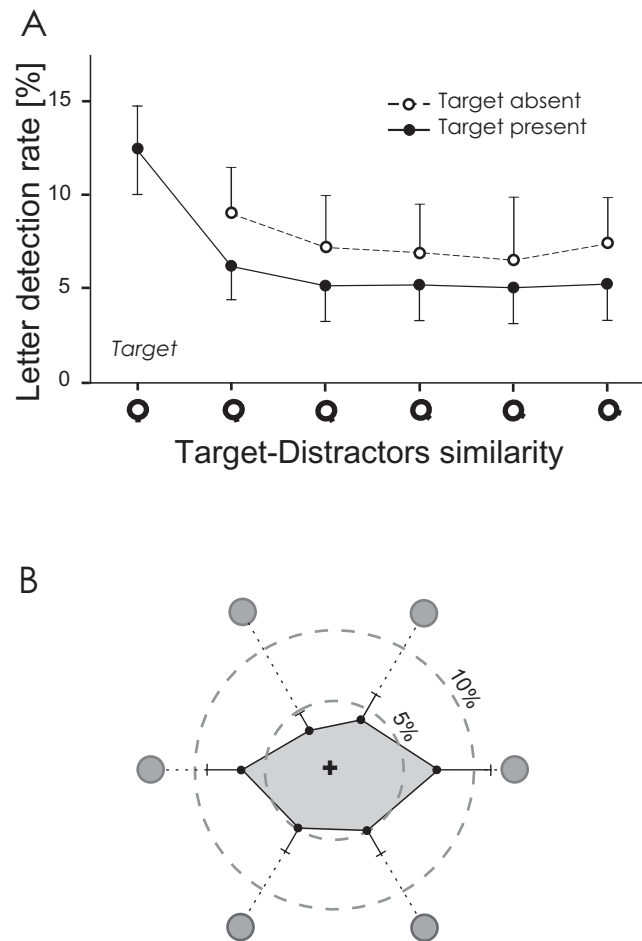


Figure II.3.2

Feature CVS performance.

A. Percentage of detection of the letters for target present (black circles, solid line) and target absent (white circles, dashed line) trials as a function of similarity between the VS item in which the letter is displayed and the target. Letters located inside the target or in the most resembling distractor are more likely to be detected.

B. Radial plot of the proportion of letters detected on each position. Item positions on the graph (grey circles) correspond to the real positions seen by subjects. Letters located on the horizontal meridian were more likely to be reported.

We found that letters flashed later during a given trial were more likely to be reported than letters flashed earlier ($F_{17,153}=98.62$, $p<0.001$). Several factors could account for this result. One possible explanation is that subjects adopted a deliberate task-ordering strategy that consisted, first, in finding the CVS target and, second, in detecting as many letters as possible. However, this interpretation is doubtful since we found the same result in the control Experiment A ($F_{17,85}=9.18$, $p<0.001$), in which, in the SINGLE LETTER task, subjects only had to perform the letter reporting task. Moreover, the difference between the presentation times of the reported letters when the letter task was performed alone or in association with the VS task was much too small (centroids of the time distributions of letter detection in the dual task: 611.1 ± 38.7 ms in the dual task and 568.35 ± 64.35 ms in the single letter reporting task) to allow subjects to perform the VS task within this interval. Therefore, rather than a task priority effect, the finding that letters flashed later were more likely reported, could reveal a masking phenomenon and/or a memory limitation. Indeed,

as a letter is flashed early on, several other symbols, including other letters, were subsequently displayed at the same location, and these symbols may act as masks on the previously displayed letter. Regarding the memory issue, the delay between detection and report was, by definition longer for letters flashed early, increasing the probability of memory trace decay.

II.3.3.2.1 Lack of attentional shift in feature CVS

To determine whether attentional shifts occurred during CVS, we focused on trials in which subjects reported at least two letters (48 ± 22 % of the trials; mean $\pm$ SD; $n=10$) and we compared the probability of reporting two letters flashed either inside the same VS item or inside two different VS items. This analysis was only performed on pairs of letters separated by 1 to 9 frames (i.e. flashed at a time interval ranging from 45 to 405 ms) because, as already mentioned in Methods, the probability of reporting two letters separated by longer intervals decreased dramatically. Our prediction was that, when subjects report two letters flashed at very short intervals, these letters would be more likely to be displayed inside the same item (“preference for same”) because there was no time for attention to shift. However, if attention shifted after a certain delay, this “preference for same” should decrease progressively as the interval between letter presentations increased. In contrast, if attention does not shift during CVS, the “preference for same” should remain constant, irrespective of the interval between letter presentations.

We found that, when a letter was detected at a given location, the probability that the second reported letter was flashed inside the same item was higher ($38 \pm 16\%$) than inside a different item ($12 \pm 5\%$) (2-way RM ANOVA: main effect of SAME vs DIFFERENT: $F_{1,9}=14.01$, $p=0.005$). In order to determine how this “preference for same” was influenced by the time interval between presentation delay, we computed the relative difference (RD) between probabilities of letter report in SAME vs. DIFFERENT items for each interval ($RD = [SAME - DIFFERENT] / [SAME + DIFFERENT]$). We failed to find evidence of a significant correlation between RD and intervals ($R=0.13$, $p=0.22$, slope = -0.01 , confidence interval (CI) = $[-0.03, 0.01]$, Fig. II.3.3, red line), indicating that, within the 45-405 ms window, the “preference for same” remained constant whatever the interval between the letter presentations. This finding suggests that attention did not shift during the performance of this CVS task. Interestingly, we found similar results for trials in which the target was absent (2-way RM ANOVA: main effect of SAME vs DIFFERENT: $F_{1,9}=42.17$, $p<0.0001$; regression: $R=0.16$, $p=0.14$, slope = -0.02 , CI = $[-0.06, 0.02]$), indicating that the absence of attentional shift when the target was present cannot be explained by the fact that attention remained stationary on the target once detected. Moreover, even when the target was present, the probability of detecting two letters flashed inside the same item was identical whatever the nature of the item, target or distractor (1-way RM ANOVA: $F_{1,9}=0.15$, $p=0.71$), showing that the “preference for same” was not only applicable to the letters detected inside the target. Finally, we found that the probability of reporting successive letters at the same location did not differ between the six VS items positions (one-way RM ANOVA: $F_{5,45}=1.50$, $p=0.21$), demonstrating that this “preference for same” did not results from the spatial heterogeneity of the letter reporting probability.

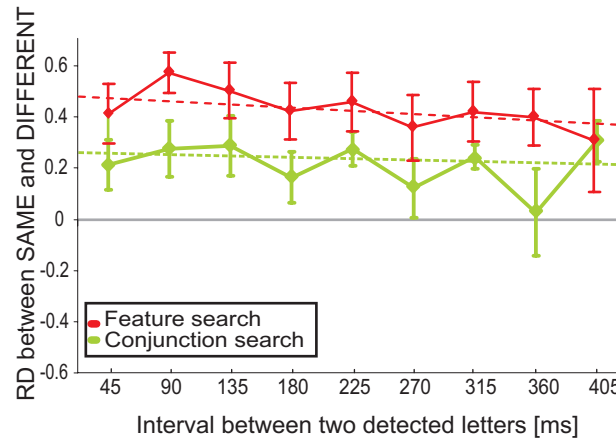


Figure II.3.3

Relative difference between same and different location in dual feature (Experiment #1) and conjunction (Experiment #2) VS experiments.

Regression line (dashed line) computed between the relative difference (RD) in detected letter location for same vs. different ($[\text{same} - \text{different}] / [\text{same} + \text{different}]$) and the delay between the first and second detected letters (in frame changes corresponding to 45 ms each). The red line corresponds to data from the dual feature VS experiment (Exp. #1) and the green line to the conjunction VS experiment (Exp. #2).

II.3.3.2.2 Interactions between CVS and letter reporting

A critical concern about dual tasks is the possible interaction between the two individual tasks namely, in the present study, the CVS and the letter reporting tasks. Indeed, it could be hypothesized that CVS was performed differently in the single and dual task conditions, hence hampering our conclusions about attentional displacements during CVS. However, several pieces of evidence do not support this assumption. Firstly, as already mentioned, we found, that the set-size slopes were identical when the CVS task was performed alone or in association with the letter task (control Experiment A), suggesting a lack of interactions between the tasks. Secondly, we computed the Attention Operating Characteristic (AOC), to estimate the additional cost of performing a dual task (Sperling & Melchner, 1978). To do so, we compared the performance of both the letter reporting task and the CVS task in the different conditions tested in the control Experiment A, i.e. SINGLE CVS, DUAL CVS, SINGLE LETTER and DUAL LETTER (see Methods). The performance in the letter reporting tasks (SINGLE LETTER, DUAL LETTER and DUAL CVS) was quantified by measuring the letter report rate and the performance in the VS tasks (SINGLE CVS, DUAL CVS and DUAL LETTER) was estimated by computing d' . We found that the letter reporting task did not affect d' (one-way ANOVA with CVS performance as a function of task conditions, SINGLE CVS, DUAL CVS and DUAL LETTER: $F_{2,10}=0.23$, $p=0.80$; Fig. II.3.4). This finding validates the use of the letter reporting task in order to monitor attention allocation during CVS. In contrast, we found that the letter report performance was significantly affected by CVS (one-way ANOVA with letter task performance in function of task conditions, SINGLE LETTER, DUAL LETTER and DUAL VS : $F_{2,10}=6.35$, $p=0.01$; Fig. II.3.4).

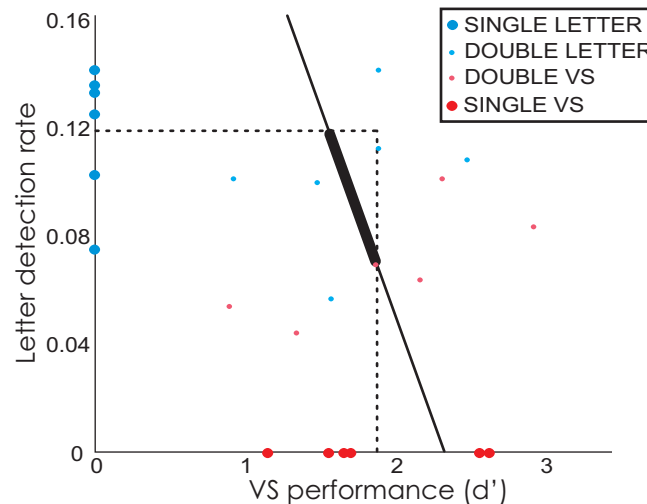


Figure II.3.4

Attention Operating Characteristic.

Large blue and large red dots correspond to data from single letter detection and single VS tasks, respectively. Small blue and small red dots correspond to dual tasks with emphasis put on the letter detection and on the VS task, respectively. The horizontal and the vertical lines are best-fits to the single tasks data; the diagonal line is best-fit to the dual tasks data (joining the means of performance for both dual task conditions); the thicker portion is the estimated Attention Operating Characteristic. The AOC line is near the “independence point”, located at the intersection of the vertical and horizontal lines, which is the point at which the subject would operate the subject can perform both search tasks simultaneously without any interference, i.e. independently of each other.

II.3.3.3 Discussion

The results of Experiment #1 demonstrate that an inefficient visual search task can be performed while attention remains stationary at a particular location. Indeed, we found that, in trials in which subjects reported several letters, those letters were mostly flashed at the same location irrespective of the delay between their presentations, indicating that attention did not shift during the task performance. This preference for detecting successive letters at constant location is not explained by asymmetries in the performance field: while letters are more likely to be reported when displayed along the horizontal meridian, the preference for same is similar in all locations. Another potential confounding factor that must be excluded is the use of a dual task paradigm. These types of paradigms can be regarded as valid provided one can demonstrate that the addition of the concurrent task - the letter reporting task in the present study - does not alter the processes underlying the main task under investigation, namely the CVS task. In particular, it could be argued that, in the dual task, subjects focus their attention strategically on a single location, in order to optimize their performance in the letter reporting task, and that, consequently, measuring attentional allocation during the dual task cannot be used to infer attentional allocation during the visual search task. We demonstrated that this issue does not confound our results, because the performance and set-size slope of the visual search task was not affected by the addition of the letter-reporting task. If visual search tasks required serial attentional shifts and that the addition of a letter reporting task prevented these attentional shifts to occur, visual search performance should drop in the dual task condition, in contrast to the present results.

Another important issue that has to be addressed when using a dual task is the possibility that the subjects could perform the two tasks sequentially instead of concomitantly. In the present study, it could be hypothesized that the subjects first performed the visual search task and that they used the remaining processing time to carry out the letter task. However, our results do not support this view since we found that the letter report probability depended on the item-target similarity, demonstrating that the letter report task is influenced by the visual search task. In addition, and more importantly, we found that the difference between the mean presentation times of the two reported letters in the single letter task and the dual task was much too small to allow the visual search to be performed within that interval. Additional evidence against this hypothesis is provided in Experiment #2.

II.3.4 EXPERIMENT #2: COVERT CONJUNCTION SEARCH

In order to replicate and extend our results, in Experiment #2, we conducted the same analysis on a conjunction visual search task. In addition, we tried to address a potential issue of Experiment #1 concerning the range of timings included in the analysis. Indeed, in Experiment #1, our analysis included more letters detected lately than early, due to the fact that letter report probability increased with the presentation delay. Therefore, it could be argued that, if attentional shifts occurred during the early period of the search, they could have been missed. To overcome this issue, in Experiment #2, we added a condition in which both the visual search items and the letters were displayed for only 405 ms.

II.3.4.1 Methods

In this task, three blue and three yellow isoluminant circles with an attached bar were displayed on the screen, at fixed eccentricity (4°). The orientation of the bar could be 0° , 20° or 40° from the vertical. The target was defined as the blue circle with a vertically oriented bar; other items were used as distractors. Additionally, while in half of the trials, a trial consisted in 18 frames (45 ms), as in Experiment #1 (see Fig. II.3.5), in the other half of the trials, a trial comprised only 9 frames. In the 18 frames condition, the letter presentation was the same as in Experiment #1 (see above). In the 9 frames trials, two different letters were always displayed simultaneously, at opposite locations, and the position of the letter pair was also modified in every frame. Therefore, after only three frames, letters had been displayed in all six possible positions and after 9 frames, three different letters had been presented in each position. The task of the subjects was the same as in Experiment #1 i.e. to detect the presence of the target, as quickly as possible, and to report as many letters as possible. Again, emphasis was put on the visual search task and not on the letter reporting task.

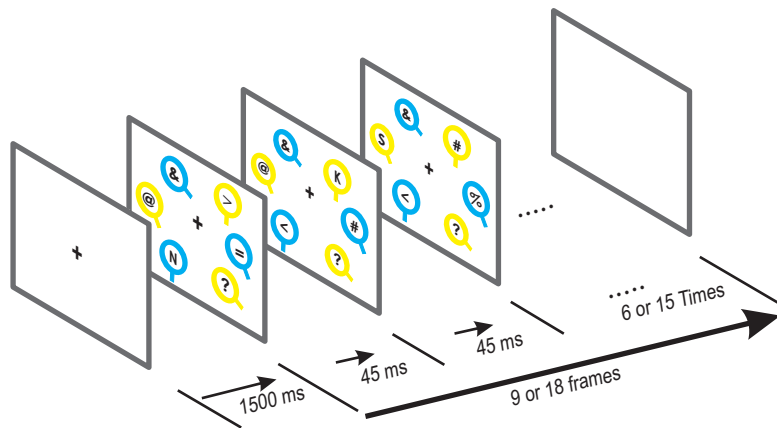


Figure II.3.5

Experimental procedure of Experiment # 2.

Visual search stimuli were either yellow or blue circles with attached lines at one of three possible orientations. The target was the blue circle with a vertical line. Equal proportions of short (9 frames) and long (18 frames) trials were randomly interleaved. Response requirements were the same as in Experiment #1.

II.3.4.1.1 Control Experiments B and C

Two additional control experiments were conducted on each subject. In control Experiment B, the display was exactly the same as in Experiment #2, but subjects had to report only the letters (SINGLE LETTER). In control Experiment C, either 4 or 6 CVS items were displayed, and subjects had only to report the presence or absence of the target (SINGLE VS).

II.3.4.2 Results

The inefficiency of this task was assessed in a single-task control experiment (control experiment C, set-size slope: 36 ms/item for target present trials and 50 ms/item for target absent trials; two-way RM ANOVA, $F_{1,7}=6.40$, $p = 0.039$). The absence of task-ordering strategy was confirmed, as in Experiment #1, by comparing the presentation times of the reported letters in a single letter report task and in the dual task. Here again, the difference was too small (centroids of the time distributions of reported letters: 437.85 ± 22.05 ms in the dual task, and 399.15 ± 43.2 ms in the letter task) to allow subjects to perform the VS task before the letter task. In the dual conjunction task, subjects reported 1.72 ± 0.64 letters (mean $\pm$ SD, $n=8$) per trial. The median RT was 1397 ± 457 ms for "target present" trials and 1429 ± 544 ms for "target absent" trials. The letter task performance was influenced by the similarity in orientation (two-way RM ANOVA, $F_{1,7}=42.81$, $p < 0.0001$) and color (two-way RM ANOVA, $F_{2,14}=22.34$, $p=0.002$) between the target and the VS item containing that letter, and also depended on their location in the display (one-way RM ANOVA, $F_{5,35}=2.43$, $p=0.05$). These effects are in agreement with the results of Experiment #1 showing that attention allocation is influenced by the similarity between the CVS item and the target. We also found a higher detection rate of letters flashed at the same location (two-way RM ANOVA, $F_{1,7}=37.62$, $p < 0.0001$) and an absence of correlation between RD and presentation intervals, suggesting also an absence of attentional shift in the conjunction CVS task ($R = 0.07$, $p = 0.54$, slope = 0.00, CI = [-0.02, 0.02], see Fig. II.3.3, green line). The RD was smaller in conjunction CVS ($RD=0.2 \pm 0.11$, mean $\pm$ SD) than in feature CVS ($RD=0.42 \pm 0.26$). This could be

explained by a more widespread distribution of attention in conjunction CVS, resulting from the grouping effect induced by color (Kim & Cave, 1999a). In agreement with this interpretation, when two letters were detected in different locations, they were more frequently detected in items sharing the same color (one-way RM ANOVA, $F_{1,7}=5.77$, $p=0.047$).

In Experiment #1 the finding that attention does not shift during CVS could be confounded because our analysis included more letters detected later than early, due to the fact that letter report probability increased with the presentation delay. In Experiment #2, we were able to investigate the early period of the search, since in 50% of trials, the display presentation lasted only 405 ms (i.e. 9 frames). The d' in this condition was much smaller than that measured in the long display duration condition (32% reduction, RM ANOVA: $F_{1,7} = 11.97$, $p = 0.01$), showing that the processing of the CVS task was not yet completed within this 405 ms presentation. In this short presentation condition, the RD analysis differed slightly because the number of trials in which more than one letter were detected was small; as a consequence, we grouped different interval conditions into only four intervals (45-90 ms, 135-180 ms, 225-270 ms and 315-360 ms). Again, these results confirmed that RD was not affected by the intervals ($R = 0.09$, $p = 0.63$), showing that even in the early stage of the search, when the target is still being looked for, no attentional shifts occurred.

II.3.4.3 Discussion

In the pioneering work of (A. M. Treisman & Gelade, 1980), parallel and serial mechanisms of visual information processing were associated with feature and conjunction VS, respectively. In feature VS, the target is defined by a single feature difference (e.g. a red target among green distractors), whereas in conjunction conditions, two or more features are combined to define the target (e.g. a red circle among red squares and green circles). To explain why conjunction VS, in contrast to feature VS, yield steep set-size slopes, Treisman and collaborators proposed the existence of multiple feature maps (e.g. orientation, color or luminance maps) in the visual system; in conjunction VS, the multiple features of the target would have to be bound together to allow the target discrimination and attention seems essential to perform this binding (A. Treisman, 1982; J. M. Wolfe & Cave, 1999). As a consequence, attention would have to select each VS item one by one to discriminate the target from the distractors. However, since then, it has been shown that the set-size slopes of both conjunction and feature CVS are distributed along a continuum, ranging from 0 to about 50 ms/item (J. M. Wolfe, 1998b). This has prompted Treisman (A. Treisman, 1999) and others (Deco, et al., 2002; Duncan, 1995; Hamker, 2004a; L. Itti & Koch, 2000; J. M. Wolfe, et al., 1989) to propose alternative models of visual search. The fact that similar set-size slopes can be obtained in conjunction and feature search tasks does not imply that inefficiency originates from the same mechanism in both types of VS. Therefore, it was critical to demonstrate, as we did in Experiment #2, that an inefficient conjunction search task can also be performed without shifting attention.

II.3.5 EXPERIMENT #3: COVERT CUED ATTENTION TASK

To strengthen the conclusion that attention does not spontaneously shift during CVS, it was crucial to prove that our method is indeed able to detect attentional

displacements in a condition where they are known to occur. To address this issue, we conducted a third experiment in which attention allocation was controlled by visual cues.

II.3.5.1 Methods

Each trial started with the presentation of a central fixation point. After 1500 ms, six grey circles (1.8 degrees wide, 4 degrees eccentricity, 50% contrast) were displayed on the screen, and ASCII signs were displayed inside each VS item and replaced on successive frames as described above. The visual search items were simple circles with no bar attached to them. The target was a slightly red circle (10% increase in red luminance). To cue attention allocation, during each trial, the contrast of two gray circles successively increased to 100% for 45 ms, at random intervals; the first cue appeared either in the 3rd, 4th or 5th frame (i.e. 135, 180 or 225 ms after the trial onset) and the second one in the 12th, 13th or 14th frame (i.e. 540, 585 or 630 ms after the trial onset). Three frames, i.e. 135 ms, after either the first or the second cue (chosen randomly in each trial), the item previously cued became the target in 40% of the trials i.e. its red luminance increased by 10%; in 10% of the trials, the target was presented in an “uncued” location and, in the remaining 50%, no target was presented (see Figure II.3.6). As before, the subjects had first to indicate whether a target was presented or not, and second, they had to report as many letters as possible.

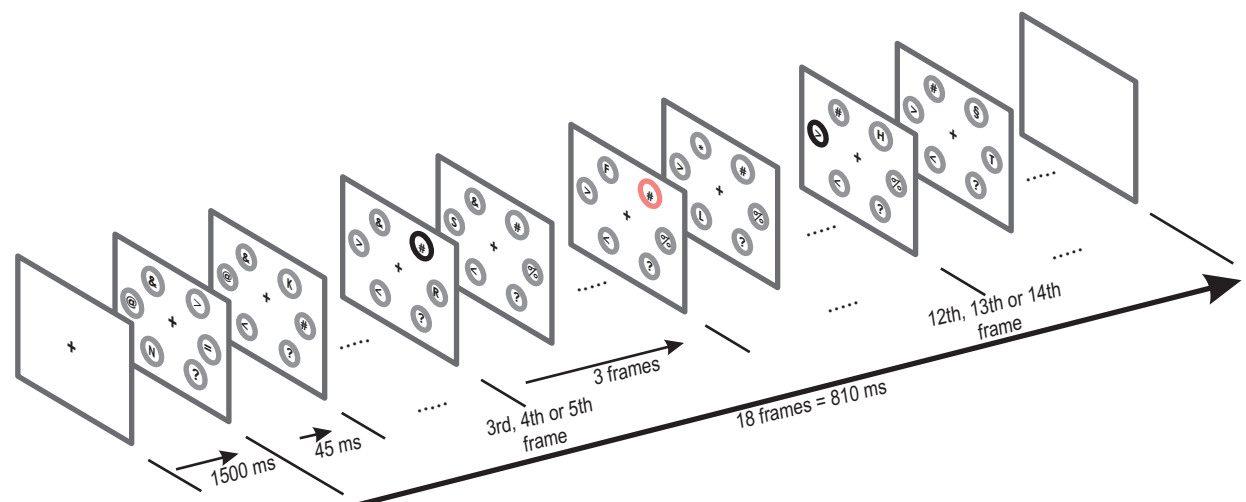


Figure II.3.6

Experimental procedure of Experiment #3.

Display items were plain circles. The cues consisted in two transient contrast changes in different display items and the target was the circle that became transiently reddish. It followed either the first (3rd, 4th or 5th frame) or the second cue (12th, 13th or 14th frame) by 3 frames. Subjects had to detect whether a target appeared and to report as many letters as possible.

II.3.5.2 Results

The results of this experiment confirm that subjects did actually make attentional shifts to the cued VS items. Indeed, the letter report rate increased significantly (one-

way RM ANOVA: $F_{7,28}=11.74$, $p<0.0001$) in the cued VS items. Figure II.3.7 shows the time course of the letter report performance in the cued location, with respect to the cue onset (the maximal performance is reached around 4 frames, i.e. ≈ 180 ms, after cue onset). As in the feature and conjunction dual tasks, we found a “preference for same”, but in this case, the slope of the regression line computed between the RD and intervals was negative ($F_{8,56}=8.83$, $p=0.004$, see Fig. II.3.8, blue line, and experimental procedure). This indicates that when an attentional shift occurred, the probability to detect two letters flashed in the same position decreased significantly with intervals, in contrast to results from both feature and conjunction VS dual tasks.

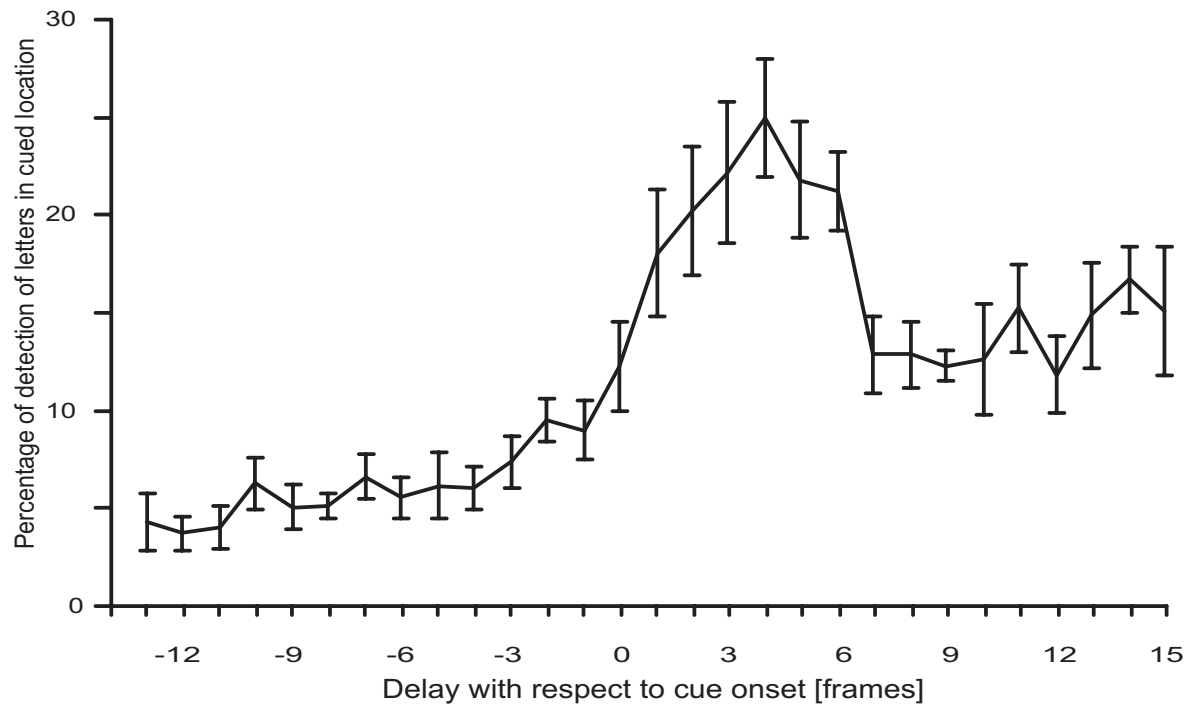


Figure II.3.7

Effect of cueing on attention allocation.

Time course, with respect to the cue onset, of the letter detection performance in the cued location ($n=8$). Error bars correspond to standard error values. The letter detection performance in the cued location increased after cue onset and reached a maximum around 4 frames (~ 180 ms) after cue onset.

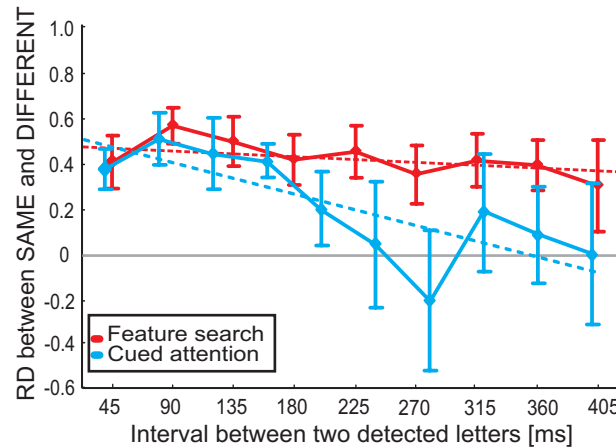


Figure II.3.8

Relative difference between same and different location in the cued attention experiment.

Same conventions as in Fig. II.3.3. Data from the cued attention experiment are shown in blue along with data from the feature VS experiment (Exp. 1) for comparison purposes.

II.3.5.3 Discussion

To be able to interpret the main finding of Experiments #1 and #2 that the high probability of reporting two letters flashed at the same location remains identical whatever the interval between their presentations, it was critical to ascertain that this “negative” result was not caused by a lack of sensitivity or by the inappropriateness of the method we used to monitor attention displacements. The results of Experiment #3 clearly demonstrate that this is not a valid criticism since when attention is successively cued on different positions, the probability of reporting letters at constant location decreases as the time interval between the detected letters increases, in sharp contrast with what we observed in Experiment #1 and #2.

II.3.6 GENERAL DISCUSSION

The present study provides support for the parallel models of VS, demonstrating experimentally a lack of attentional shifts during an inefficient CVS task. This finding is in agreement with the prediction made by the parallel visual search models that the increase in RT consequent to the addition of more distractors results from a more time consuming processing necessary to differentiate the target and distractor signals (Verghese, 2001), and not from extra attentional shifts.

Questioning the validity of the serial models of visual search is not novel and has already been done by many authors. For example, Carrasco and colleagues used informative cues to control attentional allocation during a CVS task (Carrasco & Yeshurun, 1998) and their predictions were that, according to serial models, the cue should cancel the set-size effect by suppressing the need of scanning the entire display to search for the target. In contrast, they showed that, although decreased, the set-size effect was not completely suppressed by cueing the target location, a finding regarded as incompatible with the serial models. However, the cues used in the Carrasco study were valid in only 66% of the trials, and it cannot be excluded that the incomplete disappearance of the set-size effect was due to the partial validity of the cue, instead of the parallel nature of the search process. Along the same line,

Eckstein, Palmer and colleagues used a model of parallel search, based on signal detection theory to predict accurately the performance (detection threshold) of human observers on feature (Palmer, et al., 1993; Palmer, et al., 2000) or conjunction visual searches (Eckstein, et al., 2000). These studies demonstrated convincingly that parallel models are able to explain the set-size effect observed in difficult visual search tasks. However, it remains unclear whether parallel models really outperform serial models in predicting performance of real observers. For example, when comparing the fit of the parallel model and that of a serial model (Eckstein, et al., 2000), Eckstein assumed a “blind” serial model in which attentional selection was performed at random. Instead it is now demonstrated that attentional selection is biased towards items that share some features with the target (Duncan & Humphreys, 1989; J. M. Wolfe, et al., 1989; Zenon, et al., 2008) and consequently, the performance of parallel models should be compared to the accuracy of serial models assuming the existence of a guidance of visual attention. McElree and colleagues took this point into account and compared the ability of parallel and serial search models to predict speed-accuracy trade-off in a conjunction visual search (McElree & Carrasco, 1999). Because, in this condition, all distractors share a feature with the target, it was assumed that attention guidance was ineffective. However, in such conjunction tasks, it is known that one of the feature of the target is selected and that only distractors sharing this feature are actually processed (Zohary & Hochstein, 1989). Hence, the number of distractors that had to be scanned by attention under the serial model assumption in the McElree study was overestimated. In summary, all these studies were decisive in demonstrating that serial processes are not mandatory but they did not validate parallel models. The present study provides, for the first time, direct evidence for the lack of attentional shift during inefficient visual searches.

Our results can be seen as in contradiction with a classical phenomenon reported in the literature, namely the attentional blink effect (AB). Indeed, in paradigms in which two targets have to be detected in a continuous stimulus stream (RSVP tasks), a common observation is that the probability of detecting a second target is lower when presented up to 500 ms after the first one (Shapiro, Raymond, & Arnell, 1994). Similarly, in the present study, subjects had to detect letters displayed in continuous streams, and consequently, the absence of AB may appear puzzling. However, in contrast to AB paradigms, in the present study, subjects did not have to detect the occurrence of a particular “target” letter, but only had to report letters they happened to detect during the performance of the VS task. Moreover, six streams of letters were displayed instead of one in most RSVP experiments and each letter was masked by either irrelevant signs or by other letters. The mechanism underlying AB is still unknown and the necessary and sufficient experimental conditions to observe AB in RSVP tasks are still uncertain (Raymond, 2003; Visser, Bischof, & Di Lollo, 2004) but obviously these conditions were not fulfilled in the present study.

Our finding that attention does not shift serially during CVS does not imply that attention is not critically involved in CVS. Indeed, it has been shown that attention may facilitate search by selecting a single potentially relevant location, guided by stimulus-driven and goal-directed factors (H. C. Nothdurft, 2006; J. M. Wolfe, et al., 1989), hence improving the visual discrimination at that location (J. Theeuwes, et al., 1999). Intuitively, one might assume that the perceptual and computational benefits of attentional shifts during visual search compensate for the time and resource costs, but our data do not support this view and rather show that observers rely only on parallel processes for target detection. It is noteworthy, however, that the absence of any attentional shift observed in the particular context of the present study does not necessarily mean that attentional shifts never occur in other conditions. In natural conditions, when VS is performed without any time constraint, saccades are used to explore the visual scene, and attention shifts are known to precede these rapid eye

displacements (Deubel & Schneider, 1996). It can be assumed that, during CVS too, in the absence of temporal constraint, attentional shifts could also occur. The crucial point of the present study is that inefficiency in CVS is not explained by serial attentional shifts and that the value of the set-size slope is independent of the number of shifts needed to detect the target. This finding is of critical importance because serial models are still deeply anchored in the literature and widely used as a framework to interpret results from many studies on attention mechanisms which contrasted inefficient and efficient VS in order to manipulate the attentional demand (Ashbridge, et al., 1997; Behrmann, Ebert, & Black, 2004; Donner, et al., 2002; N. G. Muller, et al., 2003; Nobre, Coull, Walsh, & Frith, 2003). The present study shows that this approach is most likely invalid and that the view that attention is, like a spotlight, serially displaced in search of the target is flawed.

II.4 Saliency representation in the parietal and frontal cortex ⁴

II.4.1 ABSTRACT

Some objects in the visual field are more likely to attract attention because they are either intrinsically eye-catching or because they are relevant in the context of a particular task. These two factors, known, respectively, as stimulus-driven and goal-directed factors, are thought to be integrated into a unique saliency map, possibly located in the frontal or the parietal cortex. However, the distinct contribution of these two regions to saliency representation is difficult to establish experimentally and remains debated. In an attempt to address this issue, we designed several dual tasks composed of a letter reporting task and a visual search task, allowing us to quantify the saliency of each visual item by measuring its probability to be selected by attention. In Experiment 1, the saliency of the visual search items depended on a combination of conspicuity and relevance factors whereas, in Experiment 2, stimulus-driven and goal-directed factors were tested separately. Then, we used transcranial magnetic stimulation to interfere transiently with the function of the right angular gyrus (ANG) or right frontal eye fields (FEF) in healthy subjects performing these dual tasks. We found that interfering with the ANG and FEF function specifically altered the influence of saliency on the letter report rate, without affecting the overall letter reporting rate suggesting that these areas are involved in saliency representation. In particular, the present study suggests that ANG is involved in goal-directed saliency representation, whereas FEF would rather house a global saliency map integrating both goal-directed and stimulus-driven factors.

⁴ Published paper : Zenon A, Filali N, Duhamel JR, Olivier E., J Cogn Neurosci. 2009 Apr 14. [Epub ahead of print]

II.4.2 INTRODUCTION

The visual environment confronts us with a continuous flow of information that has to be processed as rapidly and as efficiently as possible. Many elements in this flow of information are worthless or irrelevant, but some of them, either because they move quickly, are bright or colorful, or because they show resemblance with an object we are looking for, will attract our attention. When selected, these items will be processed more efficiently by our visual system since more neural resources will be allocated to treat them (Shaw & Shaw, 1977). Attentional selection is based on *salience* (J. M. Findlay & Walker, 1999; J. P. Gottlieb, et al., 1998) resulting from the combination of these different features, even though other terminologies have been used (J. H. Fecteau & Munoz, 2006). Two types of salience factors are typically identified: 1) stimulus-driven factors (H. C. Nothdurft, 1993a) related to the physical characteristics that make a stimulus conspicuous (e.g. luminance, color, ...), and 2) goal-directed factors that are task dependent (Navalpakkam & Itti, 2005; Posner, et al., 1980). In most instances, goal-directed factors override stimulus-driven factors, allowing us to select only the visual items that are pertinent to the task at hand, without being distracted by irrelevant conspicuous objects ((Bacon & Egeth, 1994; Leber & Egeth, 2006), see however (Schreij, et al., 2008; J. Theeuwes, 2004)).

These two types of salience factors are thought to be combined into a unique salience map (L. Itti, Koch C., Niebur E., 1998; Koch & Ullman, 1985), although alternative hypotheses have been proposed (Z. Li, 2002; VanRullen, 2003). Several brain areas have been regarded as potential neural substrates for salience maps, namely the lateral intraparietal area (LIP) (J. Gottlieb, 2007; J. P. Gottlieb, et al., 1998) and area 7a (Constantinidis & Steinmetz, 2005) in monkeys and, in humans, the angular gyrus (ANG), intraparietal sulcus and temporo-parietal junction (Corbetta & Shulman, 2002; Yantis, et al., 2002). The frontal eye fields (FEF) are also considered as a possible location for salience maps (Thompson, Bichot, et al., 2005) and other brain structures, such as the superior colliculus (Krauzlis, et al., 2004) and the pulvinar (D. L. Robinson & Petersen, 1992) might also be involved in salience representation. Because, by definition, salient stimuli are also more likely to attract attention, it remains, both conceptually and experimentally, difficult to differentiate attention and salience representations, and none of the previous human studies have clearly identified the distinct contribution of the aforementioned structures to attentional shift control and/or to salience representation.

Previous transcranial magnetic stimulation (TMS) studies have shown that interfering with the right ANG and FEF function altered the performance of cueing and visual search (VS) tasks (Chambers, Payne, et al., 2004; Ellison, Rushworth, & Walsh, 2003; Grosbras & Paus, 2002; Muggleton, Cowey, & Walsh, 2008; Muggleton, et al., 2003; Rushworth & Taylor, 2006; Walsh, et al., 1999). However, because in these studies, the cue salience was always identical, it remains impossible to determine whether the performance decrease in cueing tasks caused by ANG or FEF TMS was due to impaired attentional shifts or to a reduction in the cue salience. Similarly, in VS tasks, the longer reaction time and decrease in detection performance induced by TMS can be interpreted in different ways (Muggleton, et al., 2008) and the possibility that TMS applied over ANG or FEF may have altered salience representations, affecting therefore the normal guidance of attention towards relevant items (J. M. Wolfe, et al., 1989), has never been investigated experimentally.

To address this issue, we used TMS to disrupt neural processing in either the right ANG or the right FEF, in healthy subjects performing a VS task in which the salience of each individual item was precisely measured. We chose to investigate these two areas in the right hemisphere only, because the dominance of this

hemisphere in attentional tasks has already been clearly established (Ashbridge, et al., 1997; Fierro, et al., 2006; Fierro, et al., 2001; Hodson, Mevorach, & Humphreys, 2008; Muggleton, et al., 2008; Muggleton, et al., 2003; Muggleton, et al., 2006). It is noteworthy, however, that the left parietal and frontal cortex might also be involved in salience computation. For instance, some authors have demonstrated the involvement of the left intraparietal sulcus region in the selection of global versus local shapes as a function of their stimulus-driven salience (Mevorach, Shalev, Allen, & Humphreys, 2008), suggesting a possible contribution of some left cortical regions to the guidance of spatial attention.

The present study comprises two experiments. In Experiment 1, participants had to report letters briefly flashed inside VS items while performing simultaneously a standard covert VS task ((Zenon, et al., 2008), see Methods and Fig. II.4.1). The performance in the letter reporting task allowed us to determine, a posteriori, the attentional allocation according to the salience of VS items. In Experiment 2, participants had to perform a color visual search task. In some trials, in which colored letters were displayed instead of colored VS items, participants had to report as many letters as possible (see Methods and Fig. II.4.5). By manipulating the color of the letters, we were able to determine separately the effect of goal-directed and stimulus-driven salience on attentional allocation. Our working hypothesis was that, if FEF or ANG is involved in salience representation, impeding their functions by means of TMS will modify the distribution of letter detection as a function of the salience of VS items, leaving the overall performance in the letter task unaltered.

II.4.3 EXPERIMENT 1

II.4.3.1 Materials and methods

II.4.3.1.1 Participants

Eleven healthy participants (6 women, mean age: 24 years), with normal or corrected to normal vision participated in the present study. One of them was excluded from the analyses because he performed a large number of saccades (>30% of trials) during the task. All experimental procedures were approved by the Ethics Committee of the Université catholique de Louvain, and participants gave their written informed consent. Monetary compensation was provided for their participation.

II.4.3.1.2 Task

Stimuli were presented on a 19" CRT monitor with a 100 Hz refresh rate. A PC computer running Matlab 6.5 and the Cogent toolbox was used to control stimuli presentation and to trigger TMS. After the presentation of a central fixation point for 1500 ms, 6 VS items, i.e. 6 circles appended with a bar oriented at 0°, 20°, 40°, 60°, 80° or 100° either leftward or rightward from the vertical, were displayed at a 4° eccentricity from the screen center (Fig. II.4.1). The choice of this range of bar orientation (11 possible values) was based on the results of a pilot study and aimed to provide a robust effect of the item-target similarity (see Results section). The circle with a vertical bar was defined as the target, and was displayed in 79% of trials. In the remaining 21% of the trials, the target was replaced by a distractor, randomly selected among the distractors described above. After 340 ms, a letter was flashed inside each VS item for 60 ms, followed by a 200 ms display of 6 random noise masks displayed at the same position as the VS items and randomly generated for

each trial. Participants had first to report, as fast as possible, the presence or absence of the target, by pressing with the right index finger either the right or left arrow key, respectively, and secondly, to report as many letters as possible by typing them on the keyboard. Among the target-present trials, in 7% of trials, the letters were flashed 50 ms after VS items onset and all stimuli were turned off and replaced by masks after 110 ms (control trials). This condition was added to make sure that participants did not perform the two subtasks sequentially instead of concurrently, performing the VS task first and then the letter detection task. Participants had no time constraint to type the detected letters and they triggered the next trial by pressing the spacebar. Minimum inter-trial interval was fixed at 10 seconds.

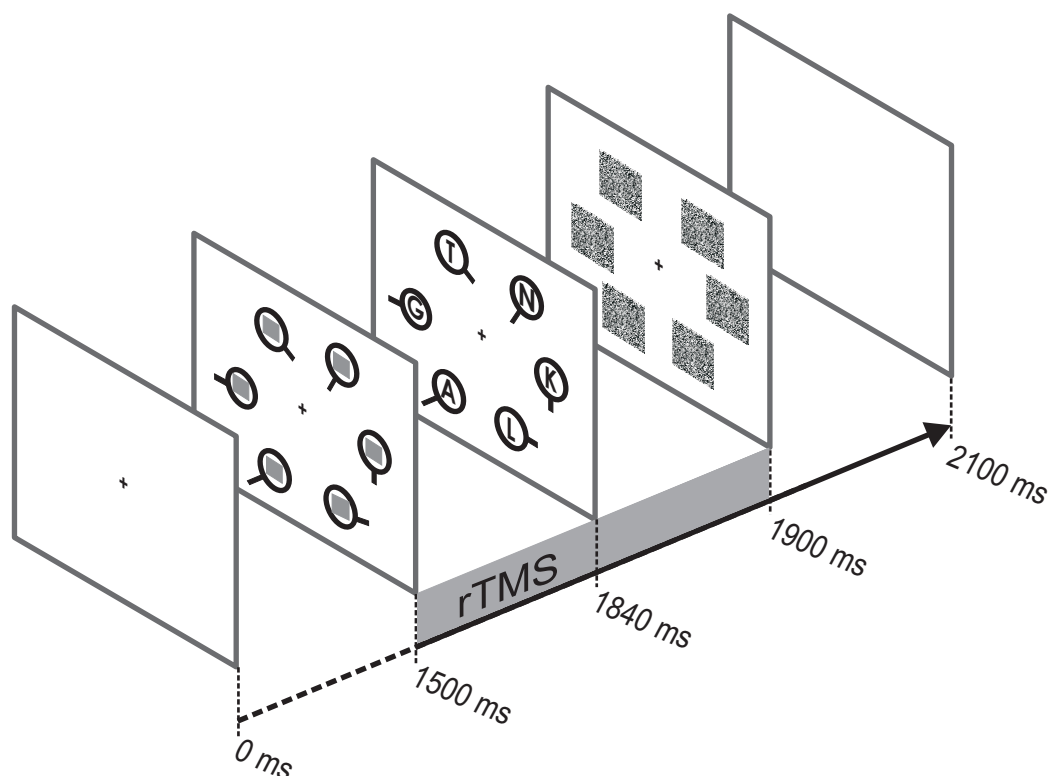


Figure II.4.1

Experimental procedure of Experiment 1. After the display of the fixation point for 1500 ms, the items of the search were switched on. The target was the circle with a vertical line. After 340 ms (50 ms in control trials), letters were flashed for 60 ms inside each VS item, and all stimuli were then replaced by masks for 200 ms. rTMS was applied during the whole VS items display duration. (5 pulses at 10 Hz).

II.4.3.1.3 Transcranial magnetic stimulation

Repetitive TMS (rTMS) was delivered with a Magstim Rapid system (Magstim Company, UK) through a 70 mm figure-of-eight induction coil, either over the right ANG or the right FEF; the vertex (VX) was used as a control site. The rTMS train (10 Hz, 5 pulses, 400 ms) was synchronized with the onset of the VS display. The intensity of stimulation was fixed at 65% stimulator output, except for FEF stimulation in two participants, in whom TMS at such intensity elicited movements of the

controlateral limb. For these two participants, the TMS intensity was reduced to 57% and 62%, respectively. For each participant, the coil position was precisely determined before each experiment by co-registering the stimulation sites onto individual anatomical MRI with a software developed in our laboratory (Noirhomme, et al., 2004). Stimulation sites were localized in each participant according to anatomical landmarks and stimulation coordinates were then normalized (Davare, Andres, Cosnard, Thonnard, & Olivier, 2006) according to the Montreal Neurological Institute atlas (see Fig. II.4.2). The ANG site was defined as the region directly adjacent to the dorsolateral projection of the superior temporal sulcus (STS) and, in the present study, the average coordinates of the stimulation site were 38.6 ± 1.8 , -77.2 ± 2.7 , 40.6 ± 3.5 mm (mean $\pm$ SE; x, y, z), corresponding to coordinates previously used to target this area (Rushworth, et al., 2001). The coil was oriented in such a way that the induced current flowed into a latero-medial direction. The FEF stimulation site was localized at the intersection between superior frontal sulcus and precentral sulcus (Muggleton, et al., 2003), at coordinates 36.8 ± 2.9 , 2.2 ± 3.1 , 60.9 ± 1.9 mm, consistently with previous experiments (J. O'Shea, et al., 2006). The direction of the induced current was antero-lateral. The vertex was defined as a point midway between theinion and the nasion, and was localized, on average, at the following coordinates: -0.5 ± 1.4 , -15.6 ± 5.3 , 71 ± 2.8 mm. The induced current, when applied on the vertex, flowed in a postero-anterior direction.

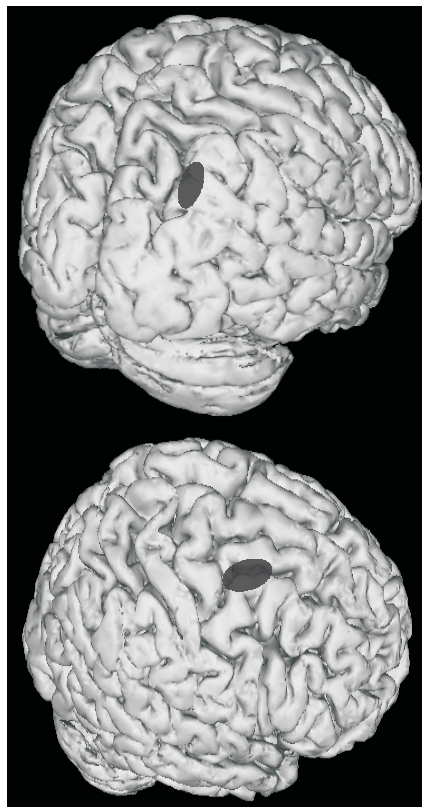


Figure II.4.2

Co-registration of TMS sites

Mean location of stimulation sites over ANG (upper brain image) and FEF (lower brain image) after normalization into the MNI coordinate system. The ellipse surface indicates the 95% confidence interval. MRI scans were obtained in separate test

sessions.

Each participant had to perform 12 blocks of 28 trials in one session. TMS was delivered in every trial. In each block, the stimulation site was pseudo-randomly selected, with a total of four blocks per stimulation site (ANG, FEF and VX).

II.4.3.1.4 Data acquisition and analysis

Eye movements were monitored and recorded by means of an infrared camera (Thomas Recording®). An online saccade detection process permitted to give a feedback to the participants about their fixation performance: if a saccade was detected during a trial, a message was displayed on the screen for 1 second at the end of the trial to inform the subject. Trials in which a saccade or a blink was detected during the stimuli presentation were discarded (12 ± 15 trials per session, mean $\pm$ SD). Trials in which no target was present (21% of trials) and control trials (110 ms stimuli duration, 7% of trials) were not analyzed either. Statistical analyses were conducted on reaction times (RT), target and letter report rates.

II.4.3.1.5 Inefficiency of the VS task: control task A

The control task A was performed in five out of the eleven participants; it consisted in reporting the presence or absence of the target without paying attention to the letters flashed inside the VS items, in displays containing either six or eight items. The visual items used this control task were identical to those used in the dual task (see above). This task was performed on the same day, at the end of the main experiment and involved no TMS.

II.4.3.1.6 Stimulus-driven effect of horizontally and vertically oriented items: control task B

In the control task B, 8 different participants (4 women, mean age: 25 years) had to perform a dual VS task comparable to that used in the main experiment but in which the orientation of the search items was irrelevant, the target being no longer defined by the orientation but by the length of its attached bar. The bar of the target was larger than that of the distractors for which the bar length was constant. The orientation of the bars, although irrelevant here, was different for each item, and varied from 0° to 360°, by steps of 15°. In that experiment, we analyzed the letter report rate as a function of the ORIENTATION of VS item bars. Each possible orientation was categorized on the basis of its angle difference with respect to the horizontal, irrespective of the side (left or right) of the bar, yielding 13 different orientations.

II.4.3.1.7 Statistical analysis

RT and target detection rate were compared across conditions by means of a two-way RM ANOVA with TARGET POSITION ($n=6$) and TMS SITE (VX, FEF or ANG) as independent variables. Letter report rate was studied by means of a four-way RM ANOVA with the ORIENTATION of the VS item in which the letter was displayed, LETTER POSITION on the screen, TARGET SIDE (left or right hemifield) and TMS SITE (VX, FEF or ANG) as independent variables. Post-hoc comparisons are described in the

Results section.

To achieve normality, an arcsine-root transformation was systematically applied on percentages of detection (Zar, 1996).

II.4.3.2 RESULTS

II.4.3.2.1 TMS experiment: behavioral results

Overall, the VS target detection rate in the TMS experiment was $63 \pm 10\%$ (mean $\pm$ SD) and the false alarm rate was $35 \pm 11\%$. RT for target detection was 1311 ± 454 ms and, on average, participants reported 3.08 ± 0.79 letters per trial (mean $\pm$ SD). Only $47 \pm 7\%$ of these letters were correct, leading to a letter detection rate of 1.43 ± 0.46 letter per trial. This value was not significantly different in regular and control trials in which the letters were displayed only 50 ms after VS stimuli onset (one-way RM ANOVA: $F_{1,9} = 3.11$, $p = 0.11$); this indicates clearly that participants did not systematically execute the subtasks in a given order, performing for instance the VS task before the letter detection task because, if it was the case, the letter detection rate would have been reduced dramatically in these control trials. The control task A, performed on 6 or 8 VS items (see Methods), proved that the VS task used in the present study was inefficient since the RT increased as a function of the number of VS items (1-way ANOVA RM: $F_{1,4} = 16.93$, $p = 0.015$, slope = 32 ± 56 ms/item). In the TMS experiment, we found that the letter report rate was influenced by the ORIENTATION (RM ANOVA: $F_{5,45} = 10.50$, $p < 0.0001$, Fig. II.4.3) and LETTER POSITION in the display ($F_{5,45} = 3.90$, $p = 0.005$). The variation in the letter report rate as a function of the VS item orientation was nonlinear: letters were detected more often when displayed in items with an orientation very similar (including the target itself) or very dissimilar to the target than in items with intermediate orientations. Letters were also better detected when displayed in VS items located along the horizontal meridian.

Similarly to the letter detection rate, the target detection performance was influenced by the TARGET POSITION (target detection rate: $F_{5,45} = 2.48$, $p = 0.045$, RT: $F_{5,45} = 4.45$, $p = 0.002$). Post-hoc analyses (Tukey) showed a higher target detection rate and shorter RT when the target was located along the horizontal meridian (all $p < 0.05$). Surprisingly, interfering with ANG or FEF function had no effect on the VS performance, irrespective of the target location (target detection rate: $F_{2,18} = 0.01$, $p = 0.989$, false alarm rate: $F_{2,18} = 0.27$, $p = 0.765$, RT: $F_{2,18} = 0.2$, $p = 0.847$; all TARGET POSITION x TMS SITE interactions: all $p > 0.05$).

II.4.3.2.2 TMS experiment: effect of TMS

Regarding the effect of TMS on the letter report rate, we found a strong interaction between TMS SITE and ORIENTATION of the VS items ($F_{10,90} = 3.10$, $p = 0.002$, see Fig. II.4.3A). The main effect of TMS and all other interactions with TMS were not significant (all p values > 0.5). More specifically, we failed to find a significant interaction between TMS SITE and TARGET SIDE ($F_{1,9} = 0.25$, $p = 0.78$) or LETTER POSITION ($F_{5,45} = 0.87$, $p = 0.57$). This absence of TMS SITE x LETTER POSITION interaction indicates that TMS applied over FEF or ANG did not change the influence of the letter position in the display on their detection rates. Post-hoc analysis (comparison of the letter detection rate, for each ORIENTATION, as a function of the TMS SITE condition, corrected for multiple comparisons) of the ORIENTATION x TMS SITE interaction indicated that the letters located inside VS items with a $\pm 40^\circ$ orientation with respect to vertical were better detected following ANG than VX TMS ($p = 0.008$,

see Fig. II.4.3) whereas those located inside VS items with a $\pm 100^\circ$ orientation were less often detected when TMS was applied over the FEF than on the VX ($p = 0.044$, see Fig. II.4.3).

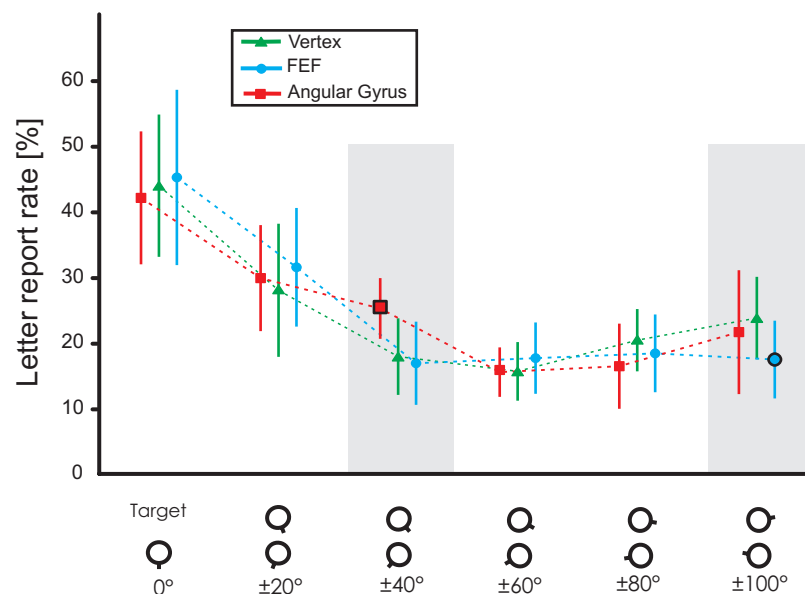


Figure II.4.3

Effect of TMS on the letter report percentage as a function of orientation.

Effect of TMS condition (color and shape code) and orientation of the search items (X-axis) on letter report percentage (Y-axis). Error bars represent standard deviation from the mean. Significant differences between TMS site conditions are indicated by shaded areas and larger data points, outlined in black.

These interactions, while somewhat in agreement with our working hypothesis about the role of ANG and FEF in salience representation, are difficult to interpret without understanding the origin of the non-linear relationship between the letter report rate and orientation of VS items found in the control (VX) condition (see Fig. II.4.3). The results in the left part of this curve are easy to interpret and can be regarded as an effect of the goal-directed salience related to the item-target similarity (Zenon, et al., 2008). In contrast, the reason why the letter report rate increased again in the right part of this curve for the VX condition is less evident and we hypothesized that this effect could unveil a stimulus-driven factor of salience related to the horizontal orientation of the VS items. Indeed, vertical and horizontal orientations have been shown to be detected more easily (Foster & Ward, 1991; Rovamo, et al., 1982) and orientations that can be clearly categorized, such as vertical or horizontal orientations, induce pop-out in VS tasks (J. M. Wolfe, et al., 1992).

II.4.3.2.3 Control task B: Stimulus-driven effect of horizontally and vertically oriented items

To test the hypothesis that horizontally oriented items attracted attention because of their high stimulus-driven salience value, we conducted a control

experiment (control experiment B, see Methods) with a dual VS task in which orientation of the search items was irrelevant. We confirmed that the letter report rate was indeed influenced by the ORIENTATION of VS items ($F_{12,84} = 1.98$, $p = 0.036$, see Fig. II.4.4), although in this experiment this factor was irrelevant. In order to confirm our *a priori* hypothesis of a stimulus-driven effect of horizontality, we conducted a linear regression analysis of letter report probability as a function of orientation of the VS items for the four orientations close to the horizontal (-30° , -15° , 0° and 15° with respect to horizontal), corresponding to the orientations for which a stimulus-driven effect of the horizontality was suspected in the main experiment. We found that the letter report rate increased with horizontality ($R=0.92$, $p < 0.0001$, see Fig. II.4.4). Consequently, we considered that this increase in letter detection performance for items orientation close to the horizontal in the TMS experiment unveiled a stimulus-driven effect. Because, in the TMS experiment, the target orientation was vertical, we also wanted to determine the possible stimulus-driven effect of vertically oriented stimuli. To do so, we performed a comparable regression analysis on the four orientations close to the vertical. Vertically oriented items also attracted attention in this control task ($R=0.92$, $p < 0.0001$, see Fig. II.4.4). Therefore, the higher letter report rate found for vertically oriented items in the TMS experiment resulted probably from a combination of both stimulus-driven and goal-directed factors.

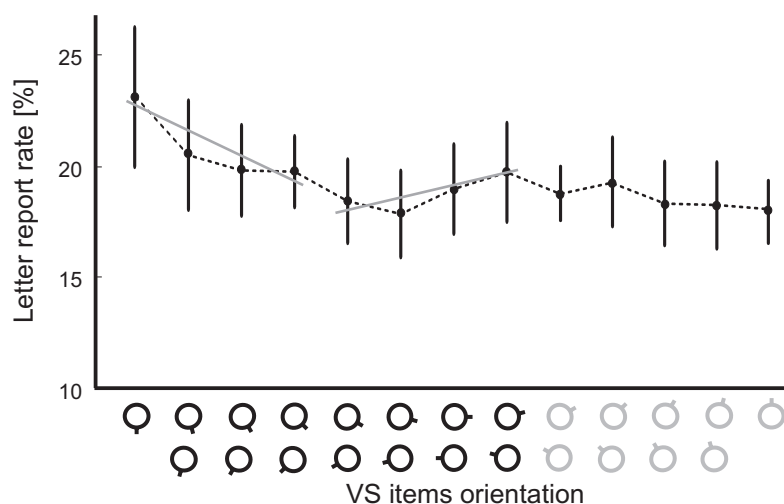


Figure II.4.4

Effect of orientation on the letter report rate in the control task.

Letter detection rate is represented as a function of the bar orientation. Error bars indicate standard deviation. The two gray lines indicate the two linear regressions performed to quantify the stimulus-driven effect of vertically- and horizontally oriented items, as described in the text (see Methods). The orientation values inside the range of orientations used in the main Experiment 1 are displayed in black on the X-axis; other orientation values are in grey.

II.4.3.3 Discussion

In Experiment 1, we found that the orientation of VS items had both a goal-directed and a stimulus-driven influence on attentional allocation. Goal-directed influence depended on the resemblance of the VS items with the target and, indeed, letters flashed inside VS items with an orientation close to the vertical were detected

with a higher probability because the target was vertically oriented. Unexpectedly, we also found that letters displayed in horizontally oriented VS items, although very different from the target, were reported with a higher probability. In control task B, we showed that even when the orientation was irrelevant to the task, participants still detected more often letters displayed in horizontally oriented items, demonstrating the stimulus-driven nature of this effect. In addition, letters displayed in vertically oriented items were also reported with a higher probability in this control task, showing that the high report rate of letters displayed in vertically oriented VS items partly originated from a stimulus-driven influence.

Interestingly, we found that interfering with the normal function of ANG or FEF did not decrease the overall letter reporting rate or the VS performance, but modified the influence of the orientation of VS items on the letter reporting probability. This effect was complex and seems to indicate that these two areas play an important role in salience representation. Indeed, we found that ANG virtual lesion improved the reporting rate of letters displayed in items showing a 40° difference with respect to the target and, because this effect specifically concerned letters displayed in items resembling the target, it could be regarded as evidence for the involvement of ANG in the representation of goal-directed salience. In contrast, TMS applied over FEF lowered the reporting rate of the letters displayed in the horizontally oriented items, suggesting an influence of FEF on stimulus-driven factors of attentional guidance.

In order to disentangle the contribution of ANG and FEF to the representation of the goal-directed and stimulus-driven salience, we conducted another experiment in which we investigated the effect of TMS on these two salience factors separately. Participants had to perform a color visual search task but, at random, in some trials, letters were presented instead of the search items. The color of the letters was manipulated so that, except for one letter, their colors departed progressively from the color of the target in the visual search task (goal-directed letter-reporting task); in another task, the letter color was adjusted so that it yielded different degrees of feature contrast (stimulus-driven letter-reporting task). Because, in the color visual search task, participants were asked to focus on a given target color, we hypothesized that in the goal-directed letter-reporting task, letters with a color similar, or close, to that of the target would be more often reported, even though participants had to report a maximum of letters irrespective of their color. This would unveil the effect of goal-directed guidance of attention by color. In the stimulus-driven letter reporting task, we predicted that letters with a high feature-contrast would be detected more often, providing a marker of the stimulus-driven guidance of attention. Therefore, by analyzing the letter reporting performance of the participants as a function of the color of the letters, we should be able to measure independently stimulus-driven and goal-directed effects on attentional allocation.

II.4.4 EXPERIMENT 2

II.4.4.1 Materials and methods

II.4.4.1.1 Participants

Nine healthy participants (3 women, mean age: 25 years), with normal or corrected to normal vision participated in Experiment 2. Subjects provided their informed consent prior to the experiment and were given monetary compensation for their participation in this study. The experimental procedure was approved by the Ethics Committee of the Université catholique de Louvain.

II.4.4.1.2 Task

The experimental setup used to control the stimuli presentation and to trigger TMS was the same as that used in Experiment 1. The task began with the presentation of a central colored circle for 2 s (see Fig. II.4.5). The color of this circle was randomly selected among 10 possible isoluminant colors and used to inform the participant about the color of the target he had to search for. Colors were represented by their hue, saturation and brightness (HSV color space). Each color had the same saturation (65% of the maximum) and brightness (40% of the maximum) but differed in hue, with 36° differences between each successive color value. It is noteworthy that a constant difference in hue between two colors in the HSV color space does not necessarily imply a constant discrimination performance between these two colors, but this was not imperative in the present experiment. After the presentation of the colored circle, a central fixation point was displayed for 1 s, and then, one out of three possible displays was presented with a probability of 0.33, each display corresponding to a different task:

- 1) Orientation discrimination task: ten colored bars located on a virtual circle, at a 4° eccentricity, and at equal distance from each other, were displayed for 100 ms. Each bar had a different color - selected randomly among the same ten possible colors as the central circle - and a different orientation, chosen randomly among ten possible orientations ranging from 0° to 162° with respect to the vertical, by steps of 18° . The orientation of the target was always 18° away from the vertical, either clockwise or anticlockwise. After the presentation of the bars, ten colored 'X' letters, used as masks, were displayed at the same locations for 300 ms. The color of each 'X' letter matched that of the bar previously displayed at the corresponding location.
- 2) Goal-directed letter reporting task: ten colored letters were displayed for 100 ms on a virtual circle, at an eccentricity of 4° and at an equal distance from each other; each letter was different and had a different color. One of the letters, located at a random location, was defined as the target because it has the same color as the circle initially displayed at the trial onset. The color of the other letters became progressively more and more different from that of the target letter as their distances from the target letter increased (by step of 36° in hue value). Consequently, the color changed smoothly from one letter to the next one, avoiding abrupt color changes between neighboring letters. This ensured that no letter in the display had a higher feature contrast, and therefore a greater stimulus-driven salience, than the others. This design yielded six different letter colors: the target color, the most different color with respect to the target and four intermediate color values. Each of the intermediate color values was attributed to two letters. Following the letter presentation, '8' figures of matching colors were displayed at each letter location, for 300 ms.
- 3) Stimulus-driven letter reporting task: Ten different letters were displayed on a virtual circle, at an eccentricity of 4° , and equally distant from each other. Only two colors were used in this task to characterize the letters; each color was equally distant to the target color defined at the beginning of the trial (i.e. at 120° from each other in the hue circle, and each at 120° from the target color). Therefore, in this task, no letter in the display had the same color as the target color defined by the initial central circle. One to 3 letters (each equally likely and pseudorandomly interleaved) were of one color and 9 to 7 letters were of the other color. For each "target" color, the same pair of colors was always used, and the color used for the smallest group of letters was selected at random. After the letter presentation, '8' figures with matching colors were displayed at each letter location, for 300 ms.

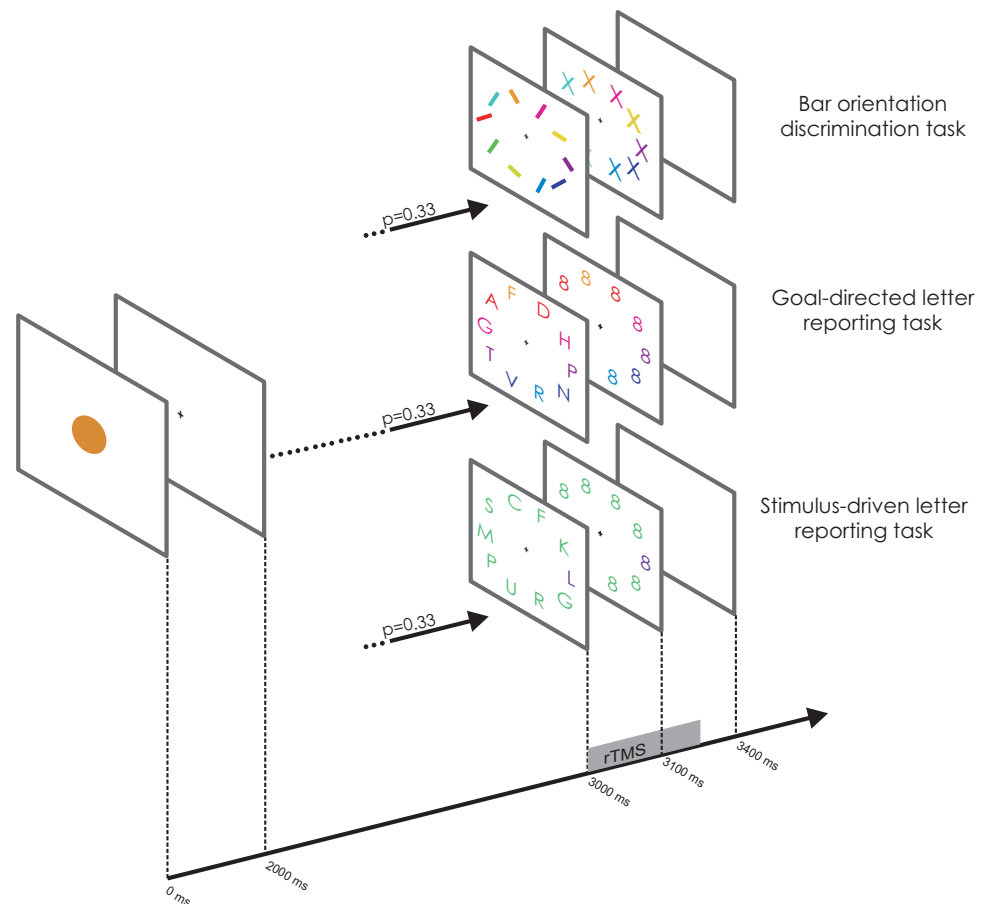


Figure II.4.5

Experimental procedure of Experiment 2. After the display of the disk indicating the target color for 2 seconds and the fixation point for 1000 ms, three different displays could appear for 100 ms, with equal probabilities, and were then replaced by masks for 300 ms. In the orientation discrimination task (upper row), ten bars were displayed with different colors and participants were required to report the orientation of the bar with the target color. In the goal-directed letter reporting task (middle row), ten different letters were displayed with a variable color difference with respect to the target color. In this case, participants had to report a maximum of letters. In the stimulus-driven letter reporting task (lower row), ten different letters were displayed with two possible colors, both equally different to the target color. The number of letters in each of the two color groups was varied. Participants were asked to report a maximum of letters. In all conditions, rTMS was applied during a period of 240 ms, aligned on stimuli onset (5 pulses at 16.66 Hz).

The task differed according to the stimuli displayed and participants were unable to predict the task they had to perform in the next trial. When the bars were displayed, the task consisted in determining the orientation of the bar matching the target color, as indicated by the colored circle initially displayed at the onset of the trial. Participants had to press either the left or right arrow key to indicate, respectively, whether the target bar was rotated counterclockwise or clockwise with respect to the vertical. Participants were encouraged to respond as quickly and as accurately as possible and they received an auditory feedback when their responses were

incorrect. When the letters were displayed, participants had to report as many letters as possible, with no time constraint. In this case, no feedback was given to the participants.

II.4.4.1.3 Transcranial magnetic stimulation

The stimulation conditions were the same as in Experiment 1, except that the frequency of the stimulation pulses was higher, the rTMS train consisting of 5 pulses delivered with an inter-pulse interval of 60 ms (16.66 Hz). This parameter was modified because the stimuli were displayed only for 100 ms and hence, it was not appropriate to have an rTMS train lasting for 400 ms. The first pulse was synchronized with the onset of the stimulus display. Stimulation was delivered at 65% of the stimulator output, except for three participants, in whom TMS at this intensity applied over FEF elicited either blinks or movements in the contralateral limb. TMS intensity was therefore reduced to 55% in two of these participants and to 58% in the third one. Stimulation sites were localized using the same procedure as that used in Experiment 1. In this experiment, the ANG, FEF and VX sites were localized, respectively, at 41.0 ± 1.0 , -79.7 ± 2.2 , 32.8 ± 3.2 mm, 38.1 ± 2.6 , 1.1 ± 2.1 , 61.8 ± 2.5 mm and -2.9 ± 1.2 , -10.5 ± 4.2 , 74.8 ± 1.2 mm (mean $\pm$ SE; x, y, z). Participants performed 12 blocks of 36 trials each, leading to a total of 432 trials.

II.4.4.2 RESULTS

Overall, the percentage of correct responses in the bar orientation discrimination task was $60 \pm 10\%$ (mean $\pm$ SD) and, on average, RT were 1040 ± 194 ms. Separate RM ANOVAs were performed to determine the effect of the bar POSITION and the effect of the bar COLOR on both the orientation discrimination rate and RT. In these ANOVAs, the independent variables were the POSITION of the bar in the display ($n=10$) and the TMS SITE ($n=3$). This analysis did not yield significant effects (percentage of correct response: main effect of POSITION: $F_{9,72} = 0.98$, $p = 0.47$, TMS SITE: $F_{2,16} = 0.22$, $p = 0.80$, POSITION x TMS SITE interaction: $F_{18,144} = 0.94$, $p = 0.53$; RT: main effect of POSITION: $F_{9,72} = 1.68$, $p = 0.11$, TMS SITE: $F_{2,16} = 0.84$, $p = 0.45$, POSITION x TMS SITE interaction: $F_{18,144} = 0.92$, $p = 0.55$). Similarly, the COLOR of the bar ($n=10$) did not affect either the orientation discrimination rate or RT, irrespective of the TMS site location (main effect of COLOR: $F_{9,72} = 1.40$, $p = 0.21$, TMS SITE: $F_{2,16} = 0.44$, $p = 0.65$, POSITION x TMS SITE interaction: $F_{18,144} = 0.97$, $p = 0.50$; RT: main effect of COLOR: $F_{9,72} = 1.62$, $p = 0.13$, TMS SITE: $F_{2,16} = 0.93$, $p = 0.41$, POSITION x TMS SITE interaction: $F_{18,144} = 0.93$, $p = 0.54$).

The letter report rate in the two letter-reporting tasks was found to depend on the color (HSV value) of the displayed letter (one way RM ANOVA: $F_{9,82} = 10.85$, $p < 0.0001$), the performance being inferior for colors in the yellow-orange range than for the other colors (Tukey post-hoc comparisons, all $p < 0.05$). However, since the target color was pseudo-randomly selected among the ten possible colors, the influence of the color on the letter detection performance does not affect the validity of the following analyses.

II.4.4.2.1 Results of the goal-directed letter reporting task

Concerning the goal-directed letter reporting task, we conducted a three-way RM ANOVA with POSITION of the letter in the display ($n=10$), TMS SITE and COLOR ($n=6$, 1 corresponding to the target color and 6 to the most different color) as independent variables. The overall letter reporting performance was significantly

influenced by COLOR and POSITION (main effect of COLOR: $F_{5,40} = 8.02$, $p < 0.0001$; main effect of POSITION: $F_{9,72} = 5.04$, $p < 0.0001$), but not by TMS (main effect of TMS SITE: $F_{2,16} = 0.49$, $p = 0.62$). Critically, the only significant interaction we found was between COLOR and TMS SITE ($F_{10,80} = 2.82$, $p = 0.005$, see Fig. II.4.6 A). Post-hoc analysis (Tukey) of the POSITION effect showed that letters located along the horizontal meridian were reported more often, with an additional bias for the right hemifield. The COLOR effect consisted in a higher report rate of letters with a color similar, or close, to the target color (see Fig. II.4.6 A, in which this effect was decomposed as a function of the TMS SITE). The COLOR x TMS SITE interaction showed that, whereas the COLOR effect in the VX control condition was small but significant (5th color level significantly different than the first and second color levels, all $p < 0.05$), the influence of COLOR on letter report probability increased when TMS was applied over ANG and FEF. In particular, the first and fourth color levels were different between the FEF and VX stimulation conditions, and the first and sixth color levels differed between the ANG and VX conditions (Post-hoc comparisons between stimulation sites, for each color value, corrected for multiple comparisons, all $p < 0.05$).

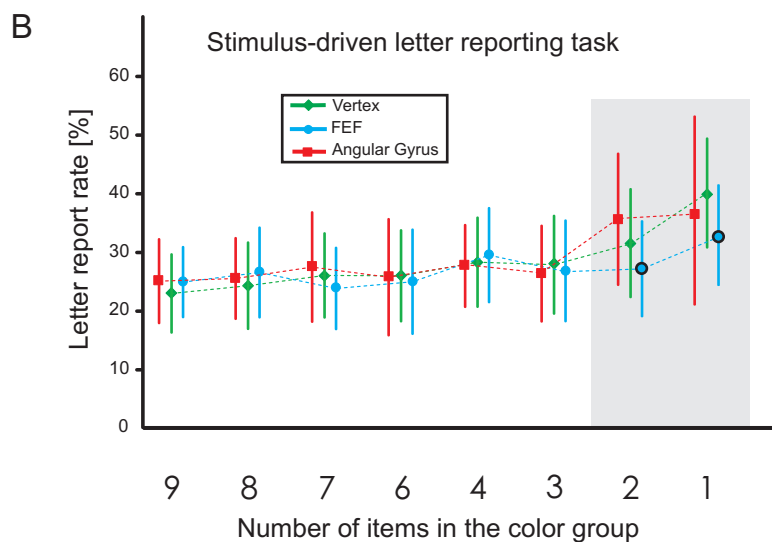
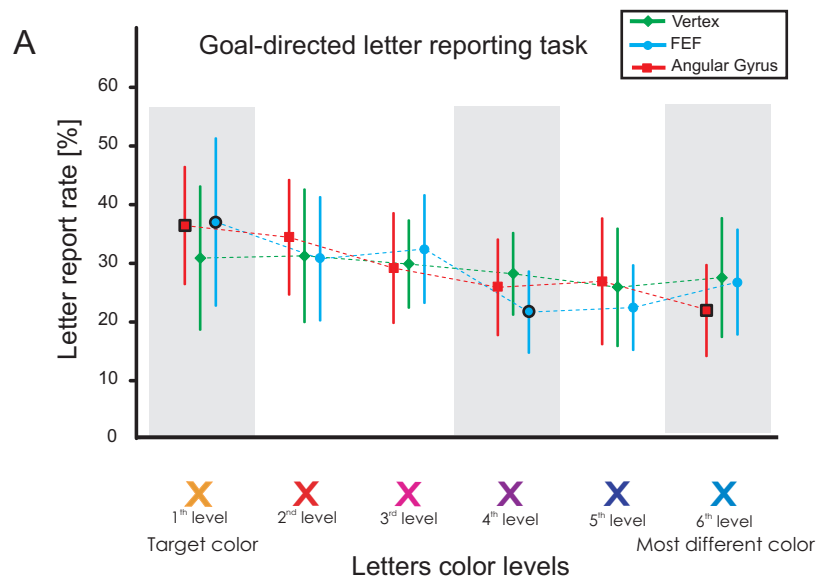


Figure II.4.6

Results of Experiment 2.

Effect of TMS condition (color and shape code) and color (X-axis) on letter report percentage (Y-axis) in the goal-directed letter reporting task (A.) and the stimulus-driven letter reporting task (B.). Error bars represent standard deviation. Significant differences between TMS site conditions are indicated by shaded areas and larger data points, outlined in black.

II.4.4.2.2 Results of the stimulus-driven letter reporting task

For the analysis of the stimulus-driven letter reporting task, we conducted a similar three-way RM ANOVA with POSITION of the letter in the display ($n=10$), TMS SITE and the number of letters in the COLOR GROUP ($n=8$, from 1 to 9, excluding 5, each value corresponding to the number of letters of the same color) as independent variables. The overall letter reporting performance was significantly influenced by COLOR GROUP and POSITION (main effect of COLOR GROUP: $F_{7,56} = 6.10$, $p < 0.0001$; main effect of POSITION: $F_{9,72} = 9.39$, $p < 0.0001$), and not by TMS (main effect of TMS SITE: $F_{2,16} = 0.27$, $p = 0.77$). Here also, the only significant interaction we found was between COLOR GROUP and TMS SITE ($F_{10,80} = 3.03$, $p = 0.001$, see Fig. II.4.6 B). Post-hoc analyses showed that the POSITION effect was the same as in the goal-directed letter reporting task, with a preference for letters located on the horizontal meridian and a bias for the right hemifield. The COLOR GROUP effect consisted in a higher detection rate of letters with a color that was unique in the display, or shared by only one other letter (see Fig. II.4.6 B). The COLOR GROUP x TMS SITE interaction showed that TMS applied over FEF impeded significantly this effect by decreasing the letter reporting rate in the color group containing 1 or 2 letters of the same color (all $p < 0.05$).

II.4.4.3 Discussion

The tasks used in Experiment 2 allowed us to determine separately the effects of stimulus-driven and goal-directed factors on attentional allocation. The bar orientation discrimination task was used to force participants to focus on the target color whereas the two letter-reporting tasks were used to measure independently the stimulus-driven and goal-directed effects of color on the letter detection rate. In the goal-directed letter reporting task, we found that participants detected more often letters with a color close to the target color, providing us with a measure of the goal-directed salience. In the stimulus-driven letter reporting task, we found that the letter reporting rate was higher for letters with a color that was unique in the display or shared by only one other letter. This so-called “feature-ratio” effect is independent of the target color, and hence, is a stimulus-driven factor of attentional guidance.

As in Experiment 1, in which TMS failed to influence the overall performance in the VS task, in Experiment 2 interfering with the ANG or FEF function had no effect on the orientation discrimination rate and RT in the bar orientation task. In contrast, TMS applied over ANG affected the letter report probability in the goal-directed task only, increasing the report rate only for letters with the same color as the target, and decreasing this rate for letters with the most different color from the target.

Additionally, interfering with FEF function affected the letter report rate in both the stimulus-driven and goal-directed tasks. In the stimulus-driven letter reporting task, TMS applied over FEF hampered the stimulus-driven effect of color in the same way as in Experiment 1 in which it decreased the stimulus-driven effect of horizontality. Moreover, we found that FEF TMS altered the letter report rate in the goal-directed letter reporting task since interfering with FEF increased the reporting rate for letters with the target color, and decreased it for letters with the fourth color level, corresponding to a 144° hue difference from the target color. As in Experiment 1, we failed to find any effect of ANG or FEF interference on the overall letter report probability.

It is noteworthy that in this experiment, in contrast to Experiment 1, we modified the salience of the letters by changing their color. Consequently, it cannot be excluded that the effects we measured in the goal-directed letter-reporting task were, at least partly, related to feature-based attention or other type of color priming phenomenon, in addition to the guidance of spatial attention by goal-directed factors.

II.4.5 GENERAL DISCUSSION

Both the parietal and frontal cortex are usually regarded as critically involved in the control of spatial attention (Corbetta & Shulman, 2002; Goldberg, Bisley, Powell, Gottlieb, & Kusunoki, 2002; Schall, 2004) and, more specifically, it has been suggested that these two brain regions could house a salience map that prioritizes the different objects present in the visual field (J. P. Gottlieb, et al., 1998; Kusunoki, et al., 2000; Thompson & Bichot, 2005). According to this view, the neural activity in those brain regions should be proportional to the conspicuity and/or the relevance of visual objects for the task at hand, and these areas should be involved in guiding attention and gaze shifts. In agreement with this latter hypothesis, our results show that interfering with the normal function of ANG or FEF hampered the influence of salience on attentional allocation without affecting the global letter report rate. In addition, the present study gives further insight into the specific role of ANG and FEF in salience representation. Indeed, the tasks we used allowed us to dissociate two different factors of salience: 1) the goal-directed effect of the item-target similarity on letter report rate, 2) the stimulus-driven effects of the horizontal orientation and of the feature-ratio effects. Interestingly, we found that TMS over ANG affected distinctly the influence of item-target similarity, whereas TMS over FEF seemed to affect both stimulus-driven and goal-directed factors of salience.

However, the present results are somewhat difficult to interpret since TMS applied over the same area induced contrasting effects, i.e. either a decrease or an increase in the letter report performance, and these effects cannot simply be regarded as a worsening or an improvement of the effect of salience factors on attentional allocation. The finding that TMS induces opposite effects on a given task is not novel. Several TMS studies have already shown that stimulation of one area can yield either disruptive or facilitative effects depending on the task at hand (Grosbras & Paus, 2002; Romei, Murray, Merabet, & Thut, 2007; Sack, et al., 2007; Walsh, Ellison, Battelli, & Cowey, 1998), the baseline level of cortical excitability (Silvanto, et al., 2008; Silvanto, Muggleton, Cowey, & Walsh, 2007), the hemifield in which the stimulus was displayed (S. Fecteau, et al., 2006; Thut, et al., 2005), or the parameters of the stimulation (Fierro, et al., 2005; Houdayer, et al., 2008; Jung, Shin, Jeong, & Shin, 2008). In the present study, several factors may have influenced the facilitative versus disruptive effects of TMS on the different tasks we investigated. First, TMS may alter the interactions between the two hemispheres: for instance, TMS could have led to a suppression of the inhibition the stimulated area normally

exerts on the homologous region of the opposite hemisphere, inducing an increased activity or excitability of the latter. If this holds true, TMS applied over right ANG would have led to an increased activity/excitability of left ANG, which could be involved in the selection of low salient stimuli (Mevorach, et al., 2008). Accordingly, the enhanced detection of items with low goal-directed salience we found in Experiment 1, could result from a disinhibition of the left ANG consequent to an interference of right ANG induced by TMS. However, this hypothesis fails to explain the results we observed in Experiment 2, in which letters with the lowest goal-directed salience value were less often detected following right ANG TMS. A second possible explanation for these contrasting effects of TMS is that a winner-take-all process of selection is implemented in the salience map, leading to the singling out of the most salient location (Bisley & Goldberg, 2003; Koch & Ullman, 1985). Applying TMS over a cortical area in which such a process takes place can lead to very complex results both by changing the level of activity in different map points and by altering the mutual interactions between them. Finally, it could be assumed that while each pulse of the TMS train induces a facilitation of cortical cells located in the stimulated area, repetitive stimulations leads to a longer lasting inhibition of these cells (Allen, Pasley, Duong, & Freeman, 2007), leading therefore to complex effects of TMS, depending on the balance between transient facilitation and more prolonged inhibition. Hence, the consequences of rTMS on behavior may vary dramatically depending on the exact timing of each pulse with respect to the time course of the process ongoing in the stimulated area.

The absence of effects of TMS applied over ANG and FEF on visual search performance in Experiment 1 and 2 contrasts strikingly with previous works (Ashbridge, et al., 1997; Kalla, et al., 2008; Muggleton, et al., 2008; Muggleton, et al., 2003; J. O'Shea, et al., 2004; Walsh, Ashbridge, et al., 1998). As far as ANG is concerned, previous studies have repeatedly found that interfering with the function of this area increases RT and alters the performance in visual search tasks. Possible explanations for a lack of effect of ANG interference on VS performance in the present study is that participants were highly trained and performed feature visual search tasks. In contrast, in their study, Walsh and colleagues showed that single pulse TMS applied over right ANG affected RT in conjunction VS and only when participants had little or no experience with the task (Walsh, et al., 1999), and most previous work found that TMS affects conjunction, but not feature, visual search (Muggleton, et al., 2008). As far as the consequences of FEF virtual lesions are concerned, previous studies have reported an increase in false alarm rate in conjunction VS (Muggleton, et al., 2003; J. O'Shea, et al., 2004). Again, because in the present study we used a feature and not a conjunction VS task, this could explain the discrepancy with previous results. In addition, in Experiment 1, the number of target-absent trials was too low to draw an unambiguous conclusion about the absence of effects of FEF interference on false alarm rate. In Experiment 2, the target was always present and participants had to perform a two alternative forced choice task, in which no false alarm can occur. Consistently with the hypothesis that ANG and FEF are involved in the computation of a salience map, the effects of TMS found on VS tasks in previous studies can be interpreted as a consequence of the disruption of salience computation and the finding that interfering with ANG and FEF only affects conjunction VS tasks, and mainly when they are novel, would suggest that these VS tasks rely more on attentional guidance than other types of VS tasks.

Beyond studies using VS, a large body of evidence supports the role of ANG and FEF in attentional processes. The implication of ANG in non-VS attentional tasks has received multiple converging evidence in TMS (Chambers & Mattingley, 2005) and fMRI studies (Culham, et al., 2001; Donner, et al., 2002; Yantis, et al., 2002). In monkeys, area 7a, the probable homologue of ANG (Rushworth, et al., 2006; Van Essen, et al., 2001), contains neurons whose activity depends on the presence of a

salient stimulus in their receptive fields (Constantinidis & Steinmetz, 2005), suggesting that area 7a contributes to salience representation. This hypothesis has been confirmed and extended in the present study, by showing a specific role for ANG in goal-directed salience representation in humans. Evidence for the FEF implication in attentional processes also comes from many studies using different approaches such as single cell recordings (Schall, 2004; Thompson, Bichot, et al., 2005), microstimulation (T. Moore & Armstrong, 2003), transient inactivation (Wardak, et al., 2006), functional neuroimaging (Simon, et al., 2004), neuropsychology (Mesulam, 1999) and TMS (Grosbras & Paus, 2002; Muggleton, et al., 2003; J. O'Shea, et al., 2004; Silvanto, et al., 2006). Some of these studies have already suggested a role of FEF in controlling shifts of attention dependant on stimulus-driven salience (Grosbras & Paus, 2002; Lavie & De Fockert, 2006; Wardak, et al., 2006) and some have suggested its implication in goal-directed factors (Smith, Jackson, & Rorden, 2005) whereas others have reported both (Kincade, et al., 2005). The present results are in line with this latter hypothesis, providing support for the contribution of FEF to both stimulus-driven and goal-directed salience computation.

In conclusion, we propose that both ANG and FEF are involved in the computation of visual salience. Whether they are also involved in the implementation of the attentional shifts, i.e. in the generation of the attentional signal that enhances sensory processing at selected spatial locations (T. Moore & Armstrong, 2003; Pessoa, Kastner, & Ungerleider, 2003) remains an open question. The finding that the disruption of their normal functions by TMS led to a deficit in attentional allocation that depends on the salience level, while it had no effect on the global letter report suggest that the capacity to shift attention was preserved and that only the processes involved in the selection of the attentional target were disrupted. The attentional signal *per se* might originate from other brain structures such as the superior colliculus (Carello & Krauzlis, 2004; Cavanaugh & Wurtz, 2004; Kustov & Robinson, 1996). Alternatively, attentional modulation might arise directly from feedback signals coming from ANG and FEF salience maps (Hamker, 2004b), requiring no additional structures. In this case, TMS, by adding noise in the system (Pascual-Leone, Walsh, & Rothwell, 2000), would perturb the selectivity of the modulation signal but would not prevent the generation of attentional shifts. This would result in a reduced effect of salience on attentional allocation without any decrease in global detection performance, as reported in the present study.

II.4.6 ACKNOWLEDGMENTS

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II.5 Cell activity in area 7a correlates with the probability to make an eye movement to a singleton⁵.

II.5.1 INTRODUCTION

In order to explore their visual environment, viewing organisms move their eyes rapidly, sampling at each eye displacement, or saccade, a small portion of the available visual information. The processes involved in the selection of the location on which to move the eyes, selecting certain pieces of information at the expense of others, influence vision dramatically. Therefore, animals have developed through evolution the capacity to select saccadic targets in order to optimize the gathering of relevant information (Najemnik & Geisler, 2005). Some authors have proposed that the processes involved in saccadic target selection rely on the building of a salience map (Koch & Ullman, 1985). The level of activity at each location of this topographic map would be proportional to the relevance and/or conspicuity of the corresponding location of the visual space, and hence, to the incentive to look at that location. Through the intervention of a winner-take-all process, the location with the greatest activation inside this map would instruct the position of the next saccadic target.

In the brain, neurons in area 7A (Constantinidis & Steinmetz, 2001b) and in the lateral intraparietal area (LIP) (Bisley & Goldberg, 2003) in the parietal cortex, in frontal eye fields (FEF) (Thompson & Bichot, 2005), and in the superior colliculus (SC) (Basso & Wurtz, 1997; Krauzlis, et al., 2004) are modulated by salience factors and are hence thought to be involved in the computation of salience. Among these structures, area 7a is the putative monkey homolog of human angular gyrus (Mort, Malhotra, et al., 2003; Rushworth, et al., 2006; Van Essen, et al., 2001) which, when damaged, is associated with hemineglect (Karnath, 1997; Mort, Malhotra, et al., 2003). Hence, understanding better the role of area 7a in salience representation could give us further insight into the mechanisms responsible for neglect. Previous studies have shown that cells in area 7a respond to conspicuous stimuli when presented in their receptive fields, irrespective of whether they are relevant for the task at hand or not (Constantinidis & Steinmetz, 2001b, 2005). In these studies, physical conspicuity was determined by the color contrast between the salient item and neighboring items. Items with high color contrast, or more generally high feature contrast, attract attention automatically (H. C. Nothdurft, 2002), in a so-called stimulus-driven way. The response of area 7a cells to conspicuity can either be interpreted as a representation of feature contrast per se, or as a representation of salience, i.e. the influence that feature contrast has on the probability to allocate attention and/or to look at a given stimulus (Hegde & Felleman, 2003). Because in these studies, the animals were required to fixate throughout the task and covert attention was not controlled, we cannot determine to what extent they allocated attention and/or planned saccades to the conspicuous items, even though they were supposed to be irrelevant. Consequently, it remains unknown whether the activity of area 7a cells depends on feature contrast or on visual salience.

⁵ Article in preparation with Joao Azzi, Suliann Ben Hamed, Etienne Olivier and Jean-René Duhamel as co-authors.

In the present study, monkeys were required to explore arrays of oriented gabors displayed on a screen while single neurons were recorded in area 7a. All but one gabor had identical orientation. The orientation difference between the unique gabor (the singleton) and the other gabors was varied, giving different feature contrast values. We then investigated whether cell activity depends more on the feature contrast of the singleton or on the salience of the singleton, taken as the incentive of the monkey to look at it. In agreement with the latter hypothesis, we found that the activity of neurons did not represent feature contrast reliably but correlated with the probability of making a saccade to the singleton.

II.5.2 EXPERIMENTAL PROCEDURE

II.5.2.1.1 Subjects and surgery

Data were collected from 2 macaque monkeys (S, N), *Macaca mulatta*, weighing 3-5 kg. The animals were cared for in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care Committee. For each monkey, a single surgery was performed under isoflurane anesthesia for stereotaxic implantation of a head restraining post and posterior parietal recording chambers (ML 5 mm and AP 12 mm, right hemisphere for monkey S, and left hemisphere for monkey N). The monkeys were then left to recover with the proper antibiotic coverage and pain-reliever was given as needed.

II.5.2.1.2 Behavioral procedure

Head-fixed animals were trained to fixate a central fixation point, using operant conditioning with positive reinforcement. Eye position was acquired thanks to an eye tracking system (EyeScan®), and its vertical and horizontal components were digitized at 250 Hz. After 1000 ms fixation, an array of 16 oriented gabors (5° wide, 1 cycle/deg) forming a 36° per 36° square grid was displayed (see Fig. II.5.1). All gabors had the same orientation at -45, -15, 15 or 45 degrees from the vertical, except one. This latter stimulus, called the SINGLETON stimulus, was located in one of the four most central positions in the array, and could be -45 or 45 degrees from the vertical (See Fig. II.5.1). As a consequence, the difference in orientation between the SINGLETON and distractors could be 0°, 30°, 60° or 90°. This difference in orientation between the SINGLETON and the distractors determined the feature contrast (FC) level of the SINGLETON. This FC level and the location of the SINGLETON were pseudo-randomly interleaved. Three hundred ms after the onset of the gabor stimuli, the fixation point was extinguished. Monkeys were rewarded for making a saccade towards any Gabor stimulus within 500 ms after fixation point extinction. Critically, the amount of reward received did not depend on the fact that the monkey fixated the SINGLETON stimulus or not. If the monkey broke fixation before the fixation point disappeared, the trial was immediately aborted, and the monkeys failed to receive the juice reward. A special procedure was used to reduce

the risk of potential saccadic biases and discourage monkeys from looking repetitively at the same location. Saccade history along the 10 last trials was used to control reward value. Reward was maximal when the first fixated stimulus after fixation point disappearance was amongst the two least fixated stimuli in the history, and minimal in the reverse situation (25% of maximal reward).

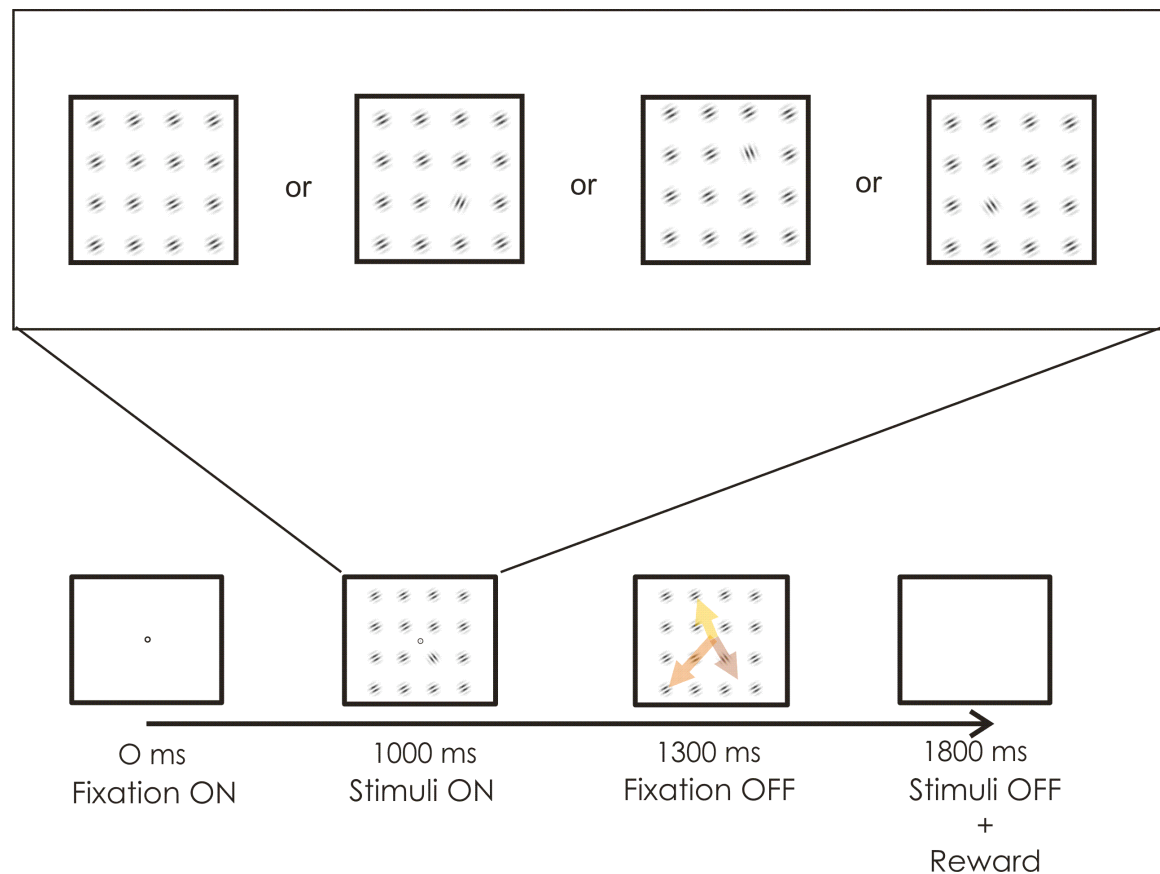


Figure II.5.1

Schematic description of the paradigm. The different epochs and the timing of the task are represented in the lower part of the figure. The inset, in the upper part of the figure, illustrates the different possible feature contrast conditions. From left to right, the represented feature contrast values are 0°, 30°, 60° and 90°.

II.5.2.1.3 Data collection

Single units were recorded with glass-coated tungsten electrodes (FHC). The electrodes were introduced through guide tubes positioned in a 1-mm-spaced grid (Crist et al. 1988) and were positioned with a hydraulic micromanipulator (Narishige). A single electrode was used during each recording session for monkey S, whereas signal was recorded simultaneously from four electrodes for monkey N. Action potentials were amplified, filtered, and discriminated using a computer-based online window discriminator (AlphaOmega) and further processed by offline cluster-based analysis. Recordings were done on the surface of the cortex lying just laterally from

the IPS. All recording sites were located on the posterior part of the IPS/inferior parietal lobule.

The activity of neurons from area 7a ($n = 67$ for monkey S and $n = 65$ for monkey N) was recorded. We used the depth of the penetration, the size of the receptive field of the cell and the timing of its saccadic response as criteria to confirm that we were recording from area 7a. Among these, 94 cells (71.2%) had a significant visual response in the main task and were selected for analysis. The receptive fields of these cells were determined at the end of the recording sessions by a computer assisted procedure. In this procedure, a single gabor stimulus was displayed on each potential location ($n=16$), chosen pseudo-randomly, during steady fixation.

II.5.2.1.4 Analysis of neural activity

We generated a spike density function for each trial by convolving action potentials with a Gaussian filter (SD : 10 ms). All analyses were conducted on 10 ms bins aligned either on stimuli onset or first saccade onset. In cell population analyses, activity in each time bin was normalized. Non parametric analyses of variance tests (Kruskal-Wallis, Friedman and Wilcoxon) and non parametric correlation tests (Spearman) were used to analyze cell data.

II.5.3 RESULTS

II.5.3.1 Behavior

We expected the monkey's oculomotor scanning behavior to be influenced by the presence of the SINGLETON amongst the distractors. When analyzing the probability of the monkey to fixate the SINGLETON, we found overall that the SINGLETON was more likely to be fixated than any other location for monkey S only (SINGLETON fixation probability: monkey S: $33\pm 8\%$, t-test against 25%: $p < 0.0001$; monkey N: $25\pm 2\%$, t-test against 25%: $p = 0.56$). However, this probability was affected by several factors. On a session by session basis, feature contrast (FC) affected SINGLETON selection probability mostly for monkey S (chi square test: $p < 0.05$ in 45% (19/42) of recording sessions of monkey S and 23% (4/17) of sessions for monkey N), and SINGLETON location affected SINGLETON selection probability for both monkeys (chi square test: monkey S: $p < 0.05$ in 79% (33/42) of sessions; monkey N: 89% of sessions (15/17)). To investigate SINGLETON selection probability across all sessions, we performed an RM ANOVA on all sessions for each monkey, with FC and SINGLETON location as independent variables. We found a significant main effect of SINGLETON location (Monkey S: $F_{3,123} = 51.70$, $p < 0.0001$; monkey N: $F_{3,48} = 7.45$, $p < 0.0001$), FC (Monkey S: $F_{6,246} = 12.20$, $p < 0.0001$; Monkey N: $F_{6,96} = 2.11$, $p = 0.059$) and a significant interaction between both factors (see Fig. II.5.2; Monkey S: $F_{18,738} = 4.99$, $p < 0.0001$; Monkey N: $F_{18,288} = 2.58$, $p = 0.0005$) for both monkeys. This effect was complex and different in both monkeys. While monkey S, fixated the SINGLETON mostly for intermediate FC levels, SINGLETONs with these FC levels were avoided by monkey N. Moreover, both monkeys exhibited a spatial bias, some locations being fixated more often than others. We did not expect the two monkeys to exhibit such differences in saccadic

behavior. In the following, we analyzed separately the cells of each monkey. We tried to determine whether neural activity in area 7a depends on the visual stimulation conditions independently of behavior, or whether it reflects the influence that visual stimulation has on behavior.

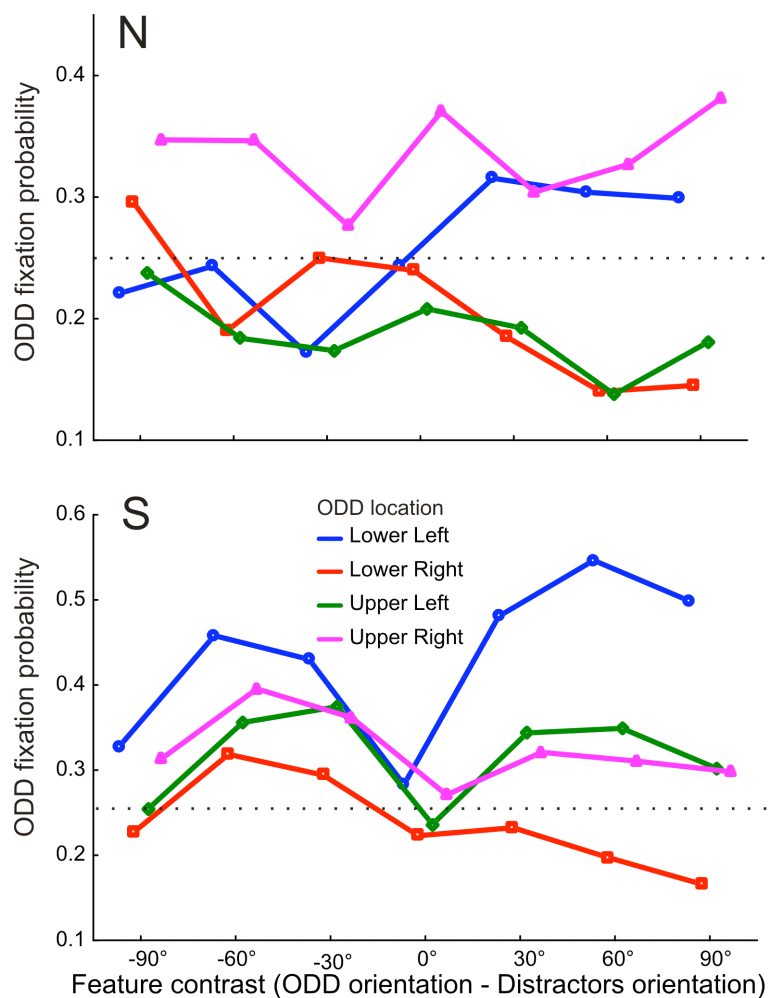


Figure II.5.2

SINGLETON fixation probability (Y axis) as a function of feature contrast (X axis) and **SINGLETON** location (color code) for both monkeys.

II.5.3.2 Neural activity

Using single gabor stimuli to estimate the receptive field (RF) size and location, we found that the mean number of effective stimulus locations across the neuronal population was 11.2 ± 3.8 (mean $\pm$ SD), out of 16 possible locations. Thus receptive fields were very large and bilateral, as expected from 7a neurons (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990). Amongst all cells, only 5 responded differently to single stimuli appearing at each of the four possible **SINGLETON** locations (non parametric Kruskal-Wallis test, $\alpha = 0.05$).

In order to analyze the representation of visual salience in area 7a, we initially determined the effect of a priori conditions (feature contrast and position of the **SINGLETON** stimulus) on neural activity. For each recorded cell, we conducted a 2-way Friedman non-parametric test with orientation difference and position as

independent factors (4x4) and mean spike rate as dependent variables, in successive 10 ms bins. Two different time windows were analyzed, aligned either on stimulus (from 0 to 300 ms after stimulus onset) or saccade onset (from -200ms to +100ms with respect to saccade onset). When aligned on saccade onset, no clear effect of any of the independent variables was observed. With regard to the alignment with stimulus onset, we found a small effect of position of the SINGLETON (max 17% of cells, $\alpha = 0.05$), and a small feature contrast X position interaction (max 15% of cells) but a more significant effect of feature contrast was observed, with up to 28% of the cells responding differently to different feature contrast levels (see Fig. II.5.3). In the following paragraphs, we will analyze this last FC effect in more detail.

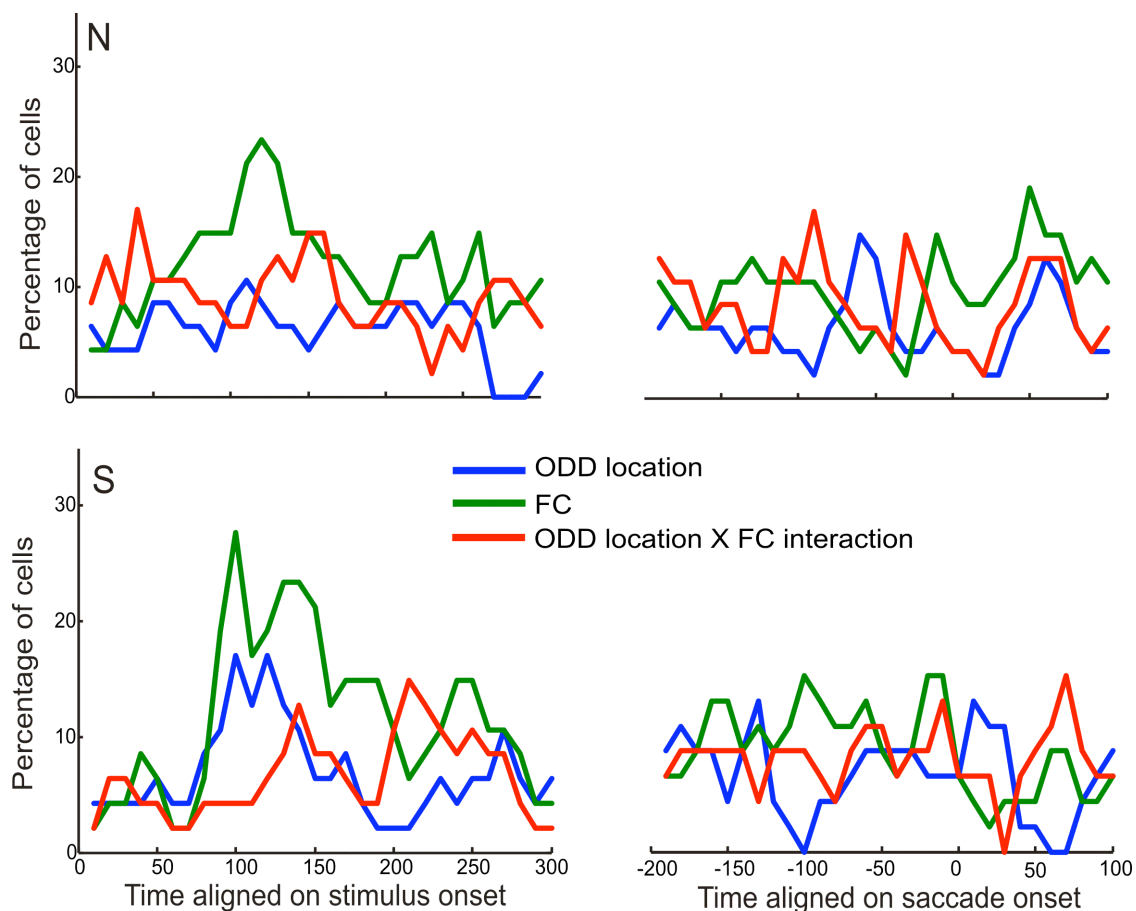


Figure II.5.3

Percentage of cells exhibiting a significant effect of either **SINGLETON** location (blue), feature contrast (green) or an interaction between these two factors (red). These percentages are shown as a function of timing with respect to stimulus onset (left part of the graphs), or saccade onset (right part of the graph).

Two hypotheses can be proposed to explain the effect of FC on neural activity. Activity could be proportional to the difference in orientation between the SINGLETON and distractor, reflecting a purely bottom-up phenomenon, or alternatively, it could reveal a correlation between the actual conspicuity of the SINGLETON - i.e. its tendency to attract gaze - and neural activity. To determine

which of these hypotheses was true, we conducted a regression analysis (multiple Spearman correlation), for each cell exhibiting a significant feature contrast effect, between the neural activity and, on the one hand, FC per se (orientation difference between SINGLETON and distractor), and on the other hand, the SINGLETON selection probability associated to each of the FC levels. This analysis was restricted to the time window during which more than 15% of the cells were modulated by FC in both monkeys (between 100 and 150 ms after stimuli onset). We then compared the distribution of the partial correlation coefficients for FC and SINGLETON selection probability. The two distributions differed significantly in both monkeys (see Fig. II.5.4; Kolmogorov-Smirnov test: monkey N : $p < 0.0001$; monkey S: $p < 0.0001$), Rho correlation coefficients being centered on a positive value for SINGLETON selection probability (Monkey S: median $\pm$ IQR = 0.30 ± 0.61 ; monkey N: median $\pm$ IQR = 0.29 ± 0.43) and on zero for FC (Monkey S: median $\pm$ IQR = -0.04 ± 0.37 ; monkey N: median $\pm$ IQR = 0.00 ± 0.22), suggesting that cell activity was affected by selection probability and not FC. An example of a cell (monkey S) whose activity is correlated to the SINGLETON selection probability is illustrated in Figure II.5.5. The same result was obtained when considering the whole cell population (Kolmogorov-Smirnov test: $p < 0.0001$ for both monkeys; median $\pm$ IQR of Rho for SINGLETON selection probability: 0.14 ± 0.64 and 0.16 ± 0.64 for monkeys S and N respectively; FC: -0.04 ± 0.57 and 0.01 ± 0.40 for monkeys S and N respectively).

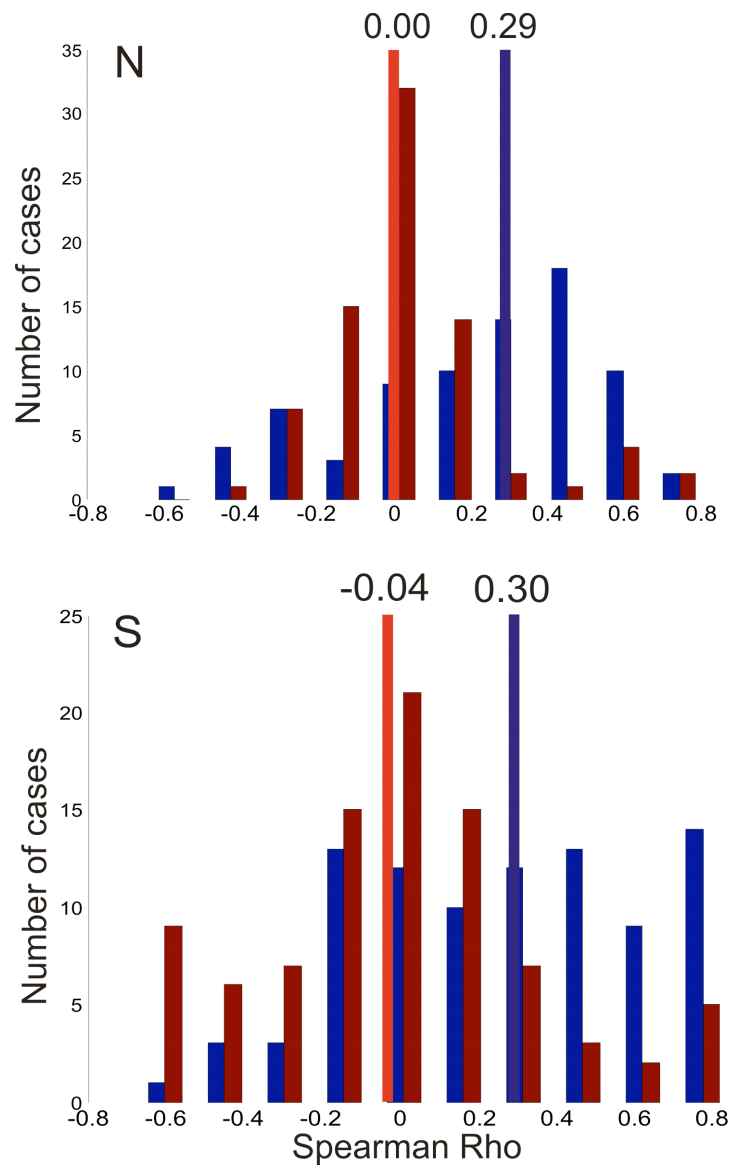


Figure II.5.4

Distribution of the spearman Rho coefficients resulting from the correlation between cell activity and either feature contrast (red) or saccadic preference (blue). The median of these coefficients is illustrated by a vertical line of the corresponding color.

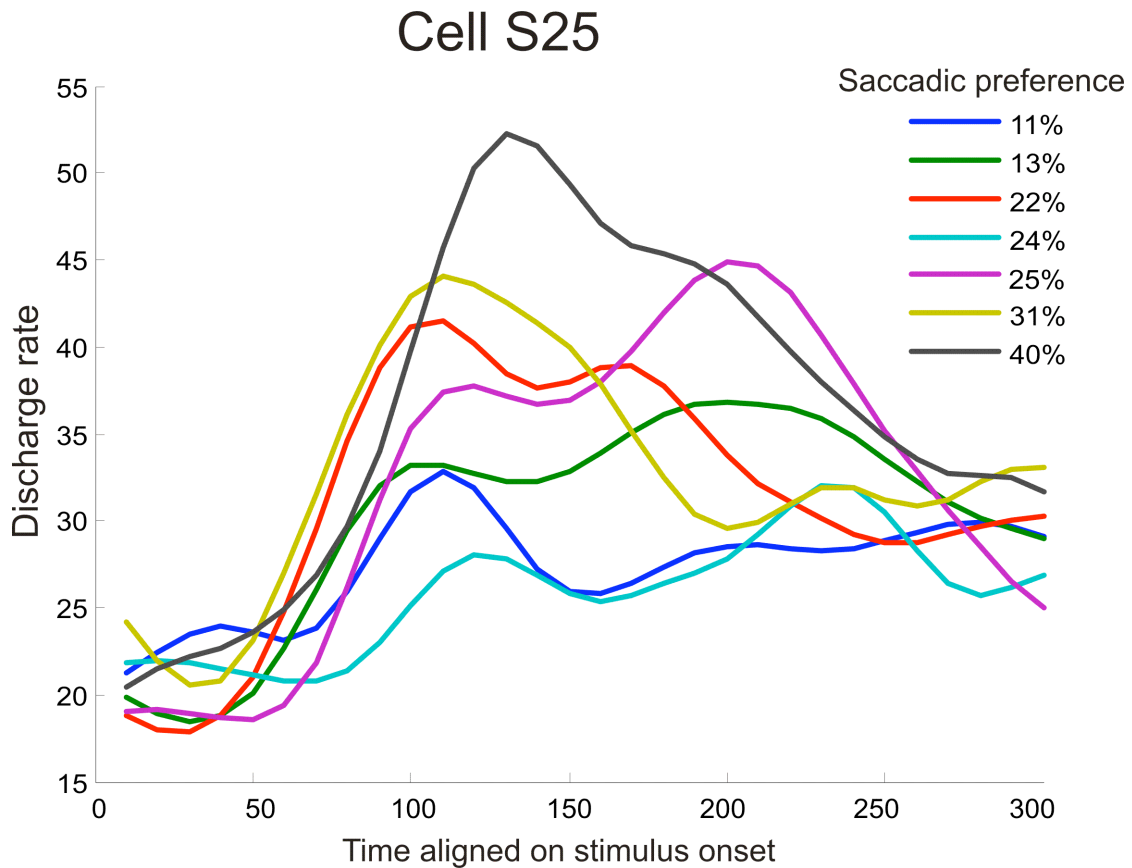


Figure II.5.5

Discharge rate as a function of time, aligned on stimulus onset, of an example cell exhibiting a significant effect of saccadic preference. The different saccadic preference values are illustrated by the color code. A 25% saccadic preference corresponds to chance selection rate. Therefore, in the present case, the SINGLETON leads either to evitement or capture by gaze.

We then assessed the correlation between SINGLETON selection probability and neural activity aligned on stimulus onset, on each time bin, on the whole cell population. We still found a significant positive correlation in both monkeys (see Fig. II.5.6; Monkey S : all $p < 0.05$, max Spearman Rho = 0.24, 7 significant time bins : 90-170 ms ; Monkey N : all $p < 0.05$, max Spearman Rho = 0.18, 4 significant time bins : 110-140 ms). For monkey N only, we also found a later negative correlation (all $p < 0.05$, min Spearman Rho = -0.13, 3 significant time bins : 250-270 ms).

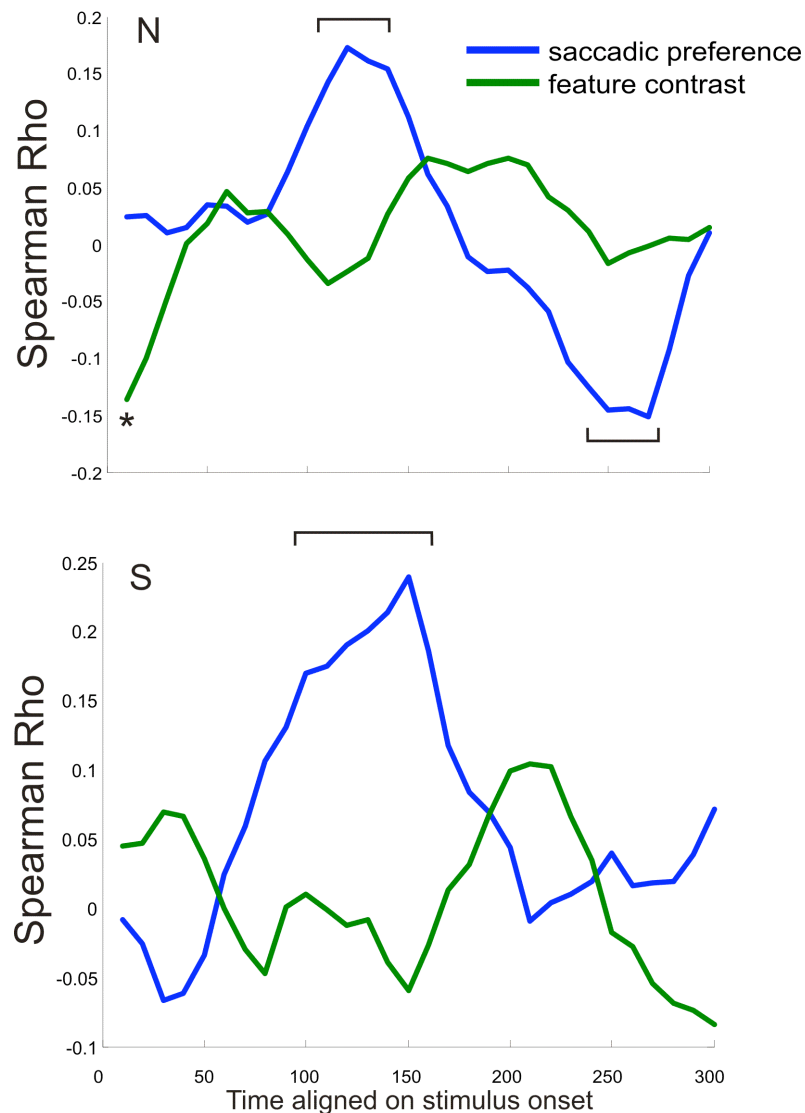


Figure II.5.6

Correlation between cell activity and feature contrast (green), or saccadic preference (blue), at the population level, as a function of time, aligned on stimulus onset. Significant coefficients are marked by brackets.

Area 7a cells are known to exhibit some selectivity for certain saccadic directions, even though this selectivity arises mainly in the post-saccadic period (Andersen, Bracewell, et al., 1990; Andersen, Essick, & Siegel, 1987; Barash, et al., 1991; Motter & Mountcastle, 1981). In the present study, when aligned on stimulus onset, the activity of up to 28% (monkey N, 280-290 ms time bins) and 19% of the cells (monkey N, 270 ms time bin) exhibited selectivity for some saccadic directions. This shows that around 300 milliseconds after stimulus onset, the saccadic target was already selected and that this selection affected cell discharge in area 7a. The proportion of selective cells increased to 40% (monkey N, 70-80 ms after saccade) and 32% (monkey S, 90 ms after saccade), when aligned on saccade onset, in the post-saccadic time window. When considering the whole cell population, a significant

effect of saccadic direction was observed in the visual (Friedman non-parametric test: monkey S: 300 ms time bin, $p = 0.032$, monkey N: 70-90 ms time window, all $p < 0.05$), and post-saccadic time windows (monkey S: 50-60 ms after saccade, all $p < 0.05$; monkey N: 30-40 and 90 ms time bins, all $p < 0.05$). Whereas leftward saccades induced significantly higher activity in monkey N cells (Wilcoxon tests : all $p < 0.05$), cells of monkey S preferred rightward saccades (Wilcoxon tests : all $p < 0.05$). Therefore, surprisingly, ipsilateral saccades induced higher activity in both monkeys.

This selectivity of the cell responses to saccadic direction could bias the correlation between neural activity in area 7a and saccadic preference that we showed before. In order to get rid of this potential confound in our results, we performed the correlation between cell activity and SINGLETON fixation probability as described above but with the addition of a covariate representing the saccade direction. The correlation remained significant (Monkey S: $p \leq 0.05$ for 80-150 ms time window; Monkey N: $p \leq 0.05$ for 120-140 ms time window).

II.5.4 DISCUSSION

The spatial selectivity of area 7a cells to salient stimuli has been investigated in several previous studies (Constantinidis & Steinmetz, 2001a, 2001b, 2005). Here, we show that the response of area 7a to the presentation of a unique stimulus embedded in an array of multiple identical stimuli does not merely depend on the feature contrast of that stimulus but rather on the incentive for the animal to look at it. The present findings are compatible with the idea that area 7a could be part of the network involved in the selection of saccadic and attentional targets, together with area LIP, FEF and superior colliculus (Carello & Krauzlis, 2004; Goldberg, et al., 2006; Thompson & Bichot, 2005). Among these structures, area 7a occupies a singular position with respect to eye movement control. First, in striking contrast to the other areas, microstimulation of area 7a in the dark does not induce saccades (Thier & Andersen, 1998). Second, connections between area 7a and oculomotor structures are weak (FEF) or inexistent (SC) connected to oculomotor structures (Andersen, Asanuma, et al., 1990; Asanuma, et al., 1985). Third, saccade-induced activity in area 7a appears after and not before the saccade (Barash, et al., 1991; Motter & Mountcastle, 1981). These peculiar features suggest that, if involved in salience computation, area 7a should intervene upstream in the process leading to the selection of the saccadic target, i.e. on the sensory side of the sensory-motor transformation process. Moreover, cells in area 7a have no or only a very broad spatial selectivity (Andersen, Asanuma, et al., 1990) that varies as a function of the task at hand (Chafee, et al., 2007; Crowe, et al., 2005), exhibit long visual response latencies (Barash, et al., 1991) and are connected mainly with high-level visual and limbic areas (Jouve, et al., 1998). These features suggest that area 7a could be involved in the cognitive control of eye movements, and possibly attention, depending on complex factors such as motivation, anticipation, social interactions, ... This hypothesis is in line with the important connectivity between area 7a and the posterior cingulate, which could have a role in the evaluation of risk and potential reward (McCoy, Crowley, Haghighian, Dean, & Platt, 2003; McCoy & Platt, 2005). In contrast, the characteristics of area 7a cells are not in agreement with a role of this structure in the implementation of gaze or attention capture by conspicuous stimuli (Remington, Johnston, & Yantis, 1992). Indeed, it is sensible to assume that this later function would require connections to low-level visual areas and shorter response latencies.

The hypothesis of a role of area 7a in the computation of cognitive factors of salience

can help to explain the small magnitude of the response modulation by salience observed in the present study. Indeed, we assessed here the correlation between cell activity and the probability to make an eye movement to the singleton stimulus. This probability is likely to depend on a multiplicity of factors. If area 7a, as we assume, is involved in the computation of only some of these factors, the correlation of the activity of area 7a cells with global salience, resulting from the integration of all factors, is expected to be small and variable. Further studies should address this question by dissociating the different factors influencing saccadic target selection, and determining separately the influence of each of these factors on the activity of the cells in area 7a.

III CONCLUSIONS

In the above studies, I tried to investigate how relevance and conspicuity interact to influence attentional allocation during visual exploration and how these factors are processed in the brain. In the three first studies I addressed three questions, central to visual search theory, which to my view lacked direct experimental evidence. The first two studies confirmed the leading view that attentional selection is guided by goal-directed and stimulus-driven factors and that this selection relies on a winner-take-all mechanism. In addition they provided some details about the role of grouping in conjunction search, the relationship between attentional selection and target detection and the shape of the attentional spotlight. In contrast, the results of the third study contradicted the widely held serial models of visual search by showing that difficult search tasks exhibiting clearly positive set-size slopes were performed in the absence of serial shifts of attention.

If we try to integrate these results into a coherent view of how visual search is processed, we can first mention that these findings provide strong support for the parallel models of visual search in which target detection does not necessarily require the scanning of the search display by attention (Chapter II.3). Instead, attention is allocated to a single (Chapter II.2) relevant and/or conspicuous (Chapter II.1) item during the search process and does not move thereafter. When search items differ from each other along two feature dimensions, in so-called conjunction searches, these features are first integrated to compute item relevance but after some delay, all items exhibiting the distractor feature in one dimension (in our study, the yellow color) become grouped and are excluded altogether from attentional selection (Chapter II.1). The extended shape of the attentional spotlight induces co-selection of neighboring items, especially when located along a common horizontal axis (Chapter II.2). Whether or not the target is selected by attention during the search process influences greatly the probability to detect the target (Chapter II.1). Results from Chapter II.1 even suggest that attentional selection of the target is necessary for detection, even though the data are not sufficient to demonstrate this statement. This interpretation, however, appears inconsistent with the conclusions of Chapter II.3 that attention does not shift during a standard difficult search task and that target detection in such a task relies on parallel processes. Indeed, if detection relies so critically on attentional allocation as suggested by results of Chapter II.1, and that attention does not shift during the search process as shown in Chapter II.3, it would follow that attentional allocation at the beginning of the trial determines entirely the success or failure of the search in the trial. Alternatively, the conclusion that attentional selection is mandatory for target detection might be overstated. In that case, as suggested by parallel models of search (Verghese, 2001), target detection would rely on parallel mechanisms and attention would only influence detection by improving the signal to noise ratio of the selected items, without being necessary for detection. Along the same line, previous studies have shown that attentional selection is not mandatory for visual tasks such as the discrimination of complex images (F. F. Li, et al., 2002; Rousselet, et al., 2002). The exact interaction between attentional selection and detection is a complex and important question that will require further investigation.

The absence of attentional shift during difficult visual search task performance may appear puzzling, given the fact that under ecological circumstances, we perform visual search by successively moving the eyes. As mentioned in the introduction of this thesis (paragraph I.1.1.3), previous studies have shown that visual search performance can be increased when preventing observers from making eye

movements during search (Zelinsky & Sheinberg, 1997). This counter-intuitive finding suggests that the computational cost associated with the programming and implementation of eye movements in some cases exceeds its benefit. The results of Chapter II.3 suggest that this might be true for attentional shifts as well. After extensive training, parallel detection processes would become very efficient in discriminating target-present and target-absent trials. In that case, displacing spatial attention successively to the most relevant items would be counter-productive. So, the reliance on serial or parallel mechanisms during search would depend on a balance between parallel search efficiency and the benefit associated with attentional shifts. Under this assumption, an experimental prediction would be that after training on a specific dual search task similar to the one used in Chapter II.3, changing the target feature, or increasing stimuli eccentricity would lead to a reinstatement of serial attentional shifts, because of a decrease in the efficiency of parallel mechanisms for target detection. Another interesting experiment allowing to test this hypothesis would consist in comparing performance in overt and covert versions of several visual search tasks, using the same technique as that described in Chapter II.3. We expect that visual searches that are performed better in covert condition should show no evidence of attentional shifts, whereas visual search tasks that benefit from eye movements should still rely on attentional shifts when performed covertly.

These three first studies pointed out the efficacy of the dual task approach in investigating visual search mechanisms. This technique, in addition to being a more direct way of unveiling attention allocation, allows reaching a higher level of spatio-temporal precision in the analysis of attentional selection. Consequently, this approach could be used instead of, or in association with classical reaction time and accuracy measurements to address the question of attentional allocation during any given visual task (see for example (Scholte, Spekreijse, & Roelfsema, 2001; Sears & Pylyshyn, 2000)). However, one must be particularly vigilant with respect to one potential flaw inherent in the use of dual tasks. Indeed, it can never be completely excluded that the addition of the letter task modifies the processing of the other visual task under investigation. In order to minimize this issue in the present studies, participants were always asked to focus mainly on the visual search task. This specific request was efficient in reducing the influence of the letter task on the visual search task, as shown in Chapter II.3. In that condition, visual search accuracy and set-size slopes were unaffected by the addition of the letter task, providing strong evidence that the visual search task processing was not significantly altered in the dual task.

In the second part of this thesis, I addressed the question of how these salience factors are processed in the brain. I focused mainly on one brain structure, namely the Angular Gyrus and its supposed homolog in the monkey brain, area 7a. In the monkey electrophysiology study (Chapter II.5), we found that, when multiple stimuli are presented, neuronal activity in this area was proportional to the incentive of the animal to look at the unique stimulus in the display, i.e. to its salience. In contrast, neural discharge rate in area 7a did not depend on the physical properties of the stimuli or on their feature contrast. While, in this study, we did not try to isolate stimulus-driven from goal-directed effects, we found in the TMS study (Chapter II.4) that Angular Gyrus seemed to be more involved in goal-directed than stimulus-driven salience guidance factors computation. However, as discussed in the Introduction, we do not believe that area 7a / Angular Gyrus can be regarded as a salience map *stricto sensu*. Even set aside the lack of functional evidence for this assertion (i.e. the absence of stimulation and inactivation studies in monkeys), spatial specificity in this area is too variable and too broad to be compatible with such a function. In addition, we would expect a salience map to be directly connected to the oculomotor structures involved in eye movements and attentional allocation, which is not the case for area 7a. We could imagine instead that this structure is involved in the

processing of high-level cognitive influences on visual exploration, such as the role of anticipation and motivation. The absence of effect of Angular Gyrus disruption on stimulus-driven guidance factors is in line with this hypothesis. These ideas could be the topic of future studies.

In addition, in the TMS study (Chapter II.4), we explored the role of the human homologue of FEF in salience computation. Under the assumption that FEF would be downstream of Angular Gyrus in the process of attentional selection, we hypothesized that FEF perturbation would lead to a deficit in attentional allocation irrespective of salience, and hence we expected to find a global effect of FEF disruption on letter detection performance, independent of salience factors. Instead, we found that FEF disruption led to consequences comparable to Angular Gyrus disruption with a modification of the attentional allocation as a function of salience factors. However, in contrast to Angular Gyrus, FEF seems to be involved in both stimulus-driven and goal-directed guidance factors computation, a finding compatible with the idea that FEF is closer to the actual decision stage of where to look or to attend next. Indeed, this function requires the integration of both goal-directed and stimulus-driven guidance factors.

In conclusion, the salience map model seems to constitute a simple and valuable approach to the study of visual exploration, providing experimental predictions that are easy to verify. However, whether this model represents an accurate description of the processing taking place in the brain remains an unresolved question. Several lines of evidence suggest that the correspondence between the salience map model and visual processing in the brain might be only partial. As proposed by Jacqueline Gottlieb in a recent review, the function of LIP might not be limited to the control of eye movements and attention but might extend to more cognitive, abstract functions (J. Gottlieb, 2007). For instance, in addition to salience computation, this structure could be used to compute magnitude (Roitman, et al., 2007; Walsh, 2003) or to categorize sensory inputs (D. J. Freedman & Assad, 2006). This idea could be extended to the other structures involved in the attentional network exposed above, such as FEF or superior colliculus. Besides, another interesting alternative to the salience model, as explained in the Introduction (paragraph 1.1.1), has been proposed by Geisler. According to his model, eye movements are made in order to optimize the gathering of visual information, taking into account the absence of acuity homogeneity across the retina. In favor of this model, Najemnik and Geisler showed that the statistics of eye fixation across natural images suggest that the visual system takes into account this retinal non-homogeneity (Najemnik & Geisler, 2008). More generally, in contrast to the salience model, this model predicts that relevant peripheral stimuli will not always attract gaze, if the predicted information gain associated with this saccade is not sufficient. Interestingly, the results obtained from monkey S in the electrophysiology study of the present thesis are compatible with this theory. Indeed, we found that fixation probability did not increase monotonically with feature contrast but exhibited a bell shape. This suggests that very conspicuous stimuli do not need to be fixated because they are discriminated with enough accuracy in peripheral vision, in accordance with Geisler's model. In future experiments, this effect could be investigated more systematically. Confirming the idea that saccadic targets are selected in order to optimize visual information gathering and not simply as a function of salience would ask for reconsideration of previous findings regarding the function of the saccadic/attentional network and would motivate new approaches to the study of the mechanisms involved in saccadic and attentional allocation.

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