Breaking the duality of vision: An experimental study of the interaction between perception and action

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List of abbreviations

ADM	Abductor digiti minimi
AIP	Anterior intraparietal area
ANOVA	Analysis of variance
APB	Abductor pollicis brevis
BOLD	Blood-oxygen-level-dependent
CIP	Caudal intraparietal area
CSE	Corticospinal excitability
DLPF	Dorsolateral prefrontal cortex
EMG	Electromyography
FDI	First dorsal interosseus
fMRI	Functional magnetic resonance imaging
GLMM	Generalised linear mixed model
ITI	Inter-trial interval
IPL	Inferior parietal lobule
IPS	Intraparietal sulcus
LGN	Lateral geniculate nucleus
LOC	Lateral occipital cortex
M1	Primary motor cortex
MEP	Motor evoked potential
MGA	Maximum grip aperture
MT	Middle temporal area
MSE	Mean square error
MST	Medial superior temporal area
PMv	Ventral premotor cortex

PMd	Dorsal premotor cortex
PSE	Point of subjective equality
RL	Response latency
rMT	Resting motor threshold
SD	Standard deviation
SE	Standard error
SMA	Supplementary motor area
SPL	Superior parietal lobule
TMS	Transcranial magnetic stimulation
TVS	Two visual systems
V1	Primary visual cortex
V2	Secondary visual cortex
V4	Visual area 4

General Introduction

Humans experience vision as a unitary phenomenon. When looking at a cookie to identify it as the favourite kind, and when keeping eyes on it to pick it up and put it into their mouth, they keep seeing the same cookie. Yet, since the 60s, research has brought evidence suggesting that vision is not a single and unified system. Instead, the mammalian visual system is dual, meaning that visual information is processed in parallel along mainly two different pathways. The reasons for the visual system to use such parallel processes have been discussed with great interest among the scientific community since their first description.

First, there was evidence for different visual components, such as colour and movement, being processed along independent and parallel subcortical pathways that provide input, respectively, to an occipitotemporal (ventral) stream responsible for object identification and an occipitoparietal (dorsal) stream responsible for object localisation (Livingstone & Hubel, 1987a; 1988; Ungerleider & Mishkin, 1982). Then, the observation that brain lesions to ventral areas were associated with impaired object recognition but with preserved reaching and grasping abilities (Milner et al., 1991), while lesions to dorsal areas were associated with the reverse pattern (*e.g.*, Perenin & Vighetto, 1988), has led Goodale and Milner (1992) to revise the role of the ventral and dorsal streams. The two visual systems (TVS) model, still the most influential in the field, assumes that the role of the ventral and dorsal streams is not so much to process different visual attributes but to process visual information for distinct purposes: the ventral stream processes visual information in a scene-based reference frame to provide long-lasting representations of the world that allow *inter alia* object identification, whereas the dorsal stream estimates the

absolute metrics of a visual target and codes them in real-time in an observer-based reference frame to support the visual control of actions.

In healthy participants, much of the support for the idea that different processes are involved in perception and action comes from studies showing that grasping movements, unlike perceptual judgments, are resistant to illusions emerging from a contrast between an object and the surrounding elements (*e.g.*, Aglioti, DeSouza & Goodale, 1995; Haffenden & Goodale, 1998). These results suggest that action, unlike perception, computes the absolute metrics of the object without being influenced by the visual context. However, these results were subsequently challenged (*e.g.*, Franz & Gegenfurtner, 2008). The debate is further complicated by the difficulty to match perceptual and action tasks, as action benefits from additional sensory information (*e.g.*, visual and proprioceptive feedback of the acting hand) that might be used to correct the error introduced by the illusion as the hand approaches the object (Franz, Hesse & Kollath, 2009). Hence, current evidence does not allow drawing firm conclusions about possible differences in the nature of the visual processes serving perception and action. Moreover, most studies investigated the overt stages of action, leaving the nature of the covert stages and thereby of the mental representations underlying action unknown.

The present thesis aims to renew current views on the duality of vision and broaden the investigation to the interaction between the two streams. To achieve this goal and overcome previous issues, I will use judgments about how one would act, which are assumed to involve the mental simulation of the judged action without actually executing the movement (Jonhson, 2000). Thereby, these prospective action judgments offer an open window on the representations and processes underlying the covert stages of action. Moreover, they allow the direct comparison with the representations and processes underlying perception, while controlling for the

additional sensory information available during action execution. I will make use of these advantages to investigate two main issues. First, I will test within the context of size processing the assumption that perception and action require specific transformations of the visual input and investigate how the ventral and dorsal streams, as well as their interaction, contribute to these processes. Second, I will investigate further the nature of prospective action judgments and, in particular, how they integrate visual and sensorimotor information. The research will thus generate novel insight into the mechanisms by which the brain interacts with the visual environment to produce adaptive behaviour.

In Chapter 1, I will first review the history of the duality of vision, from the anatomical and physiological studies evidencing the existence of two independent streams to the lesional and neuropsychological studies attributing them different functions. I will then describe in more depth the dominant TVS model that assumes that the role of the ventral and dorsal stream are respectively perception and action. This section will include the data in favour of the model, but also their criticisms, and the resulting updates considering that perception and action interact with each other. A particular emphasis will be put on the *size-contrast illusion paradigm* and what it reveals about the nature of the processes involved in perception and action. Finally, I will take stock of what is known and not known about the differences between perception and action before presenting the literature on prospective action judgments suggesting they are an open window on the representation and processes of action. In Chapter 2 to 4, I will use behavioural methods to investigate the contribution of perceptual, motor, and semantic processes, as well as and their potential interaction, to perceptual and prospective action judgments. In Chapter 5 and 6, I will use neuroimaging, brain stimulation, and psychophysiological techniques to investigate the respective contribution of the ventral and dorsal streams to these two types of judgments. Finally, I will discuss the implications of my results

for the understanding of prospective action judgments and the TVS model, and I will end with a conclusion.

Chapter 1

State of the art

1. Anatomical and physiological duality

The idea of a divided visual system emerged from the discovery that two parallel pathways composed of different types of neurons, *i.e.*, the parvo- and magnocellular pathways, run from the retina to the visual cortex through the lateral geniculate nucleus (LGN). Although these pathways are combined within the visual cortex, segregation seems partly preserved beyond this area: the parvocellular pathway mainly flows into the temporal cortex, giving rise to the ventral stream, while the magnocellular pathway mainly flows up to the parietal cortex, giving rise to the dorsal stream (Livingstone & Hubel, 1987a; 1988). This section will review the anatomical and physiological properties of the subcortical parvo- and magnocellular pathways and their continuation into the cortex.

1.1 The parvo- and magnocellular pathways

1.1.1 At the level of the lateral geniculate nucleus

Studies in cats and primates showed that mainly two groups of neurons carry information about light from the rods and cones of the eyes to the visual cortex through the LGN. In particular, the midget and parasol cells of the retina project, respectively, on the parvocellular and magnocellular neurons of the LGN. Morphological and physiological differences are already observed between the midget and parasol cells. However, it is at the level of the LGN that the segregation

between the two pathways becomes most apparent as the parvo- and magnocellular neurons not only preserve the physiological properties of their respective precursor but are also physically separated. The synapses between the midget and parvocellular neurons are grouped within the four dorsal layers of the LGN, while the synapses between the parasol and magnocellular neurons are grouped in the two ventral layers of the LGN (*e.g.*, Norton & Casagrande, 1982; Figure 1). Therefore, it is at the level of the LGN that the anatomical and functional properties of the two groups of neurons have been mainly evidenced. The parvo- and magnocellular neurons have been shown to have opposite properties, indicating that they convey complementary visual information. These properties are summarised in Table 1.

First, as their name indicates, the magnocellular neurons are large, in comparison to the parvocellular neurons, which are smaller. Magnocellular neurons also have thicker axons with more myelin and a larger receptive field aggregating information from several rods and cones. Parvocellular neurons have thin axons with less myelin and a receptive field that is two or three times smaller aggregating information from fewer rods and cones. Therefore, magnocellular neurons are characterized by fast responses that decay more rapidly than parvocellular neurons, which respond in a more sustained manner. These temporal properties allow the magnocellular neurons to follow higher temporal frequencies than the parvocellular neurons (Derrington & Lennie, 1984; Lee, Creutzfeldt & Elepfandt, 1979; Maunsell et al., 1999; Schiller & Malpeli, 1978).

Besides, the parvocellular neurons have a higher spatial resolution than the magnocellular neurons (Derrington & Lennie, 1984; Hubel & Wiesel, 1960).

Moreover, most parvocellular neurons are sensitive to differences in wavelength, and thus colour, while most magnocellular neurons are insensitive to colour contrasts. Indeed, 80 to 90% of the midget and parvocellular neurons are

colour-opponent, meaning that they oppose the input they receive from red- and green-sensitive cones. For instance, one cell can be excited in its centre by long wavelengths (*i.e.*, red) and inhibited in its surround by intermediate wavelengths (*i.e.*, green). Besides these red-on centre and green-off surround cells, there also exists red-off centre and green-on surround cells, green-on centre and red-off surround cells, and green-off centre and red-on surround cells. By combining the information coming from different colour-opponent cells, the parvocellular pathway responds in a specific manner to differences in wavelengths. On the opposite, most of the parasol and magnocellular cells (and the remaining parvocellular neurons), are excited in their centre and inhibited in their surround by the same mixture of cone types (for an example of colour-opponent and broadband cell, see Figure 1). Thereby, they are sensitive to the amount of light, but similarly for all wavelengths (De Valois, Smith, Kitai & Karoly, 1958; Schiller & Malpeli, 1978). Even by combining information from multiple neurons, the magnocellular pathway does thus respond little specifically to differences in wavelengths and is therefore often considered as colour-blind (Hubel & Livingstone, 1990).

Finally, the magnocellular neurons are more sensitive than the parvocellular neurons to small differences in luminance. When the luminance of a stimulus differs from the surrounding luminance by less than 10%, the magno- show a higher response than the parvocellular neurons. However, the response of the magnocellular neurons increases rapidly with luminance contrast and saturates at about 10-15% luminance contrast. On the contrary, the response of the parvocellular neurons increases slightly and saturates at much higher luminance contrasts (Derrington & Lennie, 1984; Hubel & Livingstone, 1990; Kaplan & Shapley, 1986). Importantly, magnocellular neurons mediate sensitivity to luminance contrast only at low spatial frequencies, while parvocellular neurons mediate luminance contrast sensitivity over a large range of spatial frequencies (Legge, 1978; Tolhurst, 1975). Hence, the

difference in luminance contrast sensitivity between the magno- and parvocellular neurons might only prevail at low spatial frequencies (Skottun & Skoyles, 2008).

Table 1. *Summary of the physiological properties of the parvo- and magnocellular geniculate neurons.*

Property	**Parvocellular neurons**	**Magnocellular neurons**
Temporal frequency	Slow sustained responses with low conduction velocity	Fast transient responses with high conduction velocity
Spatial frequency	High	Low
Colour contrast	Sensitive due to colour-opponency	Very few sensitive due to broadband mechanisms
Luminance contrast	High more efficient > 10%	Low more efficient < 10% and for low spatial frequencies

It is worth noting that the parvo- and magnocellular neurons are not the only populations of geniculate cells. Visual information reaching the retina is processed by at least 17 distinct types of ganglion cells (Dacey, 2004). However, parvo- and magnocellular neurons are particularly well characterised, represent 80% of the total population of neurons projecting on the LGN, and carry most visual functions. Indeed, when selectively destroyed, very little vision remains (Dacey, 2000; Nassi & Callaway, 2009; Schiller, Logothetis & Charles, 1990). This is why I decided to constrain the scope of this thesis to these two main types of neurons.

1.1.2 At the level of the visual cortex

Early investigations of the parvo- and magnocellular pathways found that the anatomical separation observed at the level of the LGN was largely preserved at the level of the primary (V1) and secondary (V2) visual cortices of the primate. Indeed, the magnocellular geniculate neurons project to layer 4Cα of V1, which projects, in turn, to layer 4B, which then projects to the thick stripes of V2, while the parvocellular geniculate neurons project to layer 4Cβ of V1, which projects, in turn, to layers 2 and 3 of V1 (Chatterjee & Callawey, 2003; Dacey, 2000; Hubel & Wiesel, 1972; Livingstone & Hubel, 1987a; 1987b). In some sections of layers 2 and 3, neurons assemble in a cylindrical shape called "blob" (Hendrickson, Hunt & Wu, 1981). The parvocellular neurons of layer 4Cβ project to both the blobs and inter-blobs (*i.e.*, areas between blobs). It is worth noting that the blobs also receive magnocellular input. The blobs then project to the thin stripes of V2, while the interblobs project to the pale- or inter-stripes of V2 (Chatterjee & Callawey, 2003; Dacey, 2000; Hubel & Wiesel, 1972; Livingstone & Hubel, 1982; 1987a; Figure 1). However, subsequent investigations with improved tracers have shown that the parvo- and magnocellular projections are more intermingled within V1 than initially assumed. For instance, the parvocellular neurons, on their way from layer 4Cβ to layers 2 and 3, make synapses in layers 4Cα and 4B (Callaway & Wiser, 1996; Yabuta & Callaway, 1998). Similarly, the magnocellular neurons do not only send projections from layer 4Cα to layer 4B but also project to layers 2 and 3, probably in both the blobs and interblobs (Callaway & Wiser, 1996; Yoshioka, Levitt & Lund, 1994). The projections between V1 and V2 have also been shown to be less neat than initially described. For instance, although the thin and pale stripes receive most of their input from layers 2 and 3, they also receive input from cells in layers 4A and 4B (Sincich & Horton, 2002). Hence, the projection patterns within the visual cortex allow for potential convergence of the parvo- and magnocellular inputs.

Early investigations also evidenced physiological dissociations within the visual cortex that are in line with the initial anatomical separation described above. The cells in layers 4Cα and 4B of V1, in accordance with their magnocellular input, respond to low luminance contrast and low spatial frequencies, but not colour (Hawken, Parker & Lund, 1998; Livingstone & Hubel, 1984). Moreover, they seem able to elaborate more complex information from their magnocellular geniculate input as they are sensitive to motion direction (Gur & Snodderly, 2007; Hawken et al., 1998) and binocular disparity (Poggio & Poggio, 1984). On the opposite, cells in the interblobs, in accordance with their parvocellular input, are sensitive to colour but not motion direction. Interestingly, most interblob cells do not carry information about colour *per se*, as they are not colour-opponent, but respond well to edges defined by colour-contrast irrespective of the colours. Hence, it has been suggested that they pool the colour-coded parvocellular input to identify borders. Moreover, as their geniculate homologue, their receptive field is small, and they respond thus more efficiently to high spatial frequencies (Gouras & Krüger, 1979; Gur & Snodderly, 2007; Livingstone & Hubel, 1984). Although blobs receive both parvo- and magnocellular inputs, their physiological properties are more in line with those of the parvocellular neurons: they have been found explicitly colour-coded and non-selective for motion direction or orientation (Livingstone & Hubel, 1984). Both magno-recipient layer 4B and the parvo-recipient interblobs are selective for orientation (Gur & Snodderly, 2007). In V2, a high proportion of the cells in the thick stripes are selective for motion direction, orientation, and binocular disparity, as their precursors in layers 4Cα and 4B of V1. The thin stripes, as the interblobs, are sensitive to orientation, while the pale stripes, as the blobs, are sensitive to colour (Hubel & Livingstone, 1987a).

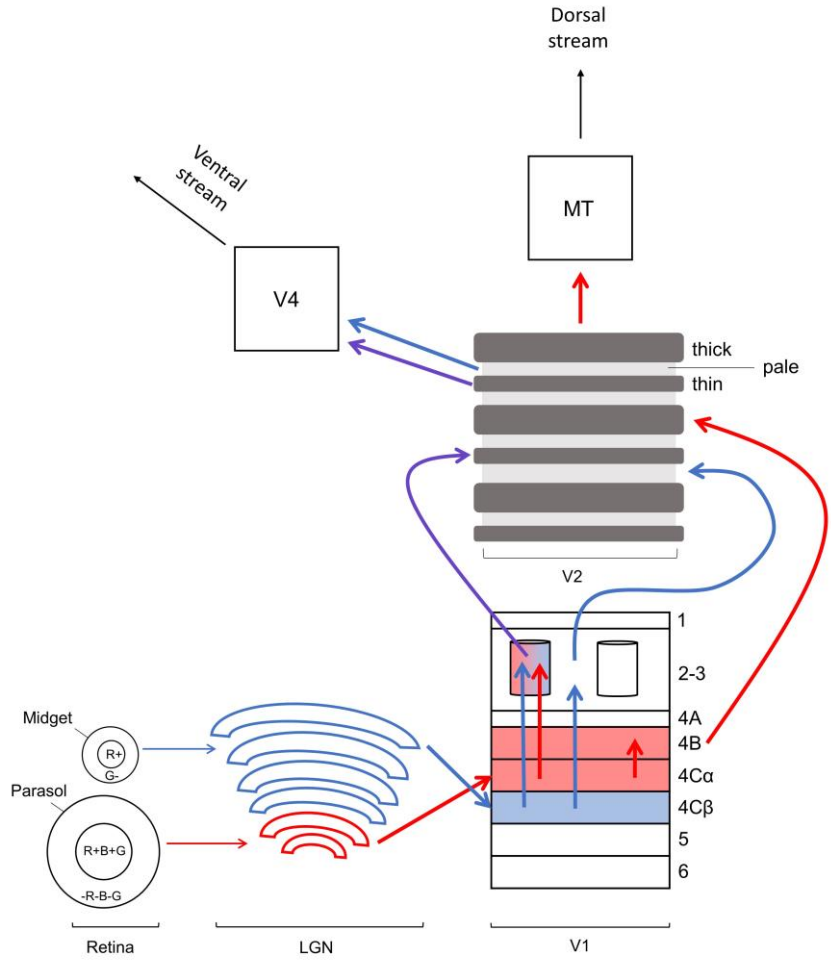

Figure 1. *Schematic representation of the parvocellular (blue) and magnocellular (red) pathways in the monkey as described by Linvgstone & Hubel (1987a). The parasol ganglion cells of the retina project to the two magnocellular ventral layers of the LGN, while the midget ganglion cells project to the four parvocellular dorsal layers. The magnocellular geniculate cells then project to layer 4Cα, which, in turn, projects to layer 4B and the blobs of layers 2-3 of V1. The parvocellular geniculate neurons project to layer 4Cβ, which, in turn, projects to the blobs and interblobs of layers 2-3. Layer 4B then projects to the thick stripes of V2, which provide input to MT and thereby the dorsal stream. The blobs project to the thin stripes of V2, while the interblobs project to the pale striped, both providing input to V4 and hence the ventral stream. LGN = lateral geniculate nucleus; V1 = primary visual cortex; V2 = secondary visual cortex; V4 = visual area 4; MT = middle temporal area.*

Based on these functional properties, Livingstone and Hubel (1987a) proposed that the magnocellular → 4B → thick stripes system supports depth and motion perception. The processing of orientation within this system might either support form perception or resolve ambiguities in motion and depth perception. The parvo- + magnocellular → blob → thin stripes system would support colour perception. Finally, the parvo → interblob → pale strip system, due to its high spatial resolution and sensitivity to orientation, would support form perception. However, as seen above, later studies showed that the parvo- and magnocellular projections in the visual cortex are actually more intermixed than initially assumed by Livingstone and Hubel (1987a; Callaway & Wiser, 1996; Sincich & Horton, 2002; Yabuta & Callaway, 1998; Yoshioka et al., 1994). Therefore, the specific physiological properties of the various portions of V1 and V2 might result from different connection patterns with the parvo- and magnocellular pathways rather than to an exclusive connection with one of the two subcortical pathways (Nassi & Callaway, 2009). Nevertheless, subsequent investigations also mitigated the tripartite division of the visual system at the functional level. Concerning V1, several studies could not find evidence for the colour-selectivity of the blobs *(e.g.*, Landisman & Ts'o, 2002; Leventhal, Thompson, Liu, Zhou & Ault, 1995). Moreover, some studies revealed that the magno-recipient layers 4Cα and 4B do respond to colour contrast though to a lesser extent than the other layers of V1 (Johnson, Hawken & Shapley, 2001), and are not the only layers within V1 to be selective to motion direction (Gur, Kagan & Snodderly, 2005; Hawken et al., 1988). Concerning V2, results are quite inconsistent, with some studies showing a high degree of functional segregation between the three types of stripes and others not (*e.g.*, Peterhans & Von der Heydt, 1993; Levitt, Kiper & Movshon, 1994; Gegenfurtner, Kiper & Festemaker, 1996).

Although the anatomical and physiological subdivision between the parvo- and magnocellular pathways proposed by Livingstone and Hubel (1987a) is less neat than first assumed, and this subdivision has been mainly characterised in monkeys and very little in humans, physiological studies on human perception are consistent with this subdivision. The study of the parvo- and magnocellular pathways in the human is challenging, mainly because the small size of the different subdivisions of the LGN and V1 makes it difficult to measure distinct signals from these subdivisions without invasive techniques. Most of the comprehension of the human visual system is thus inferred from observations in monkeys, and care must be taken when making such inferences, especially since the visual cortex might be more interconnected and disordered in humans (Tootell, Dale, Sereno & Malach, 1996). However, the subdivisions observed in the monkey are consistent with psychophysical studies on the perception of colour, high-resolution form, depth and motion in humans. These studies typically manipulate the visual properties of the stimulus to specifically activate the parvo- or magnocellular neurons. For instance, stimuli that contain colour but not luminance modulations (*i.e.*, equiluminant stimuli) should activate the parvo- but not magnocellular neurons. Under equiluminance, perception of motion (Cavanagh, Tyler & Favreau, 1984; Ramachandran & Gregory, 1978) and depth (Livingstone & Hubel, 1987a; Lu & Fender, 1972) were lost or significantly reduced, whereas perception of form was preserved. These psychophysical studies are thus in agreement with a magnocellular-dominant pathway involved in perception of depth and motion and a parvocellular-dominant pathway involved in perception of form.

1.2 The ventral and dorsal streams

After some parvo- and magnocellular convergence within the visual cortex, two new parallel streams of information run to distinct portions of the monkey cortex. A mixed pathway projects from the thin and pale stripes of V2 onto visual area 4 (V4), while a magnocellular-dominant pathway projects from the thick stripes onto the middle temporal area (MT). The projections from V4 continue to area TEO (*i.e.*, the posterior portion of the inferior temporal area) and then to the inferior temporal cortex, with a further projection to the ventral prefrontal cortex. This pathway projecting from the occipital to the temporal cortex is named the *ventral stream*. On the opposite, projections from MT continue their route to the medial superior temporal area (MST) to the posterior part of the inferior parietal lobule (IPL), with a further extension to the dorsolateral prefrontal cortex (DLPF). This pathway projecting from the visual to the parietal cortex is named the *dorsal stream* (Mishkin, Lewis, & Ungerleider, 1982; Mishkin Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982; Young, 1992).

Studies suggest that the human brain is similarly organised. In particular, studies using diffusion tensor imaging showed long parallel associative tracts running from the occipital to the parietal and temporal cortices in humans (Catani, Jones, Donato & Ffytche, 2003; Ffytche & Catani, 2005). The human ventral stream is very similar to the one evidenced in monkey, and comprises projections from V1 to V4 and then to the human homologue of the macaque inferior temporal cortex, *i.e.*, the lateral occipital cortex (LOC; Orban, Van Essen & Vanduffel, 2004). The comparative mapping of the higher visual areas in monkeys and humans indicate that the areas involved in reach and eye movements shifted from the lateral (monkey) to the medial (human) intraparietal sulcus, probably because the IPL has known more considerable expansion and gyrification in humans than in monkeys (Orban et

al., 2004; Grefkes & Fink, 2005). Therefore, the anatomical description of the dorsal stream differs slightly in humans compared to monkeys and is most often defined as the projection from V1 to V2, MT, MST, with the superior parietal lobule (SPL) as the endpoint. Studies tracing the human visual pathways indicate that the dorsal stream does not only receive input from the eye through the LGN and the cortical area V1 but also more directly through a subcortical pathway projecting from the eye to MT via the superior colliculus and the pulvinar (Leh, Chakravarty & Ptito, 2008; Sadun, Johnson & Smith, 1986; Figure 2).

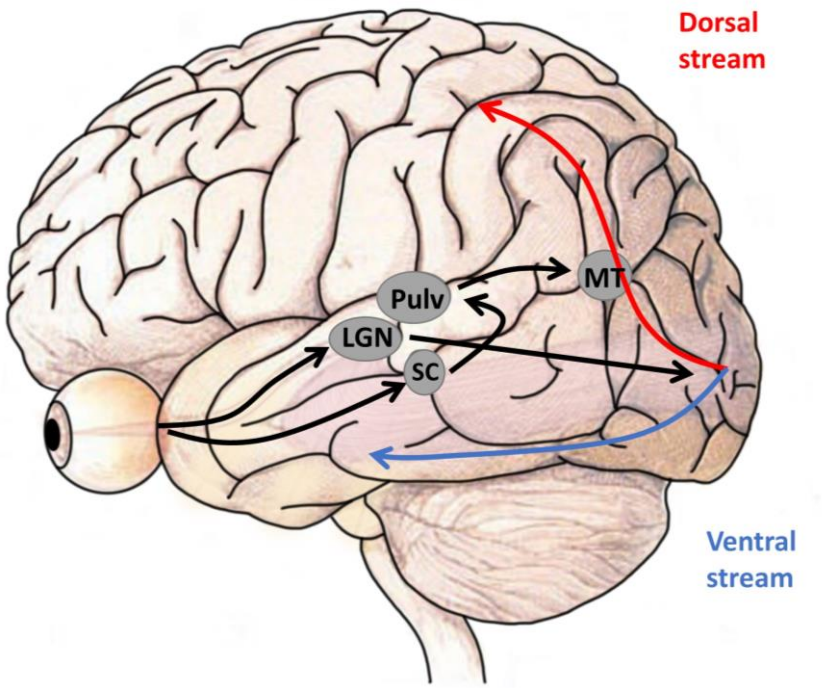

Figure 2. *Schematic representation of the ventral stream (blue) and dorsal stream (red) in humans. They both receive input from the eye via the LGN. The dorsal stream also receives direct input via the SC and then the pulvinar, which projects to MT and thereby bypasses V1. LGN = lateral geniculate nucleus; Pulv = pulvinar; SC = superior colliculus; V1 = primary visual cortex; MT = middle temporal area.*

In accordance with the idea that the ventral stream receives most parvocellular input, while the dorsal stream receives most magnocellular input, responses in ventral area V4 are characterised by colour and contour selectivity (Desimone, Schein, Moran & Ungerleider, 1985; Lueck et al., 1989; Pasupathy & Connor, 1999), while responses in dorsal area MT are characterised by motion direction and binocular disparity selectivity (Albright, 1984; DeAngelis, Cumming & Newsome, 1998; Maunsell & Van Essen, 1983). It is worth noting that activation to binocular disparity was found throughout occipital, temporal and parietal areas. However, the most significant activity and modulation to disparity were found in dorsal visual areas (*i.e.*, V3A and V7) and parietal areas (Georgieva, Peeters, Kolster, Todd & Orban, 2009; Minini, Parker & Bridge, 2010, Tsao et al., 2003). This segregation reflects the earlier segregation found between the pale and thin stripes of V2 on the one hand and the thick stripes of V2 on the other hand.

In summary, different aspects of the visual input are transmitted from the eye to the visual cortex through parallel pathways, the two main ones being the parvo- and magnocellular pathways. These pathways show opposite physiological properties so that they convey complementary information: the parvocellular pathway is sensitive to colour contrasts, low temporal frequencies and high spatial frequencies, while the magnocellular pathway is sensitive to high temporal and low spatial frequencies but very few to colour. Moreover, the magnocellular neurons are sensitive to low contrast, at least when spatial frequency is also low, while the parvocellular neurons are more efficient at high luminance contrast. After some convergence of the parvo- and magnocellular pathways in the visual cortex, two new parallel processing streams run to distinct portions of the cortex. A magno-dominant pathway specialised in motion and depth perception runs to the parietal cortex through the dorsal stream, while a mixed pathway specialised in colour and form perception runs to the temporal cortex through the ventral stream. The physiological

and psychophysical properties of the ventral and dorsal streams are in accordance with their respective input.

2. Functional duality: from input properties to output requirements

The anatomical substrate underlying the ventral and dorsal streams has been little questioned since it was initially defined by Ungerleider and Mishkin (1982), but the function attributed to each stream has been the topic of discussions since then. Initially, the ventral stream was proposed to be specialised for processing object identity (*i.e.*, "what"), and the dorsal stream for object location (*i.e.*, "where"). Goodale and Milner (1992) proposed to revise these functions after they observed that a brain-damaged patient with a lesion to the ventral stream was unable to report or describe the visual properties of an object, but was still able to use these properties to guide her actions towards the object. They took the emphasis off the input, *i.e.*, object identity *vs.* location, to put it on the output requirements, *i.e.*, perception *vs.* action. In this section, I will first describe the ancient "what *vs.* where" model and then relate the findings suggesting that the dissociation between the two streams is better explained by distinct outputs: "perception *vs.* action".

2.1 What *vs.* Where

Ungerleider and Mishkin (1982) 's proposal of a ventral stream specialised in object identification and a dorsal stream specialised in object location mostly built upon studies showing that, in both monkeys and humans, ventral lesions are associated with impaired object recognition, while dorsal lesions are associated with impaired visuospatial abilities.

The first evidence for the ventral stream being specialised in object identification came from studies on visual agnosia. Visual agnosia has been defined as a clinical impairment in object recognition following brain damage to the occipitotemporal cortex that cannot be explained by an elementary deficit in the visual modality (*e.g.*, loss in acuity or visual field) or a major impairment of another cognitive function. Patients with visual agnosia are typically impaired in describing and discriminating visual objects (*i.e.,* apperceptive visual agnosia) and/or identifying what for or how objects are used based on visual information (*i.e.*, associative visual agnosia). They remain, however, able to recognise objects through another sensory modality such as touch (Farah, 1990; Humphreys & Riddoch, 1987; Lissauer, 1890). Subsequent lesion studies in monkeys confirmed that the occipitotemporal cortex plays an indispensable role in object recognition. In particular, lesion to the inferior temporal cortex, the monkey homologue of the human LOC, caused severe deficits in the ability to discriminate between different objects. Interestingly, inferior temporal lesions did not affect the ability of the monkey to perform visuospatial tasks such as judging the distance of an object or grasping it (for a review, see Gross, 1973). Whereas occipitotemporal lesions primarily affect object recognition, human patients with damage to the right posterior parietal cortex are mostly impaired for visuospatial abilities (for a review, see Von Cramon & Kerkhoff, 1993). Similarly, posterior parietal lesions in monkeys did affect their visuospatial abilities but not their visual discrimination abilities (for a review, see Ungerleider & Mishkin, 1982).

Based on these observations, Ungerleider and Mishkin (1982) proposed the existence of two visual streams: an occipitotemporal or ventral stream mediating the visual identification of objects (*i.e.*, "what" is the object?) and an occipitoparietal or dorsal stream mediating the appreciation of spatial relationships among objects (*i.e.*, "where" is the object?). The role of the parietal cortex in spatial vision was broadly

defined so that it also included the visual guidance of movements. Their assumption is in line with precited physiological evidence showing that the ventral stream and its dominant parvocellular input are selective for visual properties that are particularly relevant for object identification, *i.e.*, colour and shape (Desimone et al., 1985; Lueck et al., 1989; Pasupathy & Connor, 1999), while the dorsal stream and its dominant magnocellular input are selective for the spatial properties of the object, *i.e.*, motion direction and depth vision (Albright, 1984; DeAngelis et al., 1998; Maunsell & Van Essen, 1983).

2.2 Perception *vs.* Action

A decade later, another brain-damaged patient with visual agnosia showing a particular pattern of impairment led Goodale and Milner (1992) to re-examine previous studies of patients with damage to the temporal and parietal cortices, which brought them to a different conclusion than Ungerleider and Mishkin (1982). While they agreed the visual system is organised into two functionally distinct streams, they argued that neuropsychological data are better explained if one assumes that the ventral stream is involved in perception and the dorsal stream in visually-guided actions.

D.F., a patient with extended lesions to the ventral stream, was diagnosed with visual agnosia. This patient was unable to recognise or copy objects and to report their size, shape or orientation. She was also unable to reproduce these dimensions manually, for instance, by rotating an object to make it correspond to the orientation of a target object or by spreading her fingers as widely as the object size (*i.e.*, matching task). So far, D.F. thus showed the typical profile of visual agnosia, which supported the role of the ventral stream in object identification. What was striking in D.F. was that she successfully performed visuomotor tasks using the very same dimensions she was unable to report or reproduce. For instance, she could pass

a plaque through a slot, even though she could not report the orientation of the slot (*i.e.*, posting task; Figure 3). Similarly, when she was asked to reach and grasp an object for which she lacked visual awareness, the opening of her hand during the reaching phase correlated with the size of the object (Goodale, Milner, Jackobson & Carey, 1991; Milner et al., 1991).

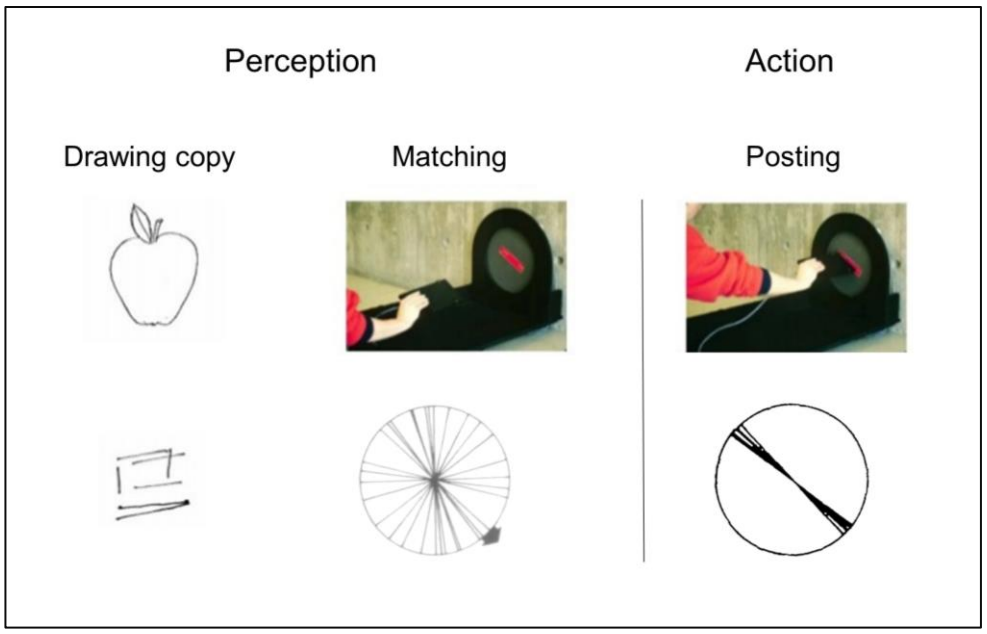

Figure 3. *Performance of patient D.F. to perceptual and action tasks. She was impaired when copying drawings of objects and when matching the orientation of a plaque with the orientation of a slot (left), but not when posting this plaque into the slot (right). The polar diagrams represent the orientation produced during the matching and posting task (adapted from Milner et al., 1991).*

Patients with optic ataxia following lesions to the posterior parietal cortex typically show the opposite pattern. Optic ataxia has been referred to as inaccuracies in visually-guided movements that cannot be explained by an elementary deficit in the motor, somatosensory or visual modality or by a visual attention disorder. These

patients are typically impaired in reaching and adjusting the opening and orientation of their hand when grasping objects located in the visual hemifield contralateral to the lesion (Perenin & Vighetto, 1988). Subtle kinematic analyses showed that their grip opened widely with no preshaping at the start of the movement and closed lately at the time of object contact (Jakobson, Archibald, Carey & Goodale, 1991; Jeannerod, 1986; Jeannerod, Decety & Michel, 1994). The "what *vs.* where" model would ascribe these deficits to impaired processing of the spatial properties of the object. However, Goodale and Milner (1992) underlined that these patients typically remain able to process object's spatial properties when they are not used to act towards the object. For instance, optic ataxic patients remained able to indicate the orientation of a stimulus verbally or with their hand, if no movement towards the stimulus itself was required (Jeannerod, 1986; Jeannerod, Decety & Michel, 1994; Perenin & Vighetto, 1988). Goodale and Milner (1992) proposed that other visuospatial disorders associated with parietal lesions might also be better explained by an impairment of the visuomotor components they involve. Overall, the double dissociation between visual agnosia and optic ataxia indicates that the processing of shape, size or orientation for perception relies on a functional system distinct from the programming of goal-oriented actions on these attributes.

In summary, early lesion studies in humans and monkeys suggested that the ventral stream is responsible for identifying what a viewed object is, while the dorsal stream is responsible for identifying where an object is. The finding that patients with visual agnosia, including D.F., were unable to recognise and discriminate objects after occipitotemporal lesions was consistent with the ventral "what" system. However, the finding that patient D.F. was still able to process objects' visual properties to guide her actions, together with the finding of the opposite pattern in patients exhibiting optic ataxia after dorsal lesions, called for a revision of the role of the dorsal stream. Goodale and Milner (1992) proposed that the dorsal stream is

crucial for processing visual attributes in order to program actions towards these attributes, but not to perceive them. Thereby, the ventral and dorsal streams do not differ so much according to the visual attributes they process than the purpose for which they process these attributes.

As the impetus shifted from the input to the output, the respective contribution of the parvo- and magnocellular pathways described in the previous sections has been little discussed within the TVS model. The late segregation between colour and motion has received a bit more attention, though. The specialisation of the ventral area V4 for colour is explained by the fact that colour is more relevant to perceive and recognise an object than to grasp it (for a review, see Tanaka, Weiskopf & Williams, 2001). On the contrary, the specialization of MT for motion and depth is explained by their particular relevance for action. Although not discussed by the model, the magnocellular input of the ventral stream could be taken into account by the model by assuming that the information it carries about motion and depth serves to resolve perceptual ambiguities. To sum up, the TVS model acknowledges there might be some specificities at the level of the input, but which mainly concern colour. So, it underlines that the main difference between the ventral and dorsal streams is the purpose for which the input is processed.

3. The two visual system model

The TVS model (Goodale & Milner, 1992) not only proposes that the ventral and dorsal streams process visual information for different purposes, but also that they have specific metrics, reference frames and timings to deal with the competing demands of perception and action. In this section, I will present the claims of the TVS model, the supporting evidence, as well as their criticisms.

3.1 Vision for perception

Perception, which refers to the conscious experience of seeing, is probably the most evident and apprehensible aim of vision because one can only experience vision through conscious percepts. These percepts consist of rich and detailed representations of the world and the objects within it. These representations are assumed to be memorised to allow, *inter alia*, object recognition when they are met again.

3.1.1 Neural substrate

Based on the case of patient D.F., Goodale and Milner (1992) proposed that the ventral stream supports not only object recognition but also perception as a whole. However, some major objections can be made to the use of these neuropsychological data to map perception onto the ventral stream. Indeed, the correspondence between a lesion site and a particular behavioural impairment is imprecise, especially in the case of visual agnosia. Most cases of visual agnosia, including D.F., suffered from carbon monoxide poisoning, which induces diffuse and widespread lesions in the whole brain. D.F.'s LOC was the most affected part of the brain, but lesions could also be seen in the left posterior parietal cortex. Moreover, atrophy was observed throughout her whole brain as evidenced by many

of her sulci being enlarged, including the posterior part of the intraparietal sulcus (IPS), the postcentral sulcus, the inferior precentral sulcus, and the parieto-occipital sulcus bilaterally, as well as the left calcarine sulcus (James, Culham, Humphrey, Milner & Goodale, 2003). Hence, it is difficult to conclude that the ventral stream plays a particular role in object recognition, and even more in all perceptual tasks. Impairment in object recognition and perception of size/orientation might result from different lesions. Subsequently, the same behavioural pattern has been described in a patient with lesions almost circumscribed to the ventral stream. It is worth noting that the damage extended to the cuneus and cingulate gyrus (Karnath, Rüter, Mandler & Himmelbach, 2009).

In healthy humans, the involvement of the ventral stream in object recognition is supported by neuroimaging studies showing that different occipitotemporal areas are specialised for processing colour, texture and form (*e.g.*, Malach et al., 1995; Price, Moore, Humphreys, Frackowiak & Friston, 1996; Puce, Allison, Asgari, Gore & McCarthy, 1996) or specific categories of objects (*e.g.*, the fusiform face area for faces: Halgren et al., 1999; the parahippocampal place area for places: Epstein & Kanwisher, 1998; the extrastriate body area for human bodies: Downing, Jiang, Shuman & Kanwisher, 2001). The LOC appears to be involved in perceiving any kind of visually presented object (for a review, see Grill-Spector, 2003). However, the neural substrate of other perceptual tasks was very little discussed within the TVS model, while there is evidence that the dorsal areas are involved. For instance, the visual comparison of two lengths, orientations or luminances was found to involve areas around the IPS as well as the premotor cortex (Dormal, Andres & Pesenti, 2012; Dormal & Pesenti, 2009; Fias, Lammertyn, Reynvoet, Dupont & Orban, 2003; Pinel, Piazza, Bihan & Dehaene, 2004), suggesting that, contrary to what is assumed by the TVS model, perception cannot be restricted to the ventral stream.

3.1.2 Metrics and reference frame

The TVS model states that recognising and identifying objects involve constancy throughout viewing points. For instance, one must remain able to recognise a chair even if presented upside down. Hence, the ventral stream would compute object representations where shape, size, colour, lightness, and location are independent of the point of view. In accordance, the LOC appeared to be largely insensitive to changes in object viewpoint (James, Humphrey, Gati, Menon & Goodale, 2002; Valyear, Culham, Sharif, Westwood & Goodale, 2006).

Moreover, the TVS model underlines that building a representation of the visual world requires the integration of the various elements of a visual scene. Therefore, the ventral stream would use a scene-based frame of reference, which computes object metrics in a relative, and not absolute, manner. This scene-based reference frame also allows perceptual representations of objects to transcend particular viewpoints. Indeed, when an object coded as "larger" than a neighbouring object, this will remain true when the observer moves around. This property of perception is reflected in size-contrast illusions where the size of an object appears smaller when surrounded by large objects and larger when surrounded by small objects (*i.e.*, the Ebbinghaus illusion). This effect is explained by the fact that any sensory magnitude is judged in a relative way, using the magnitude of the surrounding context as a reference (*i.e.*, the adaptation level theory; Helson's, 1964). The comparison of an object and its surroundings would lead to a perceptual accentuation of their differences (Coren & Miller, 1974; Massaro & Anderson, 1971). This size-contrast effect is consistently found in perceptual judgments and might thus reflect an unavoidable process of the ventral stream. The use of this illusion for comparing the metrics and frames of reference of perception and action is discussed in a separate point below (see 3.3.2 *The size-contrast illusion*

paradigm). In accordance, functional magnetic resonance imaging (fMRI) studies showed that the ventral stream was indeed activated when an object had to be coded according to another object or a landmark. However, the dorsal stream was also activated, suggesting that allocentric coding is not restricted to the ventral stream (Committeri et al., 2004; Galati et al., 2000).

3.1.3 Time scale

Another important aspect defining perception within the TVS model is the time scale over which the visual information is processed, and the resulting visual representations are available. To be able to recognise and identify objects when seen again, to attach meaning and significance to what is seen, and establish causal relationships, the representations of objects and scenes provided by the perceptual system should be available over a long period. This also implies that these representations are not directly linked to motor outputs, but rather to the cognitive system involving, among others, memory, semantics and spatial reasoning. Accordingly, the anterior part of the inferior temporal cortex is connected with memory-related areas in the frontal cortex (Takahashi, Ohki & Kim, 2007) and the limbic system (*e.g.*, amygdaloid nuclei, hippocampus; Amaral & Price 1984; Insausti et al., 1987). Moreover, inferior temporal lesions in monkeys resulted in the inability to store object representation (Mishkin & Oubre, 1976). Hence, the endpoint of the ventral stream most probably links the visual input from the visual cortices to the memory systems in the frontal cortex and limbic system.

Moreover, to build a stable and conscious perception of the visual world, the ventral stream would operate at slow speed. Indeed, such a stable representation would only emerge after recurrent processing, operating via horizontal, within-area, and feedback connections that increase response latencies (RLs; Lamme, 2001;

Lamme & Roelfsema, 2000). Accordingly, the longest responses to a visual stimulus are found in the areas of the ventral stream (i.e., 100 – 200ms; Nowak & Bullier, 1997).

The TVS model, in later developments, proposes that any use of the stored visual representations, including actions programmed on remembered objects, requires the ventral stream (*e.g.*, Goodale, 2014; Goodale & Westwood, 2004; Goodale, Westwood & Milner, 2004). This stemmed from the observation that grasping performance of patient D.F. deteriorated when goal-directed actions were performed after the object had been removed from her view. When she faced a delay of 2s between object removal and grasp initiation, her grasping movements did not show the typical correlation between object size and maximum grip aperture (MGA), which is used as an index of the in-flight adjustment of hand opening to object size (Goodale, Jackobson & Keillor, 1994). The authors assumed that D.F. could not use the memory trace of the object to guide her delayed grasping movement because visual memory for object features depends on her damaged ventral stream. More recently, these results were replicated in another patient showing visual agnosia (Cornelsen, Rennig & Himmelbach, 2016). Patients with parietal lesions showed the reverse pattern: grip scaling of optic ataxia patients was improved when grasping familiar objects or when grasping an object seen earlier but no more present (Milner, Paulignan, Dijckerman, Michel & Jeannerod, 1999). This further supports the claim of the TVS model that actions towards object features retrieved from earlier perceptual processing, presumably from long-term memory in the case of familiar objects, are driven by the intact ventral stream. In healthy individuals, the link between memory-driven actions and the perceptual system of the ventral stream is supported by the finding that this particular class of actions was sensitive to the Ebbinghaus illusion, just as perception (Hu & Goodale, 2000, but see 3.3.2 for discussion).

3.2 Vision for action

Before the 80s, providing sight was considered as the primary function of vision. The representations underlying perception were assumed to provide a ground not only for visual cognition but also for action. Goodale (1983; 1996) then proposed that acting upon the world might be the very first aim of vision. Indeed, much of vision in vertebrates consists in controlling movement in response to light stimulation, without referring to a full-blown representation of the visual world or a sense of sight comparable to the one described in humans. He further proposed that sight evolved later in a different system, *i.e.*, the aforementioned perceptual system of the ventral stream.

3.2.1 Neural substrate

Aforementioned neuropsychological findings showing that visually guided movements were preserved after ventral damage in patient D.F. but impaired after dorsal damage in optic ataxia patients led Goodale and Milner (1992) to assume that processing visual properties for controlling movement is located within the dorsal stream.

The involvement of the dorsal stream in visually-guided actions has been further supported by neuroimaging studies in healthy individuals showing fronto-parietal activations, with specific areas around the IPS being activated for different motor actions (*e.g.*, AIP, anterior part for grasping; MIP, medial part for reaching; LIP, lateral part for saccades; for a review, see Culham & Valyear, 2006). Moreover, injections of retrograde tracers in the monkey IPS indicate that this area is highly connected to the hand area of the somatosensory cortex (Lewis & Van Essen, 2000) and to the ventral (PMv) and dorsal (PMd) premotor cortices, which drives the commands of "executive" motor areas in the frontal lobe (Tanné-Gariépy, Rouiller

& Boussaoud, 2002). MRI-based tractography suggests that the functional connectivity pattern of the IPS is similar in humans (Mars et al., 2011).

The finding that some patients with lesions to V1 were still able to orient their eyes and hands, sometimes even to size their grip, towards objects presented in their blind visual field (*i.e.*, blindsight; Perenin & Jeannerod, 1975; Weiskrantz, 1986), suggests that action can also bypass V1, most probably trough the subcortical input from the pulvinar to MT (Figure 2; Weiskrantz, 1986).

3.2.2 Metrics and reference frame

The TVS model suggests that action evolved in a different stream from perception because each requires specific transformations of the visual input to meet distinct output requirements. In particular, action would require estimates of the real metrics of the objects. Transformations of the incoming input as carried out by the ventral stream might thus not be appropriate. For instance, when grasping keys, knowing that they are on the table on the left of a wallet is probably not sufficient to plan an appropriate grasp. Instead, it requires access to the actual size and position of the keys with respect to the body. This claim was supported by the finding that, contrary to perception, size-contrast illusions do not, or little, affect grasping movements, which were primarily determined by the actual size of the object to grasp (*e.g.*, Aglioti et al., 1995, but see 3.3.2).

To convert accurate metrical information about position and orientation into calibrated motor output, the TVS model assumes the dorsal stream computes them within an egocentric frame of reference, *i.e.*, with respect to oneself body. Accordingly, fMRI studies revealed that coding visual information relative to the body mainly involved the dorsal stream (Galati et al., 2000; Vallar et al., 1999). However, it should be noted that the dorsal stream was also involved when coding

visual information according to an external reference (*i.e.*, allocentric coding; Committeri et al., 2004; Galati et al., 2000). As orienting towards a visual stimulus was sometimes found impaired with hands but not eyes (Ratcliff & Davies-Jones, 1972; Riddoch, 1935), the TVS model proposed that different visuomotor modules within the dorsal stream relate to different motor outputs (Goodale, 1996). As it turned out, orienting the eyes towards an object requires information about its location to be coded in eye- and perhaps also head-based coordinates, whereas moving the hand towards the object requires limb-, hand-, and finger-based coordinates. The modular organization around the IPS, with different portions being involved in voluntary grasping or saccades, and its distinct connectivity with PMv and the frontal eye fields might make this possible (Culham & Valyear, 2006).

3.2.3 Time scale

As the observer (and sometimes the object) is moving when performing a movement, the egocentric coordinates of an object change continuously during action. Hence, contrary to the perceptual system assumed to strive for consistency, the visuomotor system is assumed to compute object coordinates fastly and in real-time. In order to support the on-line control of action, the dorsal stream would be endowed with fast feedforward connections, but very few horizontal and feedback ones (Lamme, 2001). Indeed, the neurons of dorsal areas such as MT and MST respond to a visual stimulus very shortly (~45 ms) after the neurons in V1 (~35ms). This suggests that the neurons of the dorsal stream transfer information to higher-level areas very quickly, with little time for lateral and feedback connections (Nowak & Buillier, 1997). Therefore, the parietal cortex is often qualified as the “fast” brain.

The TVS model underlines that the deployment of feedforward mechanisms in the dorsal stream is constrained by the availability of the visual input and the

programming of the action. The model assumes it would be inefficient to update the motor program repeatedly between the first appearance of the visual target and the release of the motor response, as egocentric coordinates might have changed over time. Evidence for the response-locked triggering of feedforward mechanisms comes from the observation that the kinematics of grasping movements were affected when programmed on memorised objects (*e.g.*, longer execution time, wider MGA, and earlier peak velocity; Hu, Eagleson & Goodale, 1999) and sensitive to a size-contrast illusion assumed to emerge in the ventral stream (*i.e.*, the Ebbinghaus illusion; Goodale et al., 2004, but see 3.3.2). If the computations of the dorsal stream are continuously updated for immediate use, there is no need for storage. Hence, the TVS model further specifies that computations in the dorsal stream remain shortly in memory and decay quickly (less than 2 s) after the target has been removed from view (Goodale et al., 1994). Yet, humans have a conscious visual experience of their actions. The TVS model proposes that the simultaneous processing of the visual information along the ventral stream provides us with a visual experience of the action performed via the dorsal stream (Goodale & Humphreys, 1998).

As can be noticed, consciousness plays an essential role in the dissociation between perception and action proposed by the TVS model. The authors even declared that "the visual information used to program and control those actions can never be experienced" and that only the products of the visual stream can reach visual awareness (Milner & Goodale, 2008). The most striking observation used to support their statement is blindsight, which refers to the ability of cortically blind patients with a lesion to V1 to perform actions towards visual stimuli they cannot report. Because of the limits imposed on visual awareness, the patients were surprised when they managed to grasp an object (Weisktrantz, 1986). Similarly, patient D.F. experienced with great surprise and even described as guesswork her ability to perform actions towards objects she could not recognise (Goodale et al.,

1991; Milner et al., 1991). Therefore, conscious perception was consistently opposed to non-conscious vision for action in the context of the TVS model. However, it is impossible to relate perception or action to other levels of visual awareness from those allowed by the task at hand. While most studies assessed perception with conscious measures and action with unconscious measures, a few of them indicated that, contrary to what is expected by the TVS model, the output of action is accessible to consciousness. In particular, the observation that D.F. improved her ability to discriminate two objects by verbal reports when probed just before or during a grasping movement suggests that information available during action can reach consciousness (Schenk & Milner, 2006). Moreover, patients with blindsight are not only able to perform movements towards "unseen" objects, but also to guess certain object attributes (*e.g.*, colour, location, form, and movement) when they are forced to (Stoerig & Cowey, 1997). Overall, these results are in contradiction with the TVS model's claim that the mental representations underlying action cannot reach consciousness and rather suggest that both the representations underlying perception and those underlying action can reach consciousness.

To sum up, the TVS model assumes that the anatomical segregation between the ventral and dorsal streams allows the brain to deal with the competing demands of perception and action. The ventral stream would compute object metrics (*e.g.*, size, distance) relative to the surrounding objects to give rise to an integrated representation of the visual world that is insensitive to changes in viewpoint. On the contrary, the dorsal stream would estimate the absolute metrics of a visual target and code them in real-time in an observer-based frame of reference to support the on-line control of actions. I already mentioned some of the data supporting the model as well as the issues they raised. In the next point, I will explain further how the use of size-contrast illusions contributed to study the nature of the processes involved in perception and action.

3.3 The particular case of size processing

Among the various visual attributes the TVS model expects to be processed differently by perception and action, size is undoubtedly one of the most studied. This might be partly due to Aglioti and colleagues (1995) who came up with the idea to use size-contrast illusions to put the hypotheses of the TVS model under empirical test. This paradigm has fascinated many researchers and led to numerous studies, but has also shown shortcomings leading to numerous debates. Before I describe the paradigm and the associated studies, I will make a global description of how size enters and is processed in the visual system for any purpose.

3.3.1 Size estimation

When it comes to size, the brain has to deal with a specific issue: the size of the projected image of an object on the retina (*i.e.*, retinal size) is a function not only of the real size of the object but also of the distance between the object and the observer. In particular, the retinal size is defined by the following function:

$$\alpha = \frac{\mathrm{S} \times 57.3}{\mathrm{d}}$$

where α is the retinal size (expressed in degrees of visual angle), S is the size of the object (expressed in cm), and d is the distance between the eye and the object (expressed in cm; Figure 4). This implies that an object does not have the same retinal size when its distance from the observer changes. For instance, a 70 cm-high sheep will have a retinal size that is smaller when it is at 50 m from the observer (80.22°) than when it is at 10 m from the observer (401.1°). In order to estimate the size of the sheep correctly, the brain has thus to compensate for the decrease/increase of retinal size with the increase/decrease of distance by taking into account how far the sheep is from the eyes.

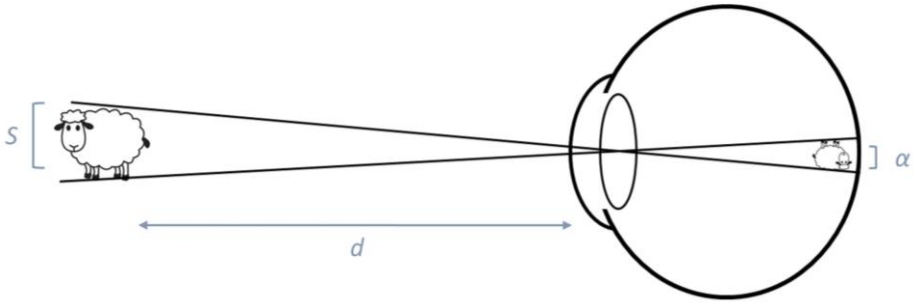

Figure 4. *Illustration of the retinal size of an object (α), which is a function of the real size of the object (S) and the distance between the eye and the object (d).*

In order to estimate the distance of an object, the brain mainly relies on the difference between the images retrieved from each eye (*i.e.*, binocular disparity). External visual cues such as relative size, relative brightness, relative position, linear perspective foreshortening, and texture gradient are other cues to distance (Gibson, 1950; Howard & Rogers, 2002; Surdick et al., 1994). Hence, the calibration of retinal size should be possible only if these cues are available. Accordingly, estimations of object size were found to be closer to retinal size under monocular than binocular vision and when presented in a dark context than when presented in a structured environment (Hastorf & Way, 1952; Holway & Boring, 1941; Gogel, 1969). Hence, size coding depends upon distance estimation.

Interestingly, external visual cues such as relative size, position and brightness are also used as cues to distance during visuomotor behaviours. For instance, the presence of a structured visual scene decreased movement undershooting that was otherwise observed in a dark context, and this decrease was even more significant under binocular vision (Conti & Beaubaton, 1980; Coello & Magne, 2000; Coello & Iwanow, 2006; Magne & Coello, 2002). More importantly,

the calibration of grip aperture to object size during grasping movements was more accurate when the object was presented with a visual background than when presented in the dark (Churchill, Hopkins, Rönnqvist & Vogt, 2000). The observation that the visual environment influences distance and size computation during reaching and grasping movements might seem in contradiction with the assumption of the TVS model that action codes absolute metrics in an egocentric reference frame that is independent of the visual context. In response to this criticism, the authors of the model suggested that one learns to use external visual cues to infer absolute distance and size for action when binocular vision is denied, but that otherwise, the motor system computes the absolute distance from binocular disparity (Marotta, Behrmann & Goodale, 1997; Marotta & Goodale, 1998). Nevertheless, this does not account for the improvement of reach and grasp movements observed in a structured compared to a dark environment, even when both environments are presented under binocular vision. This suggests that the motor system does compute the relative metrics, at least those of the different elements of a visual scene to infer the absolute metrics of the target object.

3.3.2 The size-contrast illusion paradigm

The claim that vision for perception and vision for action use different metrics in different frames of reference has been tested more systematically with size-contrast visual illusions, which are illusions that make objects appear smaller or larger than they actually are because of the visual context (for several examples, see Figure 5). Such illusions provide a unique paradigm to test the prediction that perception computes object size relative to its environment, while action estimates the real size of the object. In this point, I will concentrate on studies using the Ebbinghaus illusion, which has been extensively used to investigate the dissociation between perception and action.

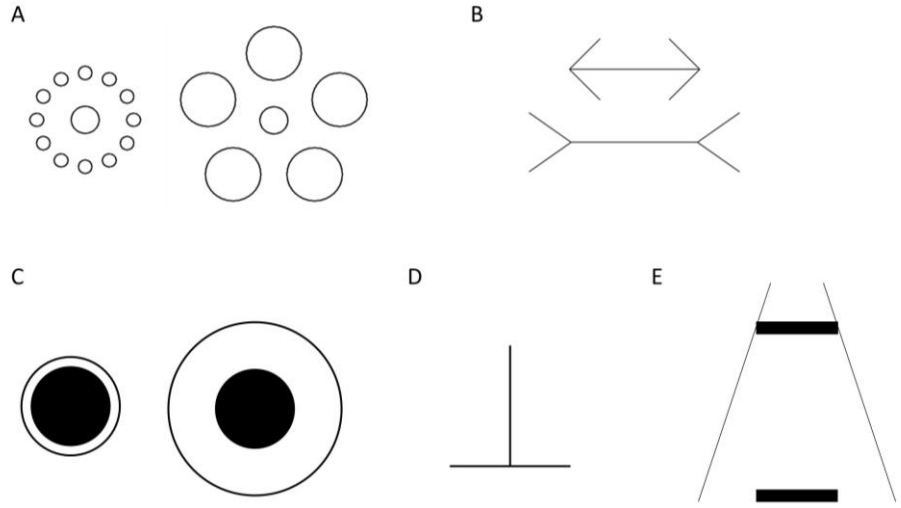

Figure 5. *Examples of size-contrast visual illusions. A. The Ebbinghaus illusion: The two central circles are of identical size, but the one surrounded by an annulus of small circles appears larger than the one surrounded by an annulus of large circles. B. The Müller-Lyer illusion: The two horizontal segments are of equal length, but the one ended by outwards-pointing arrows appears shorter than the one ended by inwards-pointing arrows. C. The Delboeuf illusion: The two inner circles are of equal size, but the one surrounded by a small external circle appears larger than the one surrounded by a large external circle. D. The Vertical-horizontal illusion: The two segments are of equal length, but the horizontal one appears shorter than the vertical one. E. The Ponzo illusion: The two rectangles are of the same size, but the upper one appears larger than the bottom one.*

The Ebbinghaus illusion consists of two circles of identical size, one surrounded by an array of large circles and the other by an array of small circles. The central circles, although physically identical, typically appear different in size: the circle surrounded by small circles appears larger than the one surrounded by large circles (Figure 5A). Aglioti and colleagues (1995) used this illusion to build an additional configuration where the two central circles appeared equivalent in size, yet of different physical sizes. They showed that perceptual judgments were strongly

affected by the illusion while grasping movements were scaled on the real size of the circle. In front of the illusion, participants were instructed to pick up the left circle if they thought the central circles were the same size or to pick up the right one if they thought they were different in size. The participants' choice (left or right) indicated they treated circles that were different as identical, and conversely, due to the illusion. On the opposite, MGA, as measured during the reaching phase with infrared markers attached to the fingers, was scaled on the real size of the selected circle, reflecting typical adjustment of grip aperture to object size (Figure 6). This dissociation was replicated in several studies using the Ebbinghaus illusion (for a review, see Goodale, 2011), and even when perceived size was assessed by requiring participants to indicate the size of the central circle by spreading their index finger and thumb without actually reaching the circle. This manual estimation was affected by the illusion, while actual grasping was much less affected (Haffenden & Goodale, 1998). These results strongly suggest that, as expected by the TVS model, perception and action process object properties (at least size) differently. Goal-directed actions only process the attributes of the relevant object, while perception processes the relevant object by bounding it to its surround to produce a unique percept. However, the dissociated effect of size-contrast illusions on perception and action has subsequently been much debated. The debate is fuelled by the difficulty to match the perception and action tasks.

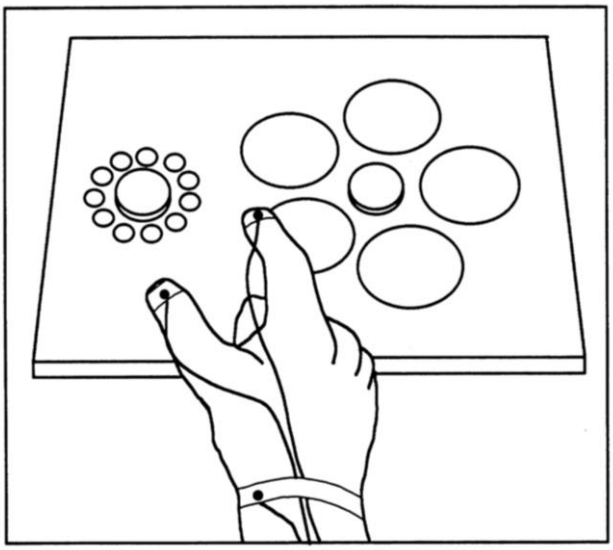

Figure 6. *The display used by Aglioti et al. (1995). The authors showed that participants judged the central circle of the left display as larger than the central circle of the right display, although they were the same size. When required to grasp the left circle, their MGA was tuned to the real size of the circle (adapted from Goodale & Humphreys, 1998).*

First, it has been shown that the greatest sensitivity of perceptual judgments to the Ebbinghaus illusion, initially observed by Aglioti and colleagues (1995), can be explained by a difference in the attentional demands of the perceptual and action tasks. In this pioneering study, the perceptual task required comparing two central circles of two Ebbinghaus displays, while grasping, and hence, attention, was directed towards one central circle. It was subsequently shown that perceptual judgments performed on a single Ebbinghaus display were much less affected by the illusion, whose effect became, in fact, similar to the one observed on grip aperture. The dissociation reported by Aglioti and colleagues (1995) might thus result from the direct comparison between two Ebbinghaus displays yielding a larger effect than one single display. It was concluded that the illusion does not provide evidence for a functional dissociation between perception and action but, on the contrary,

provides support for a common internal representation of size, influenced by the visual context, and supporting both perception and action (Franz, Gegenfurtner, Bülthoff & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti & Farnè, 1999; Vishton, Rea, Cutting & Nuñez, 1999).

Second, the distance between the central and surrounding circles might also play a role in the illusory effect on action. In the abovementioned studies, this gap was not constant across the two Ebbinghaus displays (*e.g.*, Figure 6). It has been proposed that this difference gave rise to seemingly illusory effects on action resulting, in fact, from non-illusory visuomotor mechanisms such as obstacle avoidance. Indeed, when a target is surrounded by flankers, participants typically use a smaller grasp, most probably to avoid the flankers, which are treated as potential obstacles. The difference between the grip aperture used to grasp the circle surrounded by small circles or the one surrounded by large circles might thus reflect the need to avoid obstacles leaving more or less space to place one's fingers on the contours of the central circle. When the gap between the central and peripheral circles was kept constant, two studies showed that the illusion conditions did not give rise to any difference in grip aperture (Haffenden & Goodale, 2000; Haffenden, Schiff & Goodale, 2001), but two other studies using a larger sample of participants did find an effect of the illusion on grasping (Bruno, 2001; Kopiske, Bruno, Hesse, Schenk & Franz, 2016). The latter suggests that obstacle avoidance is not responsible for the size-contrast illusion observed on grasping movements.

Third, the reason the illusory effect observed on grasping was typically of a smaller size than the one observed on perception might lie in the scale of the measures used to estimate the perceptual and motor biases induced by the illusion. Most studies that found a significant difference between perception and action used manual estimation as a perceptual measure, *i.e.*, spreading fingers at a remote distance until one estimates that space in-between the index and thumb fits the object

size. This measure was found more sensitive to object size variations than the MGA measured during reach-and-grasp movements. For instance, an increase of object size by 1 mm was associated with an increase in manual estimation by 1.6 mm, while it was associated with an increase in MGA by only 0.82 mm. One can infer from this difference in the scaling of grip aperture to object size that MGA is less likely to reflect illusory size distortions than manual estimation. When correcting for the different slopes of the linear function relating the physical size to manual estimation or MGA, the measures revealed a similar effect of Ebbinghaus illusion on perception and action (Franz & Gegenfurtner, 2008).

Finally, the effect of the illusion on grip aperture might vary as the movement evolves. MGA typically occurs in the late stages of the movement, approximately at two-thirds of the reaching phase. Tracking grip aperture during the whole movement showed that the illusion exerted a large effect on the early stages of the grasping movement and decreased as the hand approached the circle (Glover & Dixon, 2001; 2002). This suggests that the movement is influenced by the illusion during the planning phase and is then corrected during execution. This might be because the hand partly occludes the visual context when approaching the central circle of the illusion. The visual context might then have less impact. Moreover, as the hand gets closer to the target, direct visual feedback might allow the participants to refine the comparison between their actual grip aperture and target size. Action would thus benefit from visual and proprioceptive information about the acting hand, offering additional opportunities to correct the error introduced by the illusion. This is supported by the finding that the effect of the size-contrast Müller-Lyer illusion (Figure 5B) on grasping increased while the amount of visual feedback about the hand decreased (Franz & Bruno, 2008). Many studies addressed this issue by preventing vision about both the hand and the stimulus. However, the TVS model predicts that removing the stimulus from view leads to retrieving object features

from a memory trace computed in the ventral stream. Moreover, even when hiding only the hand, the proprioceptive feedback of the acting hand remains. Removing this proprioceptive information has never been done, probably because technically challenging. However, it is essential to exclude a compensatory role of proprioceptive feedback in the comparison of grip aperture with object size and the subsequent implementation of one-line corrections during movement (Prablanc, Pelisson & Goodale, 1986).

To summarise, seminal studies on size-contrast illusions supported the claim that perception and action process object size differently by showing that action, contrary to perception, is immune to such illusions. However, several methodological constraints undermine this result. The most recent studies rather suggest that grasping movements are sensitive to the illusion in the earliest stages, but that the visual and proprioceptive feedback allows correcting the error introduced by the illusion during the course of the movement. Hence, contrary to what is predicted by the TVS model, both perception and action would be affected by the visual context, but action would benefit from additional information to refine object size estimate. However, as this additional feedback is complicated to eliminate, its contribution remains to be defined.

3.4 Revisions of the model

An alternative view promoting the idea of shared processes between perception and action emerged from the evidence challenging the TVS model. Goodale and Milner more recently acknowledged they overestimated the independence of the two visual streams in their early version of the TVS model and proposed a series of amendments. They recognise perception and action have to inform each other in several ways to produce adaptive behaviour (*e.g.*, Goodale, 2011; Milner & Goodale, 2008).

3.4.1 Contribution of perception to action

First, Goodale and Milner proposed that perception contributes to action by identifying objects, their semantic as well as their material properties, in order to select the most appropriate way to interact with these objects. This would include selecting the appropriate hand posture (*e.g.*, power or precision grip) for the planned action. For instance, the authors assume one would have to recognise a scissor to know one has to grasp it by putting fingers into the holes to cut out a sheet. However, the implementation, including the specification and on-line control of the kinematic parameters of the selected action, would be handled by the dorsal stream. Hence, Goodale and Milner make a distinction between the planning, at a quite abstract level, and the precise programming of action. Consistent with the involvement of the ventral stream in grasping objects to use them functionally, neuroimaging data in healthy individuals showed that imagined grasp movements towards objects with a handle were associated with additional activation within the middle temporal and fusiform gyri compared to imagined grasping of neutral shapes (Creem-Regehr & Lee, 2005). More broadly, the use of tools is typically associated with activation in both the ventral and dorsal streams (e.g., Brandi, Wohlschläger, Sorg & Hermsdörfer, 2014; Chao, Haxby & Martin, 1999). In addition, grasping objects appropriately by their handle to use them was found to be affected by a concurrent task involving the processing of words of the same semantic category than the grasped object (*e.g.*, "soup" when grasping a spoon). Participants made errors such as picking up the object by the wrong side or grasping it by the handle but in a manner that would be ineffective if they had to use it. Such interference was not observed when the concurrent motor task was visuospatial (Creem & Proffitt, 2001). Altogether, these results suggest that grasping objects appropriately for their use requires accessing semantic knowledge stored in the ventral stream.

Second, ventral-stream processing would intrude into the visual guidance of novel, unpractised or awkward actions that require cognitive supervision. Once the action is well practised and automatised, the dorsal stream would take over the control of its complete execution (Milner & Goodale, 2008). The authors support their claim with the finding that visual illusions, considered here as a signature of ventral processing, had a larger effect on awkward than typical precision grips during grasping, which disappeared after practice (Gonzalez, Ganel, Whitwell, Morrissey & Goodale, 2008). Moreover, right-handers were more sensitive to the Ebbinghaus illusion when performing grasping movements with the left hand compared to when performing them with the right hand (Gonzalez, Ganel & Goodale, 2006). These results were taken as evidence that unfamiliar movements involved the ventral stream until they became automatic.

Third, object properties that are not directly specified in the available visual information have to be inferred from information learnt in previous grasps. For instance, weight is inferred from previous associations between certain visual attributes (*e.g.*, size, texture) and weight estimates derived from past experience of grasping (Johansson & Westling, 1984; van Polanen & Davare, 2015b). According to the revised TVS model, the ventral stream stores these learnt associations and is thus required to make such inferences. Evidence for this comes from fMRI studies showing that the weight of an object modulated brain activity in both the ventral and dorsal streams (Chouinard, Large, Change & Goodale, 2009; Gallivan, Cant, Goodale & Flanagan, 2014).

Other authors suggested that the ventral stream also provides support to the dorsal stream for delayed action (*e.g.*, Pisella, Binkofski, Lasek, Toni & Rossetti, 2006; Schenk & McIntosh, 2010). Goodale and colleagues (2004) initially proposed a switch from the dorsal to the ventral stream when a delay is introduced between target onset and movement initiation. This was supported by the observation that

action performance improved with a delay in optic ataxia patients with a lesioned dorsal stream (Milner et al., 1999). However, studies in healthy individuals showed that the LOC was found to be re-activated, in addition to dorsal areas, when the delayed action was executed on an object that was no longer present (Singhal, Monaco, Kaufman & Culham, 2013). Moreover, interruptive transcranial magnetic stimulation (TMS) applied over a dorsal area (*i.e.*, IPS) affected both immediate and delayed actions, while TMS over a ventral area (*i.e.*, LOC) only affected delayed actions (Cohen, Cross, Tunik, Grafton & Culham, 2009). Overall, the existing evidence thus suggests that delayed actions depend on the collaboration of the ventral and dorsal streams and not the substitution of the latter by the first.

To summarise, if we consider the behaviours described by Goodale and Milner and those described by other authors, most every-day actions require visuo-semantic information from the ventral stream to be transmitted to the visuomotor processes of the dorsal stream. It might even be the case for any action since perception is required before voluntary action can be planned. For instance, patients with blindsight never initiate an action spontaneously but need a go signal (*e.g.*, Weiskrantz, 1986). Hence, perception (or at least the cognitive system) seems to provide the signal for the sensorimotor system to perform any action.

3.4.2 Contribution of action to perception

The question of how action can support perception has been far less discussed within the context of the TVS model. In fact, before Milner's revision in 2017, it did not consider any situation where this would be the case. In this later review, Milner (2017) recognised two situations where the motor system of the dorsal stream might support the perceptual system of the ventral stream.

First, Milner (2017) proposed that the visuomotor processes at hand can provide cues to perceptual discrimination. This stemmed from the observation that D.F. improved her performance in perceptual tasks by performing concurrent visuomotor behaviours. For instance, when required to grasp one out of two different shapes that she could not discriminate verbally (*i.e.*, a circle and a rectangle), she often reached for the wrong object at the beginning of her movement, but then changed her trajectory mid-way so that she eventually grasped the right object (Murphy, Racicot, & Goodale, 1996). When performing a concurrent grasping task, she could also name the target object at a significantly higher level than when she had to name the object without performing a grasping movement towards it (Schenk & Milner, 2006). These results suggest that internal cues can be derived from visuomotor processing to influence perceptual discrimination.

Second, based on the observation that D.F. performance in judging the orientation of an object is better under binocular than monocular viewing, Milner (2017) proposed that depth is computed in the dorsal stream and might inform the perceptual system by dorsal-to-ventral interactions. This claim is further supported by the observation that 3D-shapes categorisation in macaques involved both the inferotemporal cortex in the ventral stream and the caudal intraparietal area (CIP) in the dorsal stream and that the reversible inactivation of CIP hampered performance and reduced activity within the inferotemporal cortex (Van Dromme, Premereur, Verhoef, Vanduffel & Janssen, 2016).

In the interactions envisaged by the TVS model, the information provided by the dorsal stream to the perceptual system of the ventral stream is quite primitive (*i.e.*, elementary object features), while the ventral stream provides more complex information (*i.e.*, semantic) to the dorsal stream allowing meaning to be attributed to one's actions.

However, data discussed outside the context of the model evidenced other situations where action contributes to perception by providing more complex information, and which the TVS should also account for. First, action might shape the perception of space. Indeed, the perception of the immediate environment is influenced by the ability to act in this environment. For instance, objects were judged as closer when participants held a tool extending their reaching capability compared to when holding no tool (Witt, Proffitt & Epstein, 2005). Similarly, distances were perceived as longer when participants had to judge them while wearing a heavy backpack than when not wearing a backpack (Proffitt, 2006). These and other related findings (*e.g.*, Grade, Pesenti & Edwards, 2015; Iachini, Ruggiero, Ruotolo & Vinciguerra, 2014) are quite consistent with the idea that action capability influences the perception of space.

Second, action might also play a functional role in the recognition of manipulable objects as suggested by action priming paradigms. Objects were recognised more accurately when primed with movies of movements that were congruent compared to incongruent with the use of these objects (Helbig, Graf & Kiefer, 2006; Helbig, Steinwender, Graf & Kiefer, 2010). This action-priming effect was associated with reduced brain activity in frontal and parietal areas, but also in temporal areas associated with object recognition, suggesting that the previous observation of a congruent action reduces the cognitive effort of object recognition (Sim, Helbig, Graf & Kiefer, 2015).

Third, it has been proposed that the constant exchange of action- and visual-related information between the two streams allows a richer internal representation about how to grasp new objects to be built. For instance, tactile information available during grasping is integrated with visual information to build an internal object representation that can be used in future grasps to predict object weight and scale

fingertip force anticipatively. This is supported by the observation that the weight experienced in a previous grasp influences subsequent lifting force, but also the verbal estimates of weight not implying any movement (van Polanen & Davare, 2015b).

Hence, in addition to the interactions proposed by the TVS model, numerous others have been identified between perception and action, leading to the general idea that most complex visual and motor behaviours require the collaboration of both the perceptual and motor systems.

3.4.3 Connectivity between the ventral and dorsal streams

Tracing studies in both monkeys and humans evidenced cross-connections between the two streams, providing the neural foundation for the aforementioned interactions. In the monkey, tracer fluids revealed that the inferior temporal area TE is connected to the IPS, IPL, and prefrontal areas (Borra, Belmalih, Gerbella, Rozzi & Luppino, 2010; Zhong & Rockland, 2003). Similarly, the temporal area TEO has been found to have connexions with the lateral IPS (Distler, Boussaoud, Desimone & Ungerleider, 1993). The combination of reversible inactivation and fMRI further evidenced a causal flow of visual information about depth from the dorsal to the ventral stream. Indeed, reversible inactivation of the macaque CIP during a depth categorisation task reduced fMRI activity within the inferotemporal cortex and decreased performance (Van Dromme et al., 2016). In humans, studies using diffusion tensor imaging evidenced white matter tracts between the middle temporal gyrus and IPL (in the context of tool use; Ramayya, Glasser & Rilling, 2010; and pantomime of object use; Vry et al., 2012; 2015). Functional connectivity was also evidenced between ventral and dorsal areas in the context of mental rotation (Koshino, Carpenter, Keller & Just, 2005). Overall, these results indicate that the ventral and dorsal streams are able to communicate with each other.

These interactions, even if more numerous than those envisaged by the TVS model, do not exclude the existence of segregation and specialisation between the two streams. They simply indicate that, if there is such a specialisation, a dynamic interplay is at hand in most behaviour. So, they do not inform about the existence of specific visual processes taking place in the ventral and dorsal streams and make the investigation of this hypothesis even more complicated by blurring the respective contribution of the ventral and dorsal stream in any investigated behaviour.

3.5 Status quo

The TVS model assumes not only that perception and action rely on different anatomical streams, but also that they compute very specific transformations to the visual input to meet their respective output requirements.

Concerning the anatomical segregation, neuropsychological data of patients with visual agnosia and optic ataxia indicate that perception and action are functionally distinct and must rely on different brain areas. However, mapping them respectively onto the ventral and dorsal streams based on these neuropsychological data is perilous. Brain lesions are often extended and diffuse and functional deficits plurals, making the correspondence unprecise. Neuroimaging data in healthy participants come in support here, and they generally agree that object recognition mainly recruits the ventral stream, while controlling movement execution mainly recruits the dorsal stream. However, the role of the ventral stream cannot be generalised to perception in its entirety. Indeed, some perceptual tasks, such as matching or comparing two stimuli, seem rather recruiting the dorsal stream. Moreover, the selective recruitment of one stream seems restricted to very simple aspects of object recognition and goal-direction action, such as colour identification

or automatic on-line movement corrections, any more complex behaviour, such as recognising or grasping tools, recruiting both streams.

Concerning the processes underlying perception and action, there is not much support for a dissociation. The main line of evidence for perception and action relying on different metrics and frames of reference is that they are not equally sensitive to size-contrast illusions, suggesting that action, contrary to perception, estimates the real metrics of the object regardless of its visual context. However, these findings have been challenged as recent studies rather suggest that the smaller effect of the illusion observed in action in some studies is better explained by the additional sensory feedback from which action benefits during its overt stages. Nevertheless, no firm conclusion is possible as long as perception and action have not been completely matched regarding the sensory feedback. Yet, observing an illusion effect has frequently been considered by the authors of the model as the signature of the visual processes of the ventral stream being into play in the task investigated. This is a recurrent issue in the TVS model: the processes put forward by the model are considered as inherent to perception and action without being tested systematically. Another example is the claim that action, unlike perception, is necessarily unconscious, but the measures taken during perceptual and action tasks do not allow comparing the level of consciousness reached in the two tasks. Yet, data discussed outside the context of the model suggest that information gathered during action can reach consciousness and that the products of both perception and action can be conscious or not. The cross-cutting issue is that perception and action were not properly matched in previous experimental studies, either according to the available sensory information or the level of awareness.

To conclude, there is good evidence that some restricted aspects of perception and action rely, respectively, on the ventral and dorsal streams. However, the existing evidence does not allow these observations to be generalised to all

perceptual and motor tasks. More importantly, there is no conclusive evidence that perception and action compute different transformations on the visual input to meet their specific goals. Hence, there is a severe lack of data supporting the very fundamental assumption of the TVS model that perception and action rely on distinct anatomical streams due to their need for specific visual processes. This is mainly because of (1) the difficulty in assessing perception and action in identical conditions and (2) the existing crosstalks between the ventral and dorsal streams that make it complicated to disentangle whether the effects observed on perception or action originate from the ventral or dorsal stream. In the next section, I will explain how investigating the covert stages of action may allow us to overcome these issues and open up new perspectives on the interactions between perception and action.

4. Towards the covert stages of action

As discussed in the previous section, the nature of the processes at stake in perception and action have not been appropriately compared because of difficulties in matching perceptual and action measures, notably in terms of available sensory information and awareness. To overcome these issues, I propose to use judgments about how one would act, thus implying no movement, in place of overt actions. These prospective action judgments not only allow the investigation of the covert stages of action, which have received little interest in the TVS model, but also the close matching with perceptual tasks. In this section, I will review findings supporting the view that prospective action judgments involve the mental simulation of the judged actions, but also their limitations and alternative views suggesting that perceptual processes may be sufficient to accomplish these judgments. Finally, I will explain further why these judgments can be of particular interest to test the TVS model.

4.1 Mental simulation theory

Judgments about how one would perform an action are assumed to be made by mentally simulating this action (Jeannerod, 2001; Johnson, 2000). For instance, judgments about the capability to reach and grasp an object would be solved by mentally simulating a grasping movement towards the object without performing any overt movement. The mental simulation of action has been shown to be analogous to action execution, in the sense that action simulation recruits the same representations and processes but at a covert level, *i.e.*, without activating the muscles required for the overt execution of that action. Prospective action judgments would thus offer an open window on the covert stages of action.

There is abundant evidence for equivalence between the mental simulation of an action and its physical execution. For instance, chronometric studies showed that the time required to simulate mentally an action was equivalent to the time required to actually execute this action (Decety, Jeannerod & Prablanc, 1989; Decety & Michel, 1989). Studies using fMRI further showed that imagined and executed movements were associated with partially overlapping activity within the parietal and frontal cortices including the contralateral primary motor cortex (M1), which is usually considered as a purely executive area (Gerardin et al., 2000). In several studies, motor imagery also modulated cortico-spinal (*e.g.*, Fadiga et al., 1998; Kasai, Kawai & Kawanishi, & Yahagi, 1997) and muscle (*e.g.*, Bird, 1984; Livesay & Samaras, 1988) activity, following similar patterns to action execution, although no actual motor output was produced. Similarly, autonomous responses such as heart rate, CO^2 pressure, and breathing frequency were enhanced during imagined physical effort (Decety, Jeannerod, Durozard, Baverel, 1993; Decety. Jeannerod, Germain & Pastene, 1991). Physical effort is also reflected in the duration of the mental simulation. For instance, participants took more time to imagine themselves

walking a certain distance when they were wearing a heavy backpack than without a backpack (Decety et al., 1989). Hence, motor imagery complies with Fitts' law, stating that difficult movements take longer to be executed than easy ones (Fitts, 1954). Finally, the existence of common cognitive processes best explains the positive transfer observed between the mental practice of a movement and its physical performance, thereby making motor imagery training a great tool for the recovery of motor skills after stroke (Denis, 1985; Carrasco & Cantalapiedra, 2016; Landers, 1983; MacKay, 1981). Mental movements thus mimic their actual counterpart both in their temporal organisation and their neural and physiological correlates.

The involvement of motor imagery in prospective action judgments is supported by their common resemblance with action. Indeed, action judgments are extremely veridical and affected by the biomechanical constraints of the related action. For instance, when making reachability judgments (*i.e.*, judging whether one would be able to reach an object), participants were sensitive to the motor constraints imposed by the posture in which the reaching would have been done (*e.g.*, while standing vs. sitting) or by the environment (*e.g.*, height and layout of the surface to be reached), although some were quite complex biomechanically (Carello, Grosofsky, Reichel, Solomon & Turvey, 1989; Cordova & Gabbard, 2014; Gabbard, Cordova & Lee, 2007; Rochat & Wraga, 1997). This was also reflected in the time required to make these judgments, with the time required to define the grip one would use to grasp a dowel increasing as a function of the angular distance of the wrist rotation along the most biologically plausible path rather than along the shortest path (Johnson, 2000). The causal involvement of the cognitive processes of action was further supported by studies showing that performing a concurrent hand motor task interfered with reachability judgments by increasing RLs or by suppressing effects indexing typical performance (Grade et al., 2015; Witt & Proffitt,

2008). Finally, neuroimaging studies have shown that prospective action judgments activated the dorsal stream, including the IPL, SPL, IPS and precuneus. Additional activations were found in the frontal structures, including the premotor cortex, and cerebellum. These areas are typically involved in motor planning and control of the corresponding action, hence, suggesting that these judgments rely, like motor imagery, on the sensorimotor representations computed in the dorsal stream (Bartolo et al., 2014; Johnson et al., 2002).

Based on these remarkable similarities between prospective action judgments, motor imagery and physical action, Johnson (2000) proposed that these judgments are solved by (1) encoding the visual properties of the object (*e.g.*, orientation, size, location), (2) activating the sensorimotor representations of the effectors implied in the judged action, and (3) applying to these representations the visuomotor transformations required by the visual properties of the object in a manner that respects the biomechanical constraints. Although these simulations are implicit and should be very rapid regarding the numbers of response options to simulate (about 100/s), they are assumed to operate in a way analogous to real actions.

4.2 Limitations and alternatives

Some limitations must be evoked with regard to the pieces of evidence supporting the involvement of motor simulation in prospective action judgments. At the behavioural level, the main evidence consists of the observation that prospective action judgments take into account the limits of the body. However, this effect has also been observed in patients born without upper limbs and, thus, lacking the associated sensorimotor representations. For instance, when judging the laterality of a depicted hand, both normally limbed individuals and a patient with congenitally absent upper limbs were sensitive to the biomechanical constraints imposed by left-

and right-hand movements. In particular, responses to the hand pictures were slower when they depicted positions difficult to adopt than when they depicted postures that can be easily adopted (Vannuscorps, Pillon & Andres, 2012). Similar effects of biomechanical constraints have been evidenced in several patients with a congenital absence of upper limbs using a range of task assumed to involved motor simulation (*e.g.*, action recognition, perception of apparent body movement; Vannuscorps & Caramazza, 2015; 2016a; 2016b). In addition, transient lesions to the motor system induced with TMS do not suppress the effect of the biomechanical constraints (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Pelgrims, Michaux, Olivier, & Andres, 2010; Sauner, Bestmann, Siebner, & Rothwell, 2006). Hence, observing that performance is modulated by the biomechanical constraints cannot be considered as proof that sensorimotor representations are being activated and manipulated within the motor system.

An alternative view assumes that the perceptual system can represent the biomechanical constraints associated with the human body, visually, without necessarily interacting with the somatosensory and motor representations. Human bodies, as faces, are recognised by identifying the spatial relations between their different parts. Presenting a body upside down would affect this configural processing, and therefore, impaired its recognition (Reed, Stone, Bozova & Tanaka, 2003). However, this is only true when the structural constraints of a standard human body are respected (Petit & Harris, 2005). The visual system would thus be endowed with a structural representation of the human body describing the different body parts and their spatial relations to allow subsequent recognition (Biederman, 1987; Cave & Kosslyn, 1993; Marr & Vaina, 1982). This visual representation could also include the biomechanical constraints of the body in movement (Shiffrar & Freyd, 1993; Vannuscorps et al., 2012). This is further supported by neuroimaging studies showing that the occipitotemporal areas are sensitive to violations of the

biomechanical constraints when observing dynamic actions (Costantini et al., 2005; Stevens, Fonlupt, Shiffrar, & Decety, 2000).

Although these two views were mostly discussed within the context of hand laterality judgments and motion perception, the same debate about the involvement of perceptual or sensorimotor representations can be applied to prospective action judgments. The effect of the biomechanical constraints on these judgments does not necessarily imply they access the sensorimotor representations of the body as they might alternatively access the visual representation of one's body and its limits. It is worth noting that the two views are not mutually exclusive. It has been previously hypothesised that the performance of healthy participants in the hand laterality judgment task is performed, first, by comparing the hand to its structural representation in the visual system, and then, as a verification strategy, by mentally moving one's hand into the judged hand posture (Parsons, 1987). Similarly, prospective action judgments might involve both perceptual and motor strategies: patients who lack the relevant sensorimotor representations would then only rely on the perceptual processes, meaning that mental simulation is not strictly necessary and that perceptual processes are sufficient (Vannuscorps & Caramazza, 2015).

To conclude, prospective action judgments allow accessing the representations underlying the covert stages of action. However, the exact nature of these representations is still unclear. While some studies suggest that the sensorimotor representations of the effectors are involved, other studies suggest that these representations might not be not necessary and that perceptual representations of the body might be sufficient to make predictions about the outcome of an action.

4.3 Prospective action judgments to test the TVS model

For several reasons, prospective action judgments are of great interest to test whether perception and action rely on different visual processes that respectively take place in the ventral and dorsal streams.

First, they allow extending the investigation of action to its covert stages, which are still little understood. Indeed, within the context of the TVS model, action was always assessed during the overt phase of the movement, and most often near the end of the movement. The investigation of the covert stages of action will provide more precise information about the representations underlying action, before they are blurred by the mechanisms implemented during action execution, such as on-line corrections.

Second, prospective action judgments are easy to match with a perceptual task. Indeed, the absence of overt movement prevents action from benefitting of additional sensory information about the acting hand compared to perception. Moreover, prospective action judgments, just as perceptual tasks, are typically assessed through verbal reports. For instance, in this thesis, I used judgments were participants have to indicate whether they feel able to grasp an object between index finger and thumb, by answering by “yes” or “no”, and without actually grasping it. I compared them to perceptual judgments requiring participants to judge whether the object is larger than a standard by answering by “yes” or “no”. In this case, perception and action measures imply the same level of awareness and allow using the same stimuli, measures, and apparatus, with the only difference consisting of the instructions. This allows a direct comparison of the processes underlying perception and action to be made and thus to test the assumption that they are different by nature.

5. Outline of the thesis

In this first Chapter, I reviewed the literature evidencing a division of the visual system, from the retina to the higher levels of the cortex, in mainly two streams. I described in more details the evidence and challenges of the dominant TVS model that assumes that the ventral stream computes relative object metrics in a scene-based reference frame to provide an integrated representation of the visual world, while the dorsal stream computes the absolute object metrics to support visually-guided actions. I concluded on a lack (1) of conclusive evidence for perception and action to have competing demands handled by distinct anatomical streams applying very specific transformations to the visual input and (2) of investigation of the covert stages of action, leaving the underlying representations little understood. I then presented evidence for prospective action judgments to be analogous to the covert stages of action and how this can be of great interest in investigating the processes and representations underlying action in comparison with those underlying perception.

The first aim of this thesis is to test the fundamental claim of the TVS model that perception and action involve distinct visual processes by using prospective action judgments. These judgments will be used to allow the matching of perceptual and action measures, and thus the direct comparison of perceptual and motor processes. Moreover, I will investigate this duality in the particular case of size processing. Size is a visual attribute for which the hypothesis that perception and action respectively compute absolute and relative metrics in a scene-based and egocentric frame of reference can easily be tested with the well-known size-contrast illusion paradigm. In particular, I will investigate the effect of the visual context on perceptual and grasping judgments that are perfectly matched in terms of available sensory information and level of awareness. I will also investigate the respective

contribution of the ventral and dorsal streams in these processes. The second aim is to investigate further the nature of grasping judgments to get a better understanding of the representations informing action that have been overlooked by the TVS model. The investigation will be extended to the integration of both visual and sensorimotor information.

Chapter 2 investigates in a series of experiments whether the Ebbinghaus illusion and thus visual context affect the computation of object size for grasping judgments similarly than for perceptual judgments. I will also test the involvement of the sensorimotor representation of the hand in grasping judgments. To do so, I will add a concurrent hand motor task assumed to interfere with the covert activation of the motor processes of grasping judgments, but not the perceptual representation of size.

Chapter 3 investigates more deeply the nature of grasping judgments by ensuring that the effect of the concurrent motor task on grasping judgments truly reflects the integration of the somatosensory information of the hand in the prospective action plan, independently of semantic biases.

Chapter 4 investigates the potential interaction between the visual context and the somatosensory information. In particular, I will test whether the effect of the motor task observed in previous chapters depends on the presence of the illusion.

Chapter 5 investigates the neural correlates of perceptual and grasping judgments. More precisely, I will use fMRI and TMS to test whether grasping judgments, unlike perceptual judgments, involve the same motor areas of the dorsal stream than motor imagery.

Finally, Chapter 6 investigates whether the common processes observed for perceptual and grasping judgments at the behavioural level (Chapter 2) and neural

level (Chapter 5) are the result of interactions between the ventral and dorsal steams. To do so, I will manipulate the low-level visual properties of the Ebbinghaus illusion to bias its processing towards the parvocellular or magnocellular pathway and, hence, the ventral or dorsal stream and investigated the impact on size estimates and visual context integration during perceptual and grasping judgments.

Chapter 2

Visual illusions modify object size estimates for prospective action judgments

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This chapter is an adapted version of: Geers, L., Pesenti, M., & Andres, M. (2018). Visual illusions modify object size estimates for prospective action judgments. *Neuropsychologia*, *117*, 211-221.

1. Introduction

Vision provides a colourful and detailed representation of the external world and plays a major role in the guidance of actions towards the external world. For instance, vision allows one to recognise and precisely describe objects (*e.g.*, an apple), but also to reach, grasp and use them (*e.g.*, grasp an apple and bite off a piece). Neuropsychological studies have shown that some brain-damaged patients have impaired object recognition but have preserved reaching and grasping abilities (*i.e.*, visual agnosia; Farah, 1990), while other patients have the opposite pattern (*i.e.*, optic ataxia; Perenin & Vighetto, 1988). This dual role of vision is the cornerstone of the perception-action model in assuming that the visual pathways supporting perception and action remain separate from input to output. Visual perception would rely on a ventral pathway extending from the striate cortex to the inferior temporal cortex, whereas visually-guided action would rely on a dorsal pathway extending from the striate cortex to the SPL. The specialisation of these two visual pathways is motivated by the competing demands of vision for perception and for action. The

model assumes that the ventral stream computes relative size and distance in order to give rise to an integrated representation of the visual world, while the dorsal stream computes estimates of actual size and distance from an egocentric perspective to calibrate the amplitude of reaching movements and adequately shape the handgrip when grasping objects. One important prediction of this model is that the visual context because it provides relative estimates of object size is processed only within the ventral stream for perception (Goodale & Milner, 1992; Milner & Goodale, 2008).

Visual illusions that make objects appear smaller or larger than they actually are because of the visual context provide a unique paradigm to test this prediction of the perception-action model. Indeed, such illusory displays preserve the real size of the object while the visual context modifies the perception of this size. The Ebbinghaus illusion has been used extensively in recent decades to test the (in)dependence of the visual processes underlying perception and action. This illusion consists of a central circle (*i.e.*, the target) surrounded by an array of smaller or larger circles (Figure 1). Seminal studies showed that participants judged the size of a central circle surrounded by an array of small circles as larger than the same circle surrounded by large circles, while the grip aperture adopted to grasp the target circle was not affected by the illusion (Aglioti et al., 1995; Haffenden & Goodale, 1998). Perceptual judgments thus seemed strongly affected by the illusion while action seemed not to be. The finding that visual illusions do not influence action was subsequently challenged by other results. For example, an effect of the Ebbinghaus illusion on grasping was found after controlling the distance between the target and surrounding circles (Franz, Bülthoff & Fahle, 2003) or the number of illusory configurations the attention has to focus on (Franz et al., 2000; Pavani et al., 1999). In these studies, the effects on action were typically of a smaller degree than the ones observed on perception, but this has been attributed to the different scaling of

perceptual and grip responses to object size. Indeed, in the studies that used manual estimation (*i.e.*, indicating the perceived size by adjusting the opening between index finger and thumb) to assess perception, the distance between the fingers was more sensitive to object size variations than the MGA measured during reach-and-grasp movements (Franz & Gegenfurtner, 2008). However, a number of other studies carefully controlling for the aforementioned issues reported dissociated effects on perception and action (*e.g.*, Amazeen & DaSilva, 2005; Stöttinger, Soder, Pfusterschmied, Wagner & Perner, 2010; van Doorn, van der Kamp & Savelsbergh, 2007; Whitwell, Goodale, Merritt & Enns, 2017). These divergent results do not allow firm conclusions to be drawn about the possible differences in the visual processes serving perception and action. The situation is further complicated by the difficulty in matching perception and action across tasks because of the additional visual and proprioceptive information provided by the acting hand when an action is actually executed compared to mere perception (Post & Welch, 1996; but see Goodale et al., 2004). This feedback is a potential source of interference in studies investigating actual actions because it allows participants to correct the error introduced by the illusion as the hand approaches the object. To sum up, the effect of visual illusions has so far only been assessed on actual actions, and it remains unclear whether the motor system relies on object size estimates independent of the visual context.

We propose to use prospective action judgments as a proxy to test the effect of visual illusions on action while controlling the visual and proprioceptive feedback of the acting hand. Judging one's capability to make an action without actually performing it would require the mental transformation of the visual inputs into sensorimotor representations of the effectors in order to anticipate the consequences of the action (*e.g.*, Bernstein, 1967; Rosenbaum, 1991). Prospective action judgments have shown remarkable similarities to real actions. They are affected by

the biomechanical constraints of the implied movement (Frak, Paulignan & Jeannerod, 2001; Johnson, 2000; Parsons, 1987) and by motor parameters (*e.g.*, actual posture: Carello et al., 1989; Mark et al., 1997) or semantic properties known to influence real actions (*e.g.*, numerical magnitude: Andres, Davare, Pesenti, Olivier & Seron, 2004; Badets, Andres, Di Luca & Pesenti, 2007). Neurophysiological findings also indicate that prospective action judgments involve cortical processes present in actual movements, notably those involved in motor planning and action control (*e.g.*, Bartolo et al., 2014; Coello et al., 2008; Johnson et al., 2002). Prospective action judgments thus provide a unique tool to investigate the processes underlying action anticipation while at the same time avoiding the limitations inherent to actual movement.

Here we tested the hypothesis that the computation of object size for action is independent of the visual context by looking at the effect of a size-contrast illusion on a prospective grasping judgment task. This task requires participants to decide whether they think they would be able to grasp the central circle of an Ebbinghaus display without actually grasping it. Experiment 1 examined the effect of the Ebbinghaus illusion on a prospective grasping judgment task; a perceptual judgment task was used as a control measure of the illusion effect. The next two experiments further investigated the potential interaction between visual and sensorimotor information by assessing the possible influence of hand sensorimotor processes on size-contrast illusions observed during action judgments. In Experiment 2, participants made either perceptual or grasping judgments on an Ebbinghaus display while squeezing balls between the index finger and thumb of each hand. Under the assumption prospective action judgments specifically involve the covert activation of sensorimotor representations, the concurrent squeezing task should interfere with grasping judgments while leaving perceptual size judgments unaffected. Experiment 3 investigated whether the predicted interference was indeed determined by the

current hand posture by asking participants to make the opposite movement, namely spreading apart the index finger and thumb of each hand during grasping and perceptual judgments. If the interference is caused by the current hand posture, participants should underestimate their grasping ability in Experiment 2 while they should overestimate it in Experiment 3.

2. Experiment 1

2.1 Method

2.1.1 Participants

Thirty-two undergraduate students (22 females, mean age and standard deviation (SD): 23 ± 2 years) of the Université catholique de Louvain, Belgium, participated in Experiment 1. All participants had normal or corrected-to-normal vision and declared themselves as right-handed. They all gave written informed consent prior to the experiment and were unaware of the hypotheses being tested. The study was performed in accordance with the ethical standards of the Declaration of Helsinki and was approved by the Ethical Committee of the Psychological Sciences Research Institute of the Université catholique de Louvain. Half of the participants were randomly assigned to the perceptual group and the other half to the grasping judgment group (see below).

2.1.2 Apparatus and stimuli

Participants sat at a viewing distance of 75 cm from a vertical screen with their head resting on a chin rest at the centre of the screen to keep this distance constant throughout the experiment (Figure 2A). A voice key was fixed on the chin rest to record RLs. A projector (MP7740, 3 M, United States) was placed behind the screen. The resolution of the projected image was 1280×1024 pixels, with 1 pixel

corresponding to 0.19 cm and 1 cm corresponding to 0.76°. Stimulus presentation and data recording were programmed using E-prime 2 (Schneider, Eschman & Zuccolotto, 2002).

The stimuli consisted of three configurations of the Ebbinghaus illusion. The configurations varied in two aspects: the size of the central circle and the size of the surrounding circles. The size of the central circle (the target) was centred either on the MGA of the participant measured prior to the experiment or on a reference circle of 13 cm, with its diameter varying from − 4 to + 4 cm by increments of 1 cm. We assessed the MGA of each participant by asking her/him to grasp wooden bars ranging from 9 to 20 cm by 1-cm increment with the dominant hand. The MGA was given by the longest bar the participant was able to hold between the tips of the index finger and thumb. The length of the bar was used as a reference for generating the sizes used in the prospective action judgment task.

The mean size of the participants' MGA was 14.5 cm. The apparent size of the circle was manipulated by a surrounding annulus consisting of circles that were either larger or smaller than the target, making the latter appear smaller or larger respectively (referred hereafter as small and large illusory display). The large surrounding circles were twice as large, and the small surrounding circles were twice as small as the target. An additional display with surrounding circles of the same size than the target was used as a control not inducing any illusion (Figure 1). The gap between the target and the surrounding circles was always equal to the size of the target so that obstacle avoidance mechanism may not be responsible for a potential illusion effect on grasping judgments (Haffenden & Goodale, 2000; but see also Franz et al., 2003).

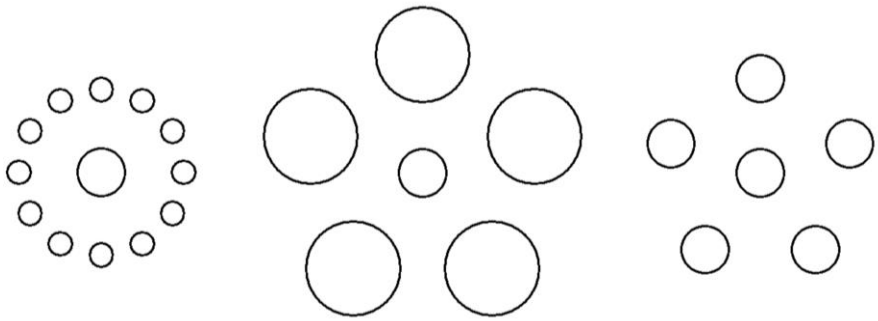

Figure 1. *Ebbinghaus displays used in the three experiments: a display with small surrounding circles making the target look larger (i.e., large display), a display with large surrounding circles making the target look smaller (i.e., small display) and a non-illusion display with surrounding circles of the same size as the target (i.e., neutral display).*

2.1.3 Tasks and procedure

Two types of judgment randomly counterbalanced across participants were used. Grasping judgments required the participants to decide whether they thought they would be able to grasp the central circle between their index finger and thumb, whereas the perceptual size judgment task was to decide whether the central circle was smaller than the in-view reference circle. The reference was displayed 80 cm to the right and 40 cm to the bottom of the centre of the screen during the whole duration of the experiment. The instructions emphasised the need to keep hands flat under a cardboard surface mounted above the surface table, in the horizontal plane, rendering the hands invisible to the participant.

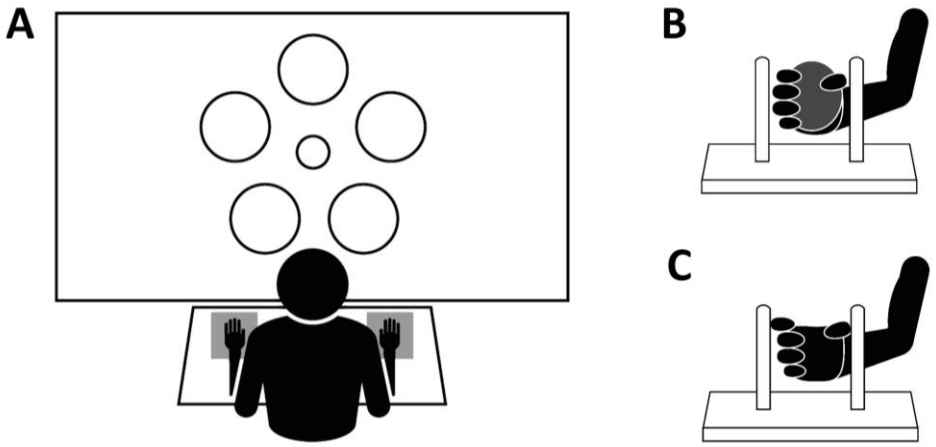

Figure 2. *Experimental setup. (A) The participants sat at a table in front of a wide screen onto which the stimuli were projected from behind. They held their hands below cardboard surfaces that made them invisible. (B) Experiment 2 included an additional condition where the participants had to squeeze foam balls between the index finger and thumb of each hand. They had to maintain a constant pressure such that the grip formed by the fingers over the ball filled the gap between two vertical iron bars placed next to each hand. (C) In Experiment 3, the participants had to spread the index finger and thumb of each hand so that they were in contact with the two vertical iron bars placed at a distance calibrated to their MGA.*

Each trial started with the presentation of a fixation cross at the centre of the screen for 500 ms, followed by the projection of an Ebbinghaus display. The participants responded "yes" or "no" aloud to indicate whether they judged the central circle as graspable (grasping judgment) or smaller than the reference circle (perceptual judgment). The image then disappeared. Participants were asked to respond as quickly and accurately as possible, and responses were encoded on-line by the experimenter. The next trial began 1500 ms after response encoding. The participants performed 6 practice trials before taking 2 blocks of 81 trials consisting of the 9 possible sizes of the central circle, repeated 3 times for each of the 3 illusion

conditions. The different combinations of circle sizes and illusion conditions were randomly mixed within each block.

2.1.4 Data analysis

Trials in which RLs were shorter than 100 ms (0.91% of the data) or in which the voice key failed to trigger (5.36%) were discarded from further analyses. In order to test whether the two judgments were of equal difficulty, the mean RLs were compared using an independent-samples t-test. We modelled the probability of judging the target circle as being graspable (grasping judgment) or smaller than the reference (perceptual judgment) as a function of its size, by applying a logistic regression to the responses of each participant. The point of subjective equality (PSE), which is the target size for which the probability of responding “yes” was 50%, was then computed for each participant and each illusory display. Participants were excluded if their estimated PSE fell outside the range of target sizes used in the study, as this indicates that they were not able to make a reliable judgment even for extreme values (*i.e.*, circles that were 4 cm smaller or larger than their grip aperture or than the reference circle). Three participants performing the grasping judgment task and one performing the perceptual judgment task were excluded for this reason. An analysis of variance (ANOVA) was conducted on the PSE obtained in the remaining participants of each group with the illusory display (small, neutral *vs.* large) as a within-subject factor. In this experiment, no direct comparison was made between groups because the instructions biased the PSE towards larger values in the perceptual judgment task relative to the grasping judgment task. Indeed, in the perceptual judgment task, a "no" response was expected for objects larger than the reference as well as for objects equal to the reference, whereas grasping judgments called for a "yes" response when object size was equal to MGA that was taken as the comparison standard in this task. The Greenhouse-Geisser correction was applied

when the sphericity assumption was violated, and the Bonferroni correction when post-hoc analyses implied multiple comparisons.

2.2 Results

A t-test showed no difference between RLs measured in the perceptual (1041 ± 250 ms) and grasping (1037 ± 200 ms) judgment tasks ($t(26) = -0.04$, $p = 0.227$).

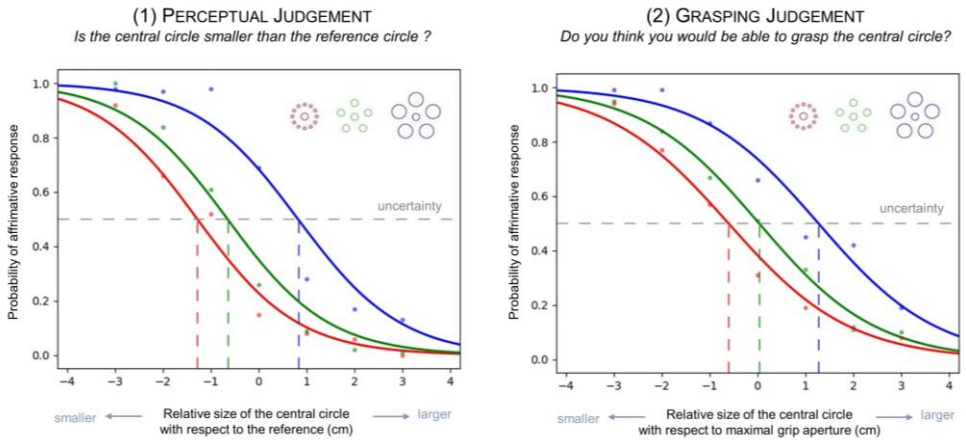

Figure 3. *Fitted curves from cumulative data showing the effect of the Ebbinghaus illusion on perceptual and grasping judgments in Experiment 1. The dots represent the average rate of affirmative responses (y-axis) as a function of the difference between (1) the actual size of the central circle and the size of the reference circle or (2) the actual size of the central circle and the participant's MGA (x-axis). Solid lines represent the predicted values obtained by means of logistic regression, while the dashed lines correspond to the PSE (i.e., circle size at which participants provide affirmative responses in 50% of the trials).*

As illustrated in Figure 3, the rate of affirmative responses decreased as the size of the central circle increased (from 0.97 for the smallest to 0.02 for the largest size for perceptual judgments and from 0.98 to 0.06 for grasping judgments). This

means that the participants were sensitive to the variations of the actual size of the central circle and performed the task correctly. Moreover, for both judgments, the curve of affirmative response probability shifted towards smaller or larger sizes according to the illusory display. Compared to the neutral display, the curve for the large illusory display shifted towards smaller sizes, indicating that the target size had to be smaller to be considered as equal to the reference circle or grip aperture. Conversely, the curve for the small illusory display shifted towards larger sizes compared to the curve for the neutral display, indicating that the target had to be larger to be considered as equal to the reference circle or grip aperture.

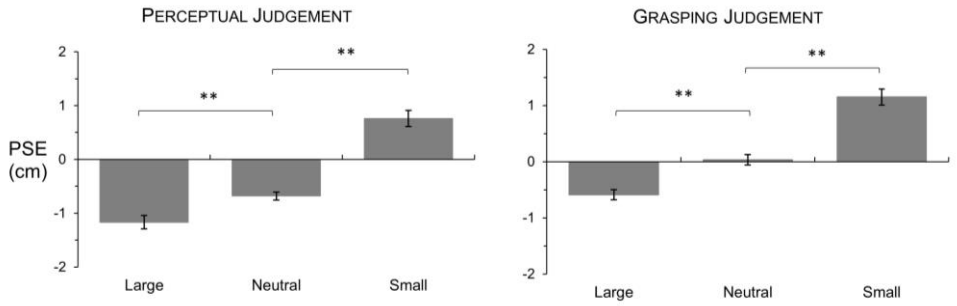

Figure 4. *Mean PSE in the grasping and perceptual judgment tasks of Experiment 1. A PSE was computed for each illusory display and participant separately. Asterisks indicate that the PSE for the large and small illusory displays were significantly smaller and larger compared to the neutral display (p < 0.001). Error bars represent standard errors corrected for within-subject designs (Cousineau, 2005). ** p-value < 0.01.*

In the perceptual size judgment task, the ANOVA revealed that the PSE was significantly influenced by the illusory display ($F(2,28) = 44.23$, $MSE = 0.34$, $p < 0.001$). Post-hoc paired *t*-tests showed that, compared to the neutral display, participants hesitated on smaller sizes when judging the central circle of the large illusory display ($t(14) = -3.50$, $p = 0.004$) and on larger sizes when judging the central circle of the small illusory display ($t(14) = 6.95$, $p < 0.001$). The mean PSE

(± SD) was equal to − 1.17 ± 0.26 cm in the large condition, − 0.68 ± 0.20 cm in the neutral condition and 0.76 ± 0.30 cm in the small condition (Figure 4).

In the grasping judgment task, the ANOVA revealed that the PSE was significantly influenced by the illusory display ($F(2,24) = 34.69$, $MSE = 0.29$, $p < 0.001$). Post-hoc paired t-tests indicated that, compared to the neutral display, participants hesitated on smaller sizes when the target was presented in the large illusory display ($t(12) = -5.05$, $p < 0.001$) and on larger sizes when the target was presented in the small illusory display ($t(12) = 4.53$, $p = 0.001$). The mean PSE (± SD) was equal to − 0.59 ± 0.42 cm in the large condition, − 0.04 ± 0.45 cm in the neutral condition and 1.15 ± 0.40 cm in the small condition (Figure 4).

3. Experiment 2

Experiment 2 extended Experiment 1 with the addition of a concurrent motor task to test whether grasping judgments involved sensorimotor processes. This manipulation also allowed us to directly investigate the interplay between size-contrast illusions and sensorimotor representations in grasping judgments. Because prospective action judgments imply the covert activation of sensorimotor representations, we expected the concurrent motor task to affect the grasping judgment task but not the perceptual judgment task.

3.1 Method

3.1.1 Participants

A new sample of 40 undergraduate students (29 females, mean age ± SD: 22.1 ± 1.9 years) of the Université catholique de Louvain, Belgium, participated in the present experiment. They had normal or corrected-to-normal vision and declared

themselves as right-handed. They all gave written informed consent prior to the experiment. The study was performed in accordance with the ethical standards of the Declaration of Helsinki and was approved by the Ethical Committee of the Psychological Science Research Institute of the Université catholique de Louvain. Participants were randomly split into two groups of 20, one making perceptual judgments, the other making grasping judgments. Experiment 1 showed that a sample size of 16 participants per task achieves a 95% power to detect a true shift of the PSE by 0.63 cm with an estimated SD of 0.44 cm with $\alpha = 0.05$ using a two-sided paired-sample *t*-test. In this new experiment, we tested 20 participants in each task to maximise the chance of detecting an effect of the illusory display.

3.1.2 Apparatus and stimuli

We used the same apparatus and stimuli than in Experiment 1, except that the size of the target circle was − 5, − 3, − 2, − 1, 0, + 1, + 2, + 3 or + 5 cm relative to the reference circle or participant's MGA.

3.1.3 Tasks and procedure

Experiment 2 followed the same procedure than Experiment 1 except for three minor modifications.

First, the instructions were matched across tasks to make the response function similar in the two tasks. In Experiment 1, the perceptual judgment task required participants to judge whether the target was smaller than the reference and thus required a "yes" response for circles of -5 to -1 cm and a "no" response for circles of +0 to +5 cm. On the other hand, the grasping judgment task required participants to judge whether they would be able to grasp the target, and thus required a "yes" response for circles of -5 to +0 cm and a "no" response for circles of +1 to +5 cm. Indeed, a circle of the size of the MGA is still graspable. Hence, the

expected size on which participants would shift from a “yes” to a “no” response was not identical in the perceptual and grasping judgment tasks. To address this issue, the perceptual judgment task of Experiment 2 required participants to judge whether the target was larger than the reference circle (instead of smaller in Experiment 1). With these new instructions, the perceptual judgment task required a “no” response for circles of -5 to +0 cm and a “yes” response for circles of +1 to +5 cm, thereby putting the expected shift between “yes” and “no” responses on the same size than in the grasping judgment task. As a corollary, central circles from -5 to +0 cm then required a “yes” response in the perceptual judgment and a “no” response in the grasping judgment task. In order to be able to interpret the effects consistently in the two tasks, a “yes” response was coded 0 for the perceptual judgment and 1 for the grasping judgment (i.e., the circle was perceived as “not large” and “graspable”), whereas a “no” response was coded 1 for the perceptual judgment and 0 for the grasping judgment (i.e., the circle was perceived as “large” and “non-graspable”).

Second, the MGA of each participant making grasping judgments was used as the reference value for a paired participant making perceptual judgments so that the same values were used as references in the two groups.

Finally, the reference circle used in perceptual judgments was displayed in front of the participant before each block and was removed during the task itself to avoid attention shifts between the target and the reference circle while making the judgment. Removing the reference from view implied that working memory was involved in this new version of the perceptual judgment task. However, grasping judgments, since they are assumed to require activating and manipulating the sensorimotor representation of the hand, should also involve working memory. Hence, the modification of the perceptual judgment task actually allowed us to match it more closely to the grasping judgment task.

In addition to these minor modifications, a concurrent motor task required participants to squeeze 7-cm foam balls between the index finger and thumb of each hand while making the perceptual or grasping judgments. Instructions emphasised the need to squeeze the ball with sufficient pressure so that the grip formed by the fingers over the ball filled the 8 cm gap between two vertical iron bars placed next to each hand (Figure 2B). The participants were asked to maintain this hand posture throughout a block of trials, and a webcam was used to monitor their performance on-line.

After 6 practice trials, the participants completed 4 blocks of 81 trials, each containing the 9 target sizes presented 3 times with each of the 3 illusory displays. The different combinations of circle size and illusion condition were randomly mixed within each block. Half of the participants kept their hands at rest on the table during the first two blocks and performed the concurrent motor task during the next two blocks, whereas this order was reversed in the other half of the participants.

3.1.4 Data analysis

An ANOVA was conducted on the median RLs with the motor condition (still *vs.* squeeze) as a within-subject factor and the type of judgment (grasping *vs.* perceptual) as a between-subject factor in order to investigate the effect of motor interference and test whether both tasks were of equal difficulty. Responses faster than 100 ms (0.28%) and failures of the voice key to trigger (9.68%) were discarded. Following the same method as in Experiment 1, a PSE was computed for each participant, illusory display and motor condition. The PSE estimated for each participant fell within the range of the target sizes used in the study. An ANOVA was thus conducted on the PSE of all participants with the type of judgment (perceptual *vs.* grasping) as between-subject factor and the illusory display (small, large *vs.* neutral) and the motor task (still *vs.* squeeze) as within-subject factors. A

separate preliminary analysis showed no main effect of the order of the motor tasks or interaction between order and the other factors. For this reason, order was not included in the subsequent analysis. The Greenhouse-Geisser correction was applied when the sphericity assumption was violated, and the Bonferroni correction when post-hoc analyses implied multiple comparisons.

3.2 Results

The ANOVA on RLs did not reveal any significant main effect or interaction. There was no difference between the latency of grasping (869 ± 135 ms) and perceptual (885 ± 135 ms) judgments ($F(1,37) = -0.14$, $MSE = 18179.63$, $p = 0.709$), and no difference between the hands at rest (868 ± 141 ms) and squeezing (870 ± 157 ms) conditions ($F(1,37) = 0.27$, $MSE = 9034.67$, $p = 0.709$).

Figure 5 illustrates the cumulative data in each group. The fitted curves indicate that in the two conditions (still *vs*. squeeze) of each judgment (grasping *vs*. perceptual), the rate of affirmative responses decreased as the size of the central circle increased (perceptual-still: from 1 to 0.02, perceptual-squeeze: from 1 to 0.01, grasping-still: from 1 to 0.05, grasping-squeeze: from 0.99 to 0.01), indicating that each group of participants performed the task correctly. Moreover, in all conditions, the probability curve of affirmative response for the large illusory display shifted towards smaller values compared to the neutral display, while the probability curve for the small illusory display shifted towards larger values.

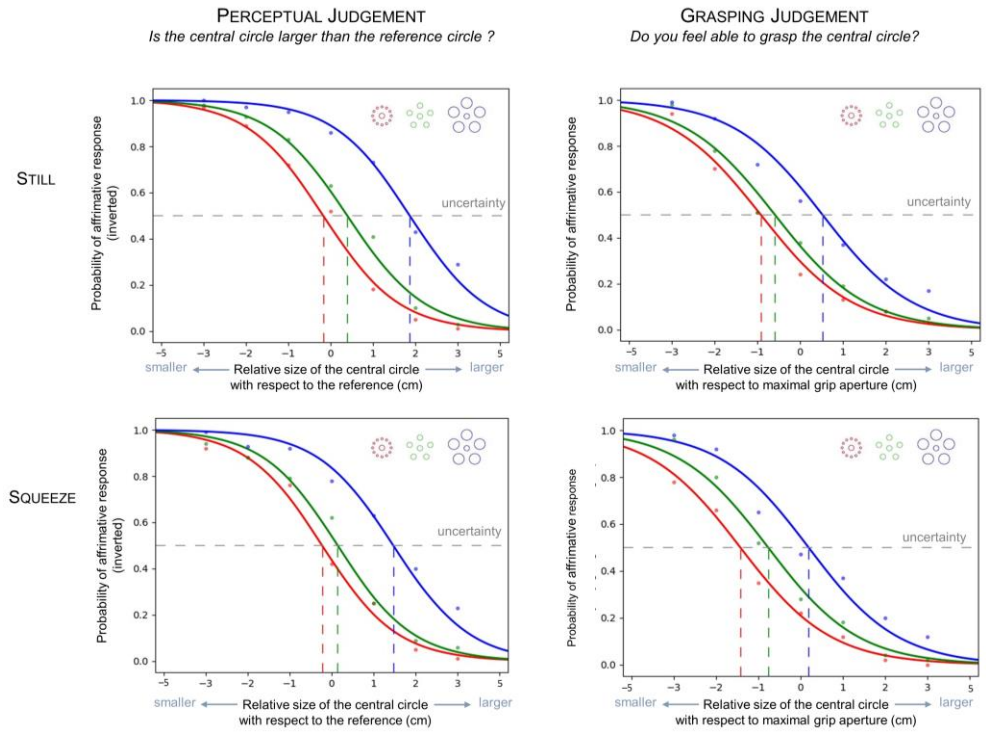

Figure 5. *Effect of the Ebbinghaus illusion on perceptual and grasping judgments in Experiment 2. The two graphs on the left side of the figure represent the cumulative data from the perceptual judgment for each motor condition (still vs. squeeze). The dots represent the average rate of affirmative responses (y-axis) as a function of the difference between the actual size of the central circle and the size of the reference circle (x-axis). The responses were inverted (i.e., "yes" was coded 0, "no" was coded 1) to allow comparison with the data from the grasping task. The two graphs on the right side of the figure represent the cumulative data from the grasping judgment for each motor condition (still vs. squeeze). The y-axis represents the rate of affirmative responses, and the x-axis represents the difference between the actual size of the central circle and participant's MGA. In all graphs, solid lines represent the predicted values obtained by means of logistic regression, while the dashed lines correspond to the PSE (i.e., circle size at which participants provide affirmative responses in 50% of the trials).*

The ANOVA on the PSE revealed a main effect of the illusory display ($F(2, 76) = 126.15$, $MSE = 0.51$, $p < 0.001$). Post-hoc paired *t*-tests indicated that, compared to the neutral display, participants hesitated on smaller sizes when the target was presented in the large illusory display ($t(39) = -7.55$, $p < 0.001$) and on larger sizes when the target was presented in the small illusory display ($t(39) = 10.53$, $p < 0.001$). The mean PSE ($\pm$ SD) was equal to -0.68 ± 0.20 cm in the large condition, -0.20 ± 0.19 cm in the neutral condition and 1.06 ± 0.22 cm in the small condition. The analysis also revealed an effect of the type of judgment ($F(1,38) = 7.27$, $p = 0.010$, $MSE = 1.52$), indicating that participants who made a grasping judgment hesitated on smaller sizes (-0.47 ± 0.28 cm) than did those who made a perceptual judgment (0.58 ± 0.28 cm). There was also a main effect of the motor task ($F(1,38) = 5.36$, $MSE = 1.01$, $p = 0.026$), showing that participants hesitated on smaller sizes when they had to squeeze balls (-0.41 ± 0.25 cm) than when they performed judgments with their hands at rest (-0.07 ± 0.22 cm). These effects were integrated into a significant three-way judgment by motor task by illusory display interaction ($F(2,76) = 4.06$, $MSE = 0.16$, $p = 0.021$).

In order to understand this interaction, we looked at the effects of the illusory display and motor condition separately for the two tasks. In the grasping judgment task, we found an effect of the illusory display ($F(2,38) = 5.58$, $MSE = 0.75$, $p = 0.029$) with participants hesitating on smaller sizes, compared to the neutral display, when they had to judge the large illusory display ($t(19) = -5.68$, $p < 0.001$) and on larger sizes when they had to judge the small illusory display ($t(19) = 7.46$, $p < 0.001$). There was also an effect of the motor task ($F(1,19) = 5.58$, $MSE = 0.75$, $p = 0.029$) with participants hesitating on smaller size when they had to squeeze a ball than with hands at rest. Finally, there was an interaction between illusory display and motor task ($F(2,38) = 3.77$, $MSE = 0.13$, $p = 0.032$). Post-hoc t-tests showed that the difference between the still and squeeze conditions was significant only when

participants made grasping judgments on the large illusory display ($t(19) = -3.23$, $p = 0.009$; Figure 6). No difference was observed when participants made grasping judgments on the neutral or small illusory display ($p > 0.1$).

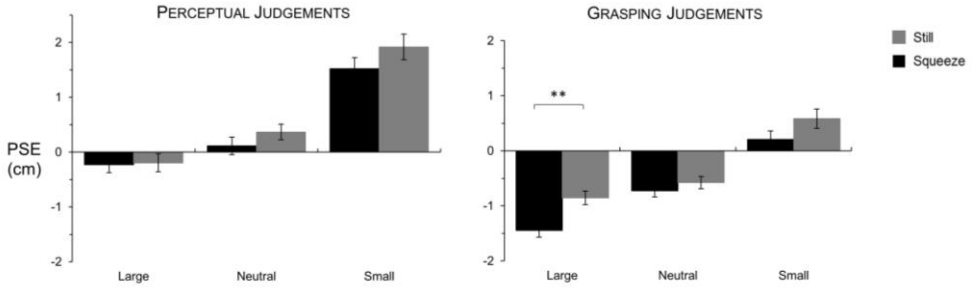

Figure 6. *Means PSE in the perceptual and grasping judgment tasks of Experiment 2. A PSE was computed for each illusory display, motor condition and participant separately. For both judgments, the mean PSE for the large and small illusory display were significantly smaller and larger compared to the neutral display (all p-values <0.05). Moreover, the mean PSE was significantly smaller when participants had to make grasping judgments on the large illusory display while squeezing a ball than with hands at rest. Error bars represent standard errors corrected for within-subject designs. ** p-value < 0.01.*

In the perceptual judgment task, there was a significant effect of the illusory display ($F(2,38) = 61.14$, $MSE = 0.67$, $p < 0.001$) with participants hesitating on smaller sizes compared to the neutral display when judging the large illusory display ($t(19) = -5.68$, $p < 0.001$) and on larger sizes when judging the small illusory display ($t(19) = 7.46$, $p < 0.001$). There was no effect of the motor task ($F(2,38) = 1.22$, $MSE = 1.27$, $p = 0.282$) and no interaction of the illusory display with the motor task ($F(2,38) = 1.78$, $MSE = 0.19$, $p = 0.183$).

4. Experiment 3

Experiment 3 aimed to test whether the effect of the motor task is due to the specific felt position of the fingers or rather a global interference effect leading participants to be conservative. To do so, we replicated Experiment 2 but changed the motor task participants had to perform during their judgment. In contrast to the previous experiment, participants were asked to spread apart index finger and thumb. We expected this task to affect grasping judgment in the opposite direction to Experiment 2. If grasping judgments rely on the sensorimotor representation of the current finger position, participants should indeed overestimate their grasping abilities when their fingers are spread at maximum.

4.1 Method

4.1.1 Participants

A new sample of 40 undergraduate students at the Université Catholique de Louvain, Belgium (35 females, mean age ± SD: 21.8 ± 1.8 years) participated in this experiment. They had normal or corrected-to-normal vision and declared themselves as right-handed. They all gave written informed consent prior to the experiment. The study was performed in accordance with the ethical standards of the Declaration of Helsinki and was approved by the Ethical Committee of the Psychological Science Research Institute of the Université catholique de Louvain. Participants were randomly split into two groups of 20, one making the perceptual judgment task, the other making the grasping judgment task.

4.1.2 Apparatus and stimuli

The same apparatus and stimuli than in Experiment 2 were used, except that the gap between the two iron bars was now set to 115% of the maximal object size the participant could grasp (Figure 2C).

4.1.3 Tasks and procedure

The same tasks and procedure than in Experiment 2 were used, except for the concurrent motor task. In Experiment 3, the concurrent motor task required participants to spread apart the index finger and thumb of each hand while making perceptual or grasping judgments. The fingers had to be spread open so that they touched two vertical iron bars placed next to the hands. The participants were asked to maintain this hand posture throughout the block of trials, and a webcam was used to monitor their performance on-line.

4.1.4 Data analysis

Eleven per cent of the trials were discarded from the analyses because the voice key failed to trigger and 0.56% because the response occurred faster than 100 ms. Two participants were excluded from the grasping judgment group because of PSE values outside the range of sizes used. The same analyses as in Experiment 2 were applied to the data.

4.2 Results

The ANOVA on the RLs did not reveal any main effect or interaction. There was no difference between the RLs for perceptual and grasping judgments (respectively: 897 ± 47 ms, 934 ± 50 ms; $F(1,36) = 0.29$, $MSE = 45616.26$, $p = 0.597$). There was also no difference between the hands-at-rest and fingers-

spread conditions (respectively: 922 ± 38 ms, 897 ± 48 ms; $F(1,36) = 0.11$, $MSE = 8977.42$, $p = 0.588$).

As illustrated in Figure 7, the rate of affirmative responses decreased as the size of the central circle increased (perceptual-still: from 1 to 0.05, perceptual-spread: from 1 to 0.06, grasping-still: from 0.98 to 0.05 and grasping-spread: from 0.99 to 0.1). Participants were thus sensitive to the variations of the actual size of the central circle and performed the task correctly. As in the previous experiments, the probability curve of affirmative response shifted towards smaller or larger sizes according to the illusory display. Compared to the neutral display, the curve for the large illusory display shifted towards smaller sizes, while the curve for the small illusory display shifted towards larger sizes.

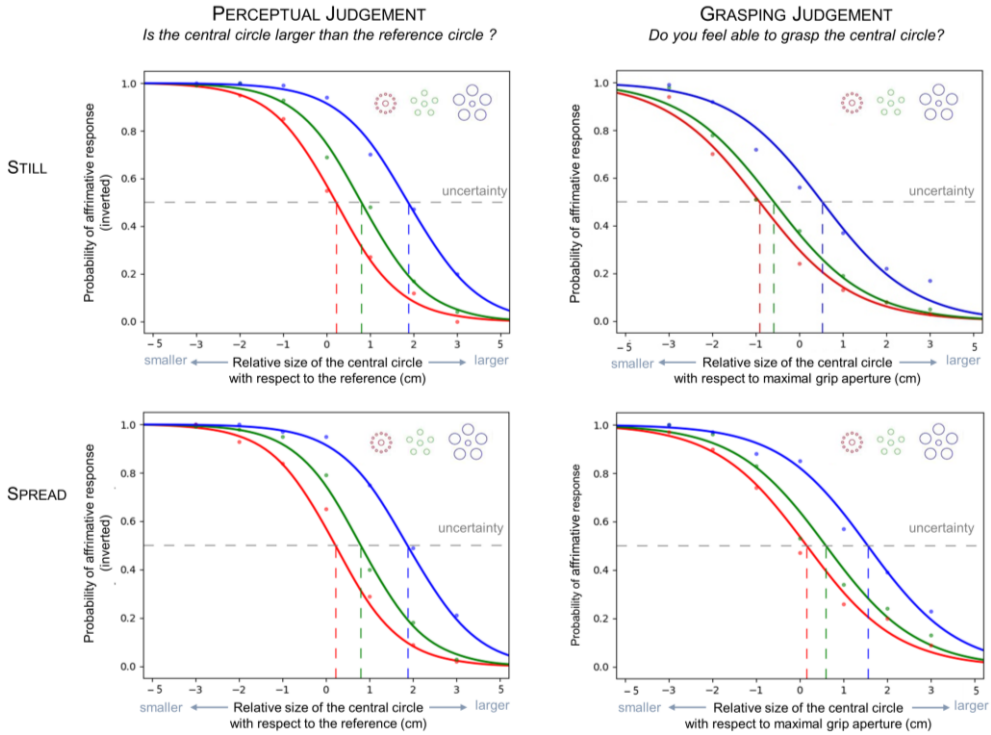

Figure 7. *Effect of the Ebbinghaus illusion on perceptual and grasping judgments in Experiment 3. The two graphs on the left side of the figure represent the cumulative data from the perceptual judgment for each motor condition (still vs. spread). The dots represent the average rate of affirmative responses (y-axis) as a function of the difference between the actual size of the central circle and the size of the reference circle (x-axis). The responses were inverted (i.e., "yes" was coded 0, "no" was coded 1) to allow comparison with the data from the grasping task. The two graphs on the right side of the figure represent the cumulative data from the grasping judgment for each motor condition (still vs. spread). The y-axis represents the rate of affirmative responses, and the x-axis represents the difference between the actual size of the central circle and participant's MGA. In all graphs, solid lines represent the predicted values obtained by means of logistic regression, while the dashed lines correspond to the PSE (i.e., circle size at which participants provide affirmative responses in 50% of the trials).*

The ANOVA on the PSE revealed a main effect of the illusion ($F(2,72) = 134.06$, $MSE = 0.44$, $p < 0.001$), indicating that, compared to the neutral display, participants hesitated on smaller sizes when making judgments on the large illusory display ($t(37) = -6.57$, $p < 0.001$) and on larger sizes when making judgments on the small illusory display ($t(37) = 12.18$, $p < 0.001$). The mean PSE ± SD was equal to -0.10 ± 0.99 cm for the large illusory display, to 0.33 ± 0.97 cm for the neutral display and to 1.34 ± 1.05 for the small illusory display. There was also a main effect of the type of judgment ($F(1,36) = 13.68$, $MSE = 4.05$, $p = 0.001$): participants who made grasping judgments hesitated on smaller sizes (0.00 ± 0.19 cm) than those who made perceptual judgments (0.99 ± 0.18 cm). A main effect of the concurrent motor task was also found ($F(1,36) = 8.60$, $MSE = 1.42$, $p = 0.006$), indicating that participants hesitated on larger sizes when they spread their fingers apart (0.73 ± 0.15 cm) than when they kept their hands at rest (0.26 ± 0.16 cm). There was also a significant interaction between the type of judgment and the concurrent motor task ($F(1,72) = 7.37$, $MSE = 0.12$, $p = 0.10$). Post-hoc t-test showed that the difference in PSE between spreading fingers apart and keeping hands at rest was significant for the grasping judgment ($t(17) = -3.23$, $p = 0.005$), indicating that participants who made the grasping judgment hesitated on larger sizes when they had to spread their fingers compared to keeping them at rest. This difference was not significant for the perceptual judgment ($t(19) = -0.21$, $p = 0.839$; Figure 8). There was no other significant interaction between factors (all p at least > 0.1).

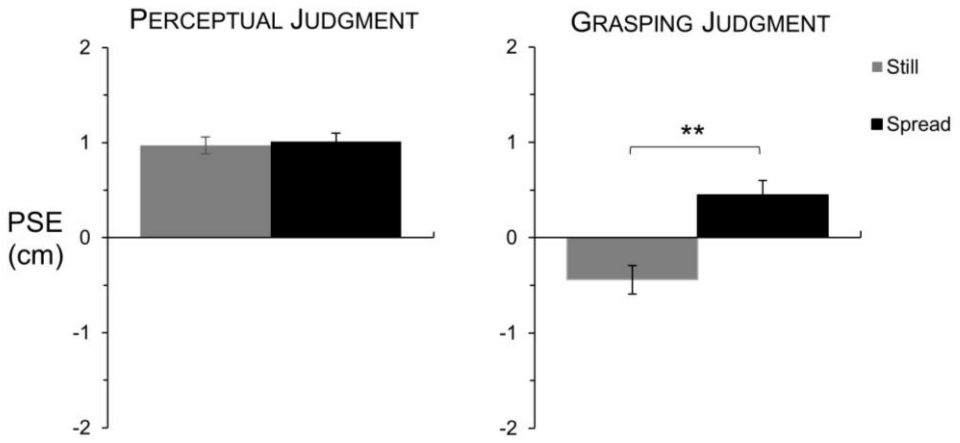

Figure 8. *Mean PSE in the perceptual and grasping judgment task of Experiment 3. PSE were computed for each illusory display, motor condition and participant separately. The mean PSE was significantly larger when participants had to make grasping judgments while spreading fingers than while keeping hands at rest. Error bars represent standard errors corrected for within-subject designs (Cousineau, 2005). ** p-value < 0.01.*

5. Discussion

The present study investigated the effect of the Ebbinghaus illusion on prospective action judgments. Experiment 1 showed that this size-contrast illusion influenced both grasping and perceptual size judgments. When participants had to make a perceptual judgment, the probability that the target circle appeared smaller than the reference circle was greater when the target was surrounded by large circles than when it was surrounded by small circles. Similarly, when participants were asked to make a grasping judgment, they estimated being less capable of grasping a target circle surrounded by small circles than a target circle of equal size surrounded by large circles. Experiment 2 investigated a potential interaction between the illusion and sensorimotor processes. The results replicated the illusory effect found on both the perceptual and the grasping judgments in Experiment 1. In addition, the concurrent motor task affected the grasping but not the perceptual judgment task. In

the grasping judgment task, participants hesitated on smaller sizes when they were squeezing a ball compared to when the hands were at rest, meaning that they underestimated their grasping abilities more in the former condition. This underestimation suggests that participants perceived their grip aperture as diminished while squeezing. Moreover, the effect of the motor task was modulated by the illusion, with the large illusory display exacerbating participants' underestimation of their grasping ability. Experiment 3 provided evidence for a selective effect of the current hand posture on grasping judgments by examining the effect of a task requiring participants to spread apart their fingers. Spreading fingers open (Experiment 3) had the opposite effect to squeezing balls (Experiment 2): finger extension led to an overestimation of the maximal object size participants thought they would be able to grasp, whereas finger abduction led to an underestimation of the maximal graspable size. The effect of the concurrent motor task on grasping judgments was thus dependent on the actual posture of the fingers during the task. Altogether, these results demonstrate that the illusion influences object size computation during action anticipation and that the contextual information is integrated with somatosensory information of the current hand posture in the prospective action plan.

In this study, prospective action judgments were used as a means to assess the effect of a visual illusion on action while controlling for the visual and proprioceptive information provided by the acting hand. Because no actual object grasping was required, on-line corrections could not interfere with the motor response. Moreover, the stimuli remained visible until the participants responded, which makes it unlikely that their judgment was based on a memory trace, an objection usually made to studies showing an illusion effect on grasping movements performed in open loop (*i.e.*, hand and stimuli hidden after movement onset). The motor interference found in the grasping judgment task indicates that this task

requires accessing sensorimotor representations and that performance is not simply mediated by perceptual processes. This selective interference of the motor task on grasping but not perceptual judgments shows that the former cannot be reduced to a perceptual comparison with a standard value that would serve to approximate the size of one's grip. The absence of difference in the latency of grasping and perceptual judgments further indicates that the selective interference of the motor task with grasping judgments does not result from increased difficulty or cognitive load compared to perceptual judgments. Moreover, Experiment 2 showed that the effect of the motor task on grasping judgments was constrained by the illusion, suggesting an interaction between the perceived object size and the perceived grip aperture. The interaction between the illusory display and the modified grip aperture was found when the grip aperture was reduced (Experiment 2) but not increased (Experiment 3). When fingers were spread apart, we expected participants to overestimate their grasping abilities significantly more when judging the small illusory display. However, as observed in the three experiments, the small illusory display yielded a greater distortion of perceived object size than the large illusory display. In other words, the overestimation of the grasping abilities yielded by the illusion of smallness was more important than the underestimation yielded by the illusion of largeness. We hypothesise that the illusion of smallness was so strong that an additive overestimation induced by spreading fingers open was unlikely to emerge in this condition. The important finding is that, under some circumstances, contextual and somatosensory information may interact, as evidenced by the interaction of the illusory display and the motor task in Experiment 2. We conclude from these results that the visuomotor processes involved in action anticipation take into account the visual context and compute estimates of object size relative to its context.

The perception-action model (Goodale & Milner, 1992; Milner & Goodale, 2008) makes no prediction for such an interaction between contextual and somatosensory information. Illusory object size might be computed by the visuomotor processes associated with the dorsal stream or supplied by the perceptual processes associated with the ventral stream to be further integrated into the action plan. If the size-contrast effect of the Ebbinghaus illusion emerges in the dorsal stream, then the dorsal stream does not exclusively compute the absolute metrics of the central circle in a reference frame centred on the hand (*i.e.*, egocentric coordinates), but also relies on contextual information in order to compute relative and scene-based metrics (*i.e.*, allocentric coordinates). Indeed, behavioural and neurofunctional studies suggest the existence of partially overlapping networks for the two reference frames, with a dual coding in allocentric and egocentric coordinates in a subset of parietal regions (Iachini, Ruggiero, Conson & Trojano, 2009; Zaehle et al., 2007). This first explanation constitutes a shift from the view that action is bound to egocentric coordinates while the computation of allocentric coordinates is the core of perception, and would thereby discard a major theoretical argument for making a distinction between a ventral stream dedicated to perception and a dorsal stream dedicated to action. An alternative explanation is that the ventral stream computes illusory object size and relays it to the dorsal stream, which would imply that the two visual streams are not as independent as hitherto assumed. The possible interactions between the two processing streams have received increased interest in recent years (*e.g.*, Cloutman, 2013; Freud, Plaut & Behrmann 2016; van Polanen & Davare, 2015a). For instance, knowing the weight of an object, a piece of conceptual information typically accessed through the ventral stream, facilitates adequate and efficient grasping of this object (Gallivan et al., 2014). Findings from the study of patients with optic ataxia also support a contribution of the ventral stream in action planning. The performance of patient AT in grasping unfamiliar

objects was improved when the target object was replaced by an object with the same shape but familiar to the patient (*i.e.*, a cylinder replaced by a lipstick tube), suggesting that object identification contributes to defining the appropriate action, including motor parameters related to grip aperture (Jeannerod et al., 1994). Milner and Goodale (2008) assumed that visual processes in the ventral and dorsal streams are separate but proposed that the output of the ventral stream may be communicated to the dorsal stream to constrain action selection. Under the hypothesis that only the ventral stream computes allocentric coordinates, our results suggest that the work of the two streams is much more integrated than initially assumed by the perception-action model. Indeed, the interaction of the illusory effect with the motor task would reveal the deep integration of the visual information related to illusory object size and the somatosensory information related to the current grip posture. This second explanation goes against the idea that interference between perceptual and somatosensory information emerges after the parallel processing of this information in the ventral and dorsal streams, respectively. It rather suggests that the two streams act in concert to integrate the relevant information for guiding motor behaviour. Direct evidence for cross-stream interactions is provided by neuroimaging studies of mental rotation of objects (Koshino et al., 2005), tool use (Ramayya et al., 2010) and motor imagery (Vry et al., 2012). The neural foundation for communication between the two streams thus exists and makes the hypothesis of a functional interplay plausible. Further behavioural and neuroimaging studies are now necessary to characterise the role of these connections and assess the respective contribution of the ventral and dorsal streams to the generation of a size-contrast illusion during motor-related behaviour. Past research has relied extensively on the effect of visual illusions on perception and action to motivate a functional dissociation between the ventral and dorsal streams while the exact involvement of the two streams in mediating this effect remains unclear. So far, neuroimaging studies investigating the

effect of visual illusions on neural activity have been limited to perceptual judgments (Weidner & Fink, 2006; Koene, Huang & Chen, 2008; Plewan, Weidner, Eickhoff & Fink, 2012).

Our view that perception and action work in concert and support each other also opens up perspectives for rehabilitation. Spared perceptual abilities may be used to remediate motor deficits, whereas a preserved access to sensorimotor information may be used to compensate perceptual deficits. Such compensation strategies have actually been reported in studies of visual agnosia, though in an anecdotal way (Murphy et al., 1996; Dijkerman & Milner, 1997). For instance, patient DF was unable to discriminate between a rectangle and a triangle by verbal reports but significantly improved her performance when the response involved grasping: when she was asked to reach and pick up one of the two shapes (*e.g.*, "grasp the triangle"), DF was attentive to the sensorimotor cues of her hand configuration to know whether she was approaching the correct object. As a result, she sometimes changed her reaching trajectory to pick up another object than the one she initially selected as the target. DF thus seemed to rely on her spared visuomotor abilities to compensate for the perceptual deficits caused by her visual agnosia. On the other hand, patient IG was able to compensate for his optic ataxia and adjust grip aperture correctly to object size when the task setup encouraged reliance on a memory representation of perceptual size (Milner et al., 2001). Further investigation on how and when perception and action can interact would thus benefit to clinical rehabilitation.

The effect of the concurrent motor task on the prospective action judgments also brings new insight concerning the nature of these judgments. Prospective action judgments are associated with a covert activation of the sensorimotor system. Several studies showed that when people make prospective action judgments, they are sensitive to the actual posture of their hand and to the complex functional

restriction arising from it (Carello et al., 1989; Mark et al., 1997). For example, squeezing a ball was found to affect judgments about one's ability to reach an object placed at a certain distance (Grade et al., 2015; Witt & Proffitt, 2008). Our study adds to these findings by showing that the hand posture adopted during a concurrent motor task also affects judgments about one's ability to grasp an object of a certain size. The reduction of the grip aperture induced by the squeezing action led objects to be considered as less graspable (Experiment 2) while spreading fingers apart led objects to be considered as more graspable (Experiment 3) than when the hand was at rest. These biases are typically ascribed to motor imagery. Motor imagery of hand actions would involve the activation of the sensorimotor representation of the hand in its actual position and the spatial transformation of this representation into a position that fits with the target size and/or orientation, with respect to the biomechanical constraints of hand movements (Johnson, 2000; Sirigu & Duhamel, 2001). However, the motor imagery hypothesis has become much debated since an effect of the biomechanical constraints of hand movement has been reported in prospective action judgments performed by individuals with no hand motor experience due to a congenital absence of upper limbs (Vannuscorps & Caramazza, 2015; 2016a; 2016b, Vannuscorps et al., 2012). The present results do not necessarily imply that prospective action judgments are solved by mentally simulating the action from one's motor repertoire. They simply provide evidence for a biased comparison between the size of the object and the size of the current grip aperture. Because the computation of the possible grip aperture is decreased while squeezing balls, the participants consider themselves less able to grasp the object. Conversely, because the felt grip aperture is increased when one spreads apart the fingers, an overestimation of grasping abilities was observed. It is worth noting that the concurrent motor tasks used in Experiment 2 and 3 were also associated with different haptic sensations: pressing a foam ball induces sensations of softness

whereas spreading fingers between two iron bars induces sensations of hardness. A previous study suggests that the association of certain haptic sensations with abstract concepts may lead to cognitive biases. For instance, the sensation of hardness made job candidates appear as more rigid and strict (Ackerman, Nocera & Bargh, 2010). However, these findings cannot explain our results that go opposite to the predictions of an haptico-cognitive bias. Indeed, the hardness of the bars should have led participants to behave in a more rigid way and thus underestimate their ability, while the softness of the ball should have led participants to adopt a less conservative behaviour and overestimate their ability. It is thus reasonable to assume that the effect of the concurrent motor task we used was driven by the somatosensory information of the current hand posture. Further studies should clarify how this information is implemented in the comparison process underlying grasping judgments, while considering alternatives to the motor imagery hypothesis, since the ability to mentally rehearse one's own motor experience is not a prerequisite for anticipating the outcome of an action (Vannuscorps & Caramazza, 2016a; 2016b).

In conclusion, our study constitutes the first demonstration that visual illusions affect prospective action judgments. Because grasping and perceptual size judgments were perfectly matched, notably in terms of visual and proprioceptive information from the acting hand, the results can be considered as strong evidence that visual illusions affect both perception and action. An interaction between illusory object size and concurrent motor activity was found in grasping judgments, suggesting an integration of the visual information of the context and the somatosensory information of the hand posture during action anticipation.

Chapter 3

Thinking ahead of action involves somatosensory integration

1. Introduction

Predicting the feasibility of an action is a fundamental aspect of human adaptive behaviour. It allows action calibration to be computed anticipatively, at no cost for the effector system. Hence, the prediction that a coffee cup is out of reach or too full to be grasped safely between finger and thumb typically triggers the search of alternative response options, such as making a step forward or lifting the cup with both hands, which will, in turn, be evaluated for their capability to achieve the expected outcome before any effort is produced (Johnson, 2000).

Previous studies showed that prospective judgments about an action are influenced by the biomechanical constraints associated with this action (Frak et al., 2001; Johnson, 2000; Mark, 1987; Warren, & Whang, 1987). For instance, reaching judgments (*i.e.*, judging whether one would be able to reach an object) are sensitive to the motor constraints imposed by the posture in which the reaching would be done (*e.g.*, reaching while standing *vs.* sitting) or by the environment (*e.g.*, texture and height of the surface, weights fixed on the wrist; Carello et al., 1989; Rochat & Wraga, 1997). We recently showed that grasping judgments (*i.e.*, judging whether one would be able to grasp an object) are influenced by the grip aperture at the time of the judgment: participants underestimate *vs.* overestimate their capability to grasp circles between their index finger and thumb when performing a concurrent motor

task that implied squeezing *vs.* spreading the fingers (Geers, Pesenti & Andres, 2018, see Chapter 2). Such interference is particularly intriguing because the judgment is based on the potential capability to grasp an object, *i.e.*, the maximal achievable grip aperture, a decision that should remain identical whether the hand is opened or closed at the time of the judgment.

It is remarkable that prospective action judgments keep track of somatosensory information to estimate general motor capabilities that are, in principle, unbound to the current state of the motor system. This suggests that current state estimation is a constitutive and unavoidable part of action prediction. However, before a precise description of its role can be proposed, the question of how hand representations are mapped to perceptual object representations in action judgments remains to be elucidated. The dominant hypothesis is that action judgments are achieved by activating the sensorimotor representation of the effector in its actual position and the spatial transformation of this representation into a position fitting with target size and/or orientation while taking into account the biomechanical constraints of hand (Johnson, 2000). According to this *somatosensory* account, the effect of grip aperture on grasping judgments reflects the direct integration of somatosensory information into the prospective plan. However, a different stream of the literature suggests that the motor system responsible for grasping communicates with the cognitive system responsible for magnitude processing (Walsh, 2003). One implication of this crosstalk is that the action of closing or opening the grip, as implied by squeezing a ball or spreading fingers, conveys magnitude information that can be used by the semantic system to instantiate the concepts of "smallness" or "largeness". For instance, several studies showed that observing the closure/aperture of a precision grip is sufficient to slow down the discrimination of large/small numbers (Badets & Pesenti, 2010) or to bias random number generation towards small or large values (Badets, Bouquet, Ric & Pesenti, 2012; Badets & Pesenti, 2011;

Grade, Badets & Pesenti, 2017). A similar bias was observed, though to a lesser extent, when precision grip was replaced by hand or mouth opening/closing (Grade et al., 2017). In turn, other studies evidenced that priming small or large numbers affected grasping behaviour (*e.g.*, Andres et al., 2004; Lindemann, Abolafia, Girardi, & Bekkering, 2007; Wood & Fischer, 2008) and grasping judgments (Badets et al., 2007; Chiou, Chang, Tzeng & Wu, 2009). Overall, these results suggest a possible *semantic* account of motor interference in grasping judgments, whereby the effect of current grip aperture would be mediated by the semantic system relating grip size to a magnitude representation shared with words and numbers (Andres, Olivier & Badets, 2008). The comprehension of the role of sensorimotor processes in action prediction is thus obstructed by the possibility that the implied movement can be converted into a magnitude representation devoid of sensorimotor content but semantically relevant for comparative judgments.

This issue is further complicated by uncertainty about the metrics used to represent object size in action judgments. While a long-standing theoretical position emphasises the need to compute veridical size estimates for optimal hand-object interactions (Goodale & Milner, 1992), diverging findings have accumulated over the past decade to suggest that action also integrates relative size estimates traditionally ascribed to visual perception (Franz & Gegenfurtner, 2008). Several studies have shown that the grip aperture adopted to grasp an object is affected by the Ebbinghaus illusion (*i.e.*, a central circle surrounded by small or large circles leads participants to perceive it as larger or smaller and adjust their grip accordingly; Franz et al., 2000; Kopiske et al., 2016). Because prospective action judgments have been used as a proxy to test the preliminary stages of action calibration, it is essential to determine whether the off-line estimation of grasping capability is based on actual object size or subjective values reflecting the way it is perceived in a given visual context.

Several results raise the counter-intuitive hypothesis that action prediction is unavoidably tied to the state of the perceptual and sensorimotor systems at the time the mental representation of one's motor capability is formed. The present study aims to test this idea while addressing other viable alternative accounts of the supporting effects. In particular, it investigates whether concurrent motor tasks affect grasping judgment through the integration of somatosensory information about current grip aperture (*i.e., somatosensory* account) or the conversion of grip size into a representation of magnitude (*i.e., semantic* account). In Experiment 1, we asked participants to estimate their capability to grasp circles of different sizes between their index finger and thumb, while performing a concurrent motor task that required to squeeze a ball between index finger and thumb (*i.e.*, precision grip) or between the two hand palms (*i.e.*, bimanual grip). The semantic account predicts that the reduction of grip aperture imposed by squeezing a ball should activate the concept of "smallness", whatever the effectors involved in the motor task, leading to an underestimation of grasping capability relative to a control condition where the hands are at rest. In contrast, the somatosensory account assumes that only the motor task modulating somatosensory information about the grip involved in the judgment, *i.e.*, the precision grip, should affect participants' judgment so that no underestimation is expected when the motor task involves a bimanual grip. In order to test the influence of the visual context on prospective action judgments, we manipulated the perceived size of the target circle using the Ebbinghaus illusion as described in previous studies (Geers et al., 2018, see Chapter 2). Experiment 2 was designed as a control experiment to exclude that the precision grip has a stronger potential to evoke the concept of "smallness" than the bimanual grip due to its more frequent association with small objects. Rather than grasping judgments, we asked participants to make numerical judgments that required comparing numbers to a standard (*i.e.*, 45). If hand posture is linked to a magnitude concept, the action of

squeezing should slow down the comparison of numbers larger than the standard due to a conflict between the small magnitude associated with the reduced grip and the large magnitude assigned to the number in the course of the numerical judgment. The effect of various hand postures (precision *vs.* bimanual grip) on grasping (Experiment 1) and numerical (Experiment 2) judgments should allow us to delineate the influence of somatosensory and semantic information associated with grip size.

2. Experiment 1

2.1 Method

2.1.1 Participants

Twenty-two French-speaking undergraduate students (Eighteen females; M_{age} = 22.9 years, SD_{age} = 7.3) of the Université catholique de Louvain, Belgium, participated in this experiment in exchange for course credits. All participants were right-handed and had a normal or corrected-to-normal vision. They were unaware of the hypotheses been tested and gave their written informed consent before the experiment. The study was performed in accordance with the ethical standards of the Declaration of Helsinki and was approved by the Ethical Committee of the Psychological Science Research Institute of the Université catholique de Louvain. The sample size was defined according to the results of previous experiments (Geers et al., 2018) showing that at least 16 participants are required to observe a true effect of the concurrent motor task (d = .69), in the context of the size-contrast illusion, with an 80% power using a one-tailed pairwise contrast (α = 0.05).

2.1.2 Apparatus and stimuli

We used the same apparatus and stimuli as in Experiment 2 and 3 of Geers and colleagues (2018, see Chapter 2). The stimuli were displayed on a vertical screen (225 x 210 cm) by a projector (MP7740, 3M United States) placed behind the screen with a 1,280 x 1,024-pixel resolution, with 1 pixel corresponding to 0.19 cm and 1 cm corresponding to 0.76° (Figure 1A). A chin rest was used to keep a 75 cm distance between the screen and the participants' head throughout the experiment. A voice key was fixed on the chin rest to record RLs. The experiment was controlled with E-prime 2 software (Schneider et al., 2002).

The stimuli consisted of Ebbinghaus displays constituted of central and peripheral circles with varying size. The size of the central circle (*i.e.*, target) differed by -5, -3, -2, -1, 0, +1, +2, +3 or +5 cm with respect to the MGA measured prior the experiment using wooden bars ranging from 9 to 20 cm. The MGA was given by the longest bar the participant could grasp comfortably between the tips of index finger and thumb of the dominant hand (M = 11.9 cm, SD = 1.3). The size of the surrounding circles was (1) twice as small as the central circle, (2) twice as larger as the central circle or (3) identical to the central circle. In the two first displays, the central circle is typically perceived as larger or smaller, respectively, than its actual size. They are referred hereafter as the small and large illusory displays. The latter display was used as a control not inducing any illusion. To avoid simulated obstacle avoidance to be responsible for a potential effect of the illusion, the distance between the target and the surrounding circles always corresponded to the size of the target (Figure 1B; Haffenden & Goodale, 2000; but see also Franz et al., 2003).

2.1.3 Tasks and procedure

We used the same grasping judgment task as Geers and colleagues (2018, see Chapter 2) consisting in judging whether one would be capable of grasping the central circle of an Ebbinghaus display between index finger and thumb, without actually grasping it. Each trial consisted of a fixation cross displayed at the centre of the screen for 500ms followed by an Ebbinghaus display. Participants were required to indicate as quickly and accurately as possible whether they judged the target as graspable or not by responding "yes" or "no" aloud. At response onset, the stimulus disappeared. The experimenter then encoded the response, and the next trial began 1500 ms later. Participants had to perform the grasping judgment while (1) keeping their hands flat on the table (*i.e.*, rest), (2) while squeezing a 7-cm foam ball between the index fingers and thumbs of each hand (*i.e.*, precision grip), and (3) while squeezing a 7-cm foam ball between their two hands fully opened, with the palms facing each other, and the fingers pointing forward (*i.e.*, bimanual grip). For the precision and bimanual grip, the instructions emphasised the need to keep constant pressure on the ball in order to fit the gap formed by two iron bars placed next to the hands (Figure 1C). The order of the motor conditions was counterbalanced across participants. Hands were kept under a cardboard surface during the entire experiment making them invisible to the participant. A webcam was used to allow the experimenter to monitor that the concurrent motor tasks were properly performed. The participants performed six practice trials before taking two blocks of trials for each of the three motor conditions. A block consisted of 81 trials presented in a random order resulting from the nine possible sizes for central circle combined with each of the three Ebbinghaus displays, repeated three times.

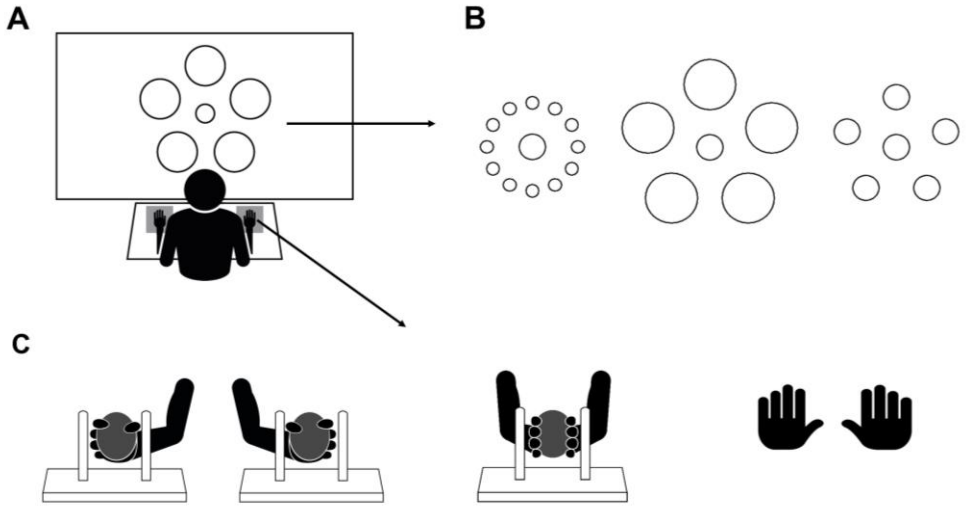

Figure 1. *Experimental set-up. (A) In Experiment 1, the stimuli were projected from behind onto a wide screen. Participants were seated in front of the screen and had to keep their hands under cardboard surfaces in such a way that they can no longer see their hand. (B) The Ebbinghaus displays used in Experiment 1 with small surrounding circles making the central circle appear larger (i.e., large display) on the left, large surrounding circles making the central circle appear smaller (i.e., small display) at the centre, and with surrounding circles of the same size than the central circle not inducing any illusion (i.e., neutral display) on the right. (C) Motor conditions of Experiment 1 and 2. Participants performed the grasping judgment (Experiment 1) or number comparison (Experiment 2) task while squeezing a foam ball between the index finger and thumb of each hand (left), squeezing a foam ball between their two hands in neutral position (i.e., open palm, no extension or flexing; centre) and keeping hands at rest (right). In the two squeezing conditions, participants had to keep constant pressure on the ball such that the grip formed by the fingers/hands over the ball, fitted into the gap formed by two vertical iron bars placed next to the hands.*

2.1.4 Data analysis

Trials where the voice key triggered due to coughs or external noises were discarded from any further analysis (2.34% of the dataset). Trials where the voice key failed to trigger (11.6% of the dataset) were discarded from the RL analysis. We

first conducted a GLMM on the RLs with the motor condition (rest, precision grip *vs.* bimanual grip) as a fixed factor to investigate the effect of motor interference and test whether the motor conditions were of equal difficulty. To investigate the effect of the motor condition, the illusion, and the size of the target on participants' estimates of grasping capability, while accounting for the variability of the slope and intercept of each participant, we computed a GLMM on the response, following a binary distribution predicted by a logistic regression model (*i.e.*, "yes" or "no", coded as 1 and 0). The size of the target (-5, -3, -2, -1, +0, +1, +2, +3 *vs.* +5 cm, relative to MGA), the illusory display (small, neutral *vs.* large), the motor condition (rest, precision grip *vs.* bimanual grip) and the interaction between motor condition and illusory display were included as fixed effects in the analysis. The model also included the differences between participants as a random intercept. Post-hoc pairwise contrasts were corrected with Bonferroni correction.

2.2 Results

The GLMM analysis on RLs revealed a main effect of motor condition, $F(3,8291) = 3262.19$, $p < .001$. Post-hoc pairwise contrasts indicated that RLs were smaller for the precision grip ($M = 835$ ms, $SE = 37$) than for the bimanual grip ($M = 856$ ms, $SE = 57$), $t(8291) = -2.43$, $p = .030$, difference (D) = -21.05, 95% CI = [-40.46, -1.64], and resting condition ($M = 864$ ms, $SE = 59$), $t(8291) = -3.25$, $p = .004$, D = -28.75, 95% CI = [-49.95, -7.55].

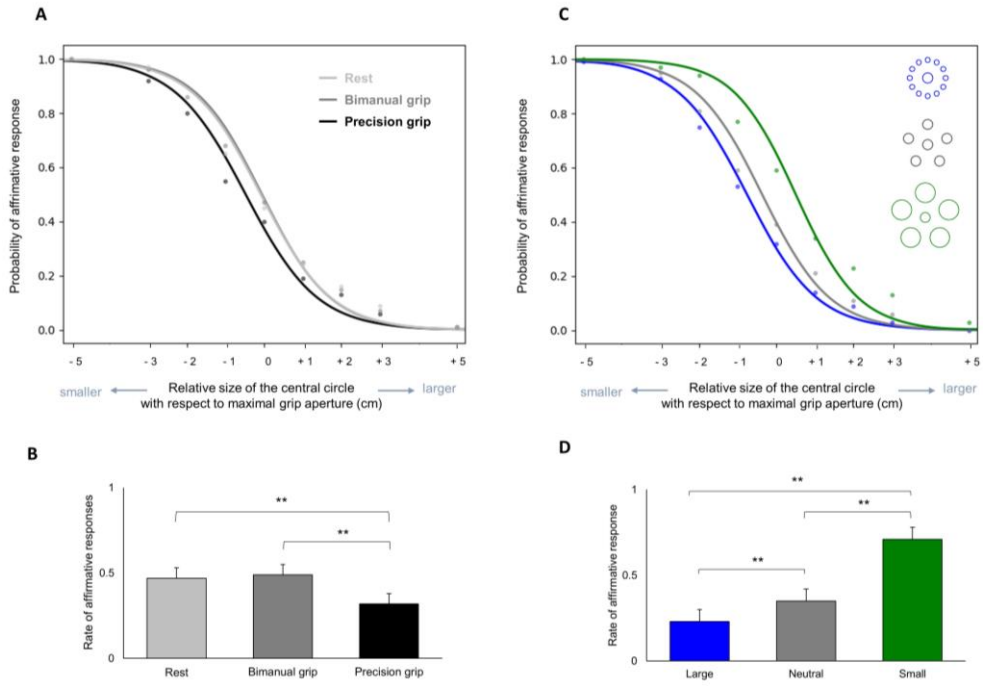

Figure 2. *Effect of the motor condition (A & B) and Ebbinghaus illusion (C & D) in Experiment 1. The two graphs in the upper part of the figure represent the cumulative data. The dots represent the average rate of affirmative response (y-axis) as a function of the difference between the actual size of the central circle and participant's MGA (x-axis). Solid lines represent the predicted values obtained by means of logistic regression. The two graphs in the lower part of the figure represent estimated means of affirmative responses, at the mean target size (i.e., +0 cm with respect to MGA). Error bars represent standard errors; **p-values < .001 corrected for multiple comparisons; * p-values < .05 corrected for multiple comparisons.*

The GLMM analysis on grasping judgment responses showed a significant effect of size, $F(1, 9525) = 1{,}792.60$, $p < .001$, with the rate of affirmative responses decreasing when size increased. There was also a main effect of the motor condition, $F(2, 9525) = 29.46$, $p < .001$. Post-hoc pairwise contrasts indicated that the mean rate of affirmative responses was significantly smaller for the precision grip ($M = .32$, $SE = .12$) than for the rest condition ($M = .47$, $SE = .14$), $t(9{,}525) = -5.25$, $p =$

.001, *D* = -.15, 95% *CI* = [-.22, -.09], and for the bimanual grip (*M* = .49 ms, *SE* = .14.), *t*(9,525) = -5.57, *p* = .001, *D* = -.16, 95% *CI* = [-.23, -.09]. There was no significant difference between the rest condition and bimanual grip, *t*(9,525) = -0.37, *p* = .706, *D* = -.01, 95% *CI* = [-.05, .04]. The analysis also showed a significant main effect of the illusion, *F*(2, 9525) = 195.98, *p* < .001. Post-hoc pairwise contrasts indicated that, compared to the neutral display (*M* = .35, *SE* = .13), the mean rate of affirmative responses was significantly smaller for the large illusory display (*M* = .23, *SE* = .10), *t*(9,525) = 3.45, *p* = .001, *D* = .12, 95% *CI* = [.05, .19], and significantly larger for the small illusory display (*M* = .71, *SE* = .12), *t*(9,525) = -13.90, *p* < .001, *D* = -.36, 95% *CI* = [-.42, -.30]. The interaction between motor condition and illusion was not significant, *F*(4, 9525) = 0.96, *p* = .428 (Figure 2).

3. Experiment 2

3.1 Method

3.1.1 Participants

A new sample of thirty undergraduate students (Twenty-nine females, M_{age} = 21.5 years, SD_{age}= 1.9 years) of the Université catholique de Louvain, Belgium, participated in this experiment in exchange for course credits. Three of them were left-handed. All had a normal or corrected-to-normal vision. They were unaware of the hypotheses being tested and gave their written informed consent before the experiment. The experiment was performed in accordance with the ethical standards established by the Declaration of Helsinki and was approved by the local Ethical Committee. A sample size analysis showed that 27 participants are required to observe a RL difference of 20 ± 40 ms (*d* = .5) between the motor interference condition and the control rest condition with an 80% power using a one-tailed pairwise contrast (α = 0.05).

3.1.2 Apparatus and stimuli

The participant sat in front of a 27-inch LCD screen on which the stimuli were displayed with a resolution of 1,920 x 1,080 pixels. A chin rest was used to keep the distance between the screen and the participants' head at 75 cm throughout the experiment. A microphone was fixed on the chin-rest to record RLs. The experiment was run with PsychoPy2 (Peirce et al., 2019).

We used the same set of stimuli as in the study of Salvaggio and colleagues (2019). The stimuli consisted of all Arabic numbers ranging from 20 to 70, except 45 used as a reference for the comparison task, and displayed on the screen with a size of 2° of visual angle. Numbers smaller and larger than 45 were divided into three categories of distance: numbers from 20 to 29 and from 61 to 70 were considered far from the reference, numbers from 30 to 39 and from 51 to 61 considered at a medium distance, and numbers from 40 to 45 and from 46 to 50 considered close to the reference. Each number was presented twice per task, except for the close numbers, which were half as many and therefore repeated four times.

3.1.3 Tasks and procedure

Each trial started with a fixation square displayed at the centre of the screen for 500 ms followed by an Arabic number displayed for 2 s. Participants were required to say aloud as quickly and accurately as possible whether the number was "smaller" or "larger" than 45. The response was encoded on-line by the experimenter before the next trial began. The inter-trial interval was 500 ms. Participants were required to perform one block of trials for each of the motor conditions described in Experiment 1. The order of the tasks was counterbalanced across participants. One block consisted of 120 trials resulting from the combination of three distance

categories (close, medium and far) and two magnitude categories (smaller and larger than the reference), with 20 trials per combination.

3.1.4 Data analysis

The data of two participants were removed before the analysis due to a technical problem with the microphone. The RL data of the remaining participants were analysed after excluding trials with noises, coughs or microphone failures (0.25% of the data set) and trials where participants answered erroneously (1.2% of the dataset). To investigate the effect of the motor condition, numerical magnitude and numerical distance on RL, while accounting for the variability of the slope of each participant, we computed a generalised linear mixed model (GLMM). The dependent variable was the RL. The numerical magnitude (smaller *vs.* larger), numerical distance (close, medium *vs*. far) and motor condition (rest, precision grip *vs.* bimanual grip), and their interactions were included as fixed effects. The numerical distance effect characterised by faster responses to numbers far from rather than close to the reference was used as an index of typical performance. The model also included the differences between participants as a random intercept. Post-hoc pairwise contrasts were corrected with Bonferroni correction.

3.2 Results

The GLMM analysis showed a significant effect of numerical distance, $F(2,10151) = 172.95$, $p < .001$, indicating that RLs increased as numerical distance decreased (M_{close} = 777 ms, SE_{close} = 22; M_{medium}= 741 ms, SE_{medium} = 22; M_{far}= 723 ms, SE_{far} = 22; Figure 3). There was also a main effect of magnitude, $F(1, 10151) = 17.34$, $p < .001$, indicating that response to numbers smaller than the standard (M = 752 ms, SE = 22) were slower than to numbers larger than the standard (M = 742 ms, SE = 22).

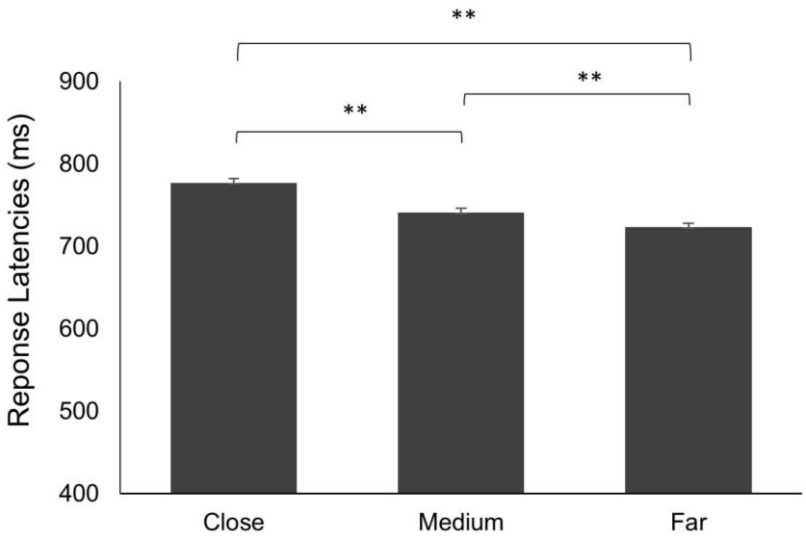

Figure 3. *Effect of numerical distance in Experiment 2. Mean RLs are expressed (in ms) for numbers at a close, medium and far distance of the. Error bars represent standard errors corrected for within-subject designs (Cousineau, 2005); **p-values < .001 corrected for multiple comparisons; * p-values < .05 corrected for multiple comparisons.*

The analysis also revealed a main effect of the motor condition, $F(1,10151) = 9.25$, $p < .001$, indicating that RLs were larger when squeezing the ball with the bimanual grip (M = 755 ms, SE = 22) than in the rest condition (M = 743 ms, SE = 22), $t(10,151) = 3.85$, $p < .001$, D = 11.28, 95% CI = [4.27, 18.28], and when squeezing with the precision grip (M = 744 ms, SE= 22), $t(10,151) = 3.57$, $p = .001$, D = 10.46, 95% CI = [3.90, 17.02]. There was no significant difference between the rest and precision grip conditions, $t(10,151) = -0.28$, $p = .781$, D = -0.81, 95% CI = [-6.56, 4.93]. More importantly, there was an interaction between numerical magnitude and motor condition, $F(2, 10161) = 6.77$, $p = .001$: squeezing a ball slowed down the comparison of numbers larger than the reference, but this was only true for the bimanual grip (M = 754 ms, SE = 21) compared to the rest condition (M=

732 ms, *SE* = 22), *t*(10161) = -5.35, *p* < .001, *D* = 22, 95% *CI* = [12.18, 31.91]. No difference was found between the precision grip (*M* = 739 ms, *SE* = 22) and the rest conditions, *t*(10161) = 1.51, *p* = .135, *D* = 6.18, 95% *CI* = [-1.93, 14.29]. The discrimination of numbers smaller than the reference was not affected by the motor conditions, all *p*-values > .05 (Figure 4).

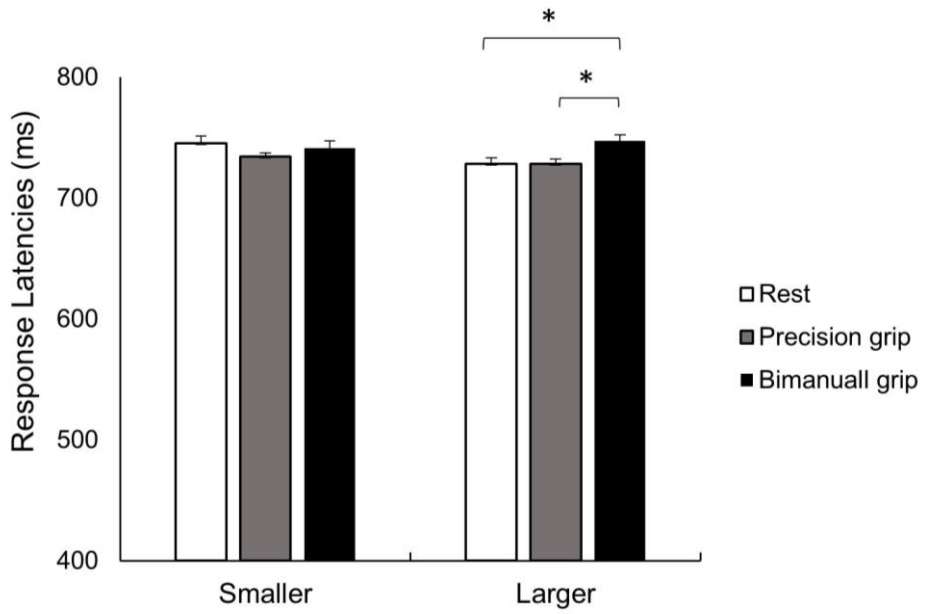

Figure 4. *Effect of the motor conditions on numbers smaller and larger than the reference in Experiment 2. Mean RLs (expressed in ms) for numbers smaller and larger than the standard are expressed for each motor condition. Error bars represent standard errors corrected for within-subject designs (Cousineau, 2005); **p-values < .001 corrected for multiple comparisons; * p-values < .05 corrected for multiple comparisons.*

4. Discussion

The present study aimed at understanding the respective contribution of sensorimotor and semantic processes to action prediction. We tested whether the effect of concurrent motor tasks on grasping judgments reflects the integration of somatosensory information about the current state of the effectors or the semantic information about the magnitude associated with the grip. Experiment 1 showed that participants underestimated their capability to grasp circles when a squeezing movement was performed with a precision grip, but not when it was performed with a bimanual grip. This finding suggests that subjective estimates of grasping capability are bound to available somatosensory information from the effectors involved in the judged action. In Experiment 2, we tested whether this result could be explained by the precision grip evoking the concept of "smallness" more strongly than the bimanual grip due to its more frequent association with small objects in everyday life. To do so, we looked at the influence of the precision and bimanual grips on a concomitant numerical judgment. We found that the bimanual grip but not the precision grip slowed down magnitude comparison on numbers larger than the reference. Thus, whereas squeezing a ball between the two hands was not detrimental to action judgments, it interfered with the semantic processing of large numbers. Furthermore, we replicated the observation that grasping judgments are strongly biased by the size-contrast illusion created by surrounding circles smaller or larger than the target circle. This finding indicates that not only sensorimotor estimates relative to grip size but also visual estimates relative to object size are tied to the environmental constraints. Overall, our results converge to show that, at least for ordinary gestures such as grasping, current state estimation is a constitutive and unavoidable part of action prediction.

The present results are in line with those of previous studies showing, for example, that squeezing a ball between finger and thumb affects judgments about one's capability to reach an object placed at a certain distance (Grade et al., 2015; Witt & Proffitt, 2008). In these studies, motor interference was inferred from increased RLs, decreased accuracy, or the disappearance of other classical effects affecting reaching judgments. These observations were interpreted as reflecting an interference of the concurrent motor task with the mental simulation of the relevant action to solve this judgment, in line with the literature showing high similarities between action prediction and execution (*e.g.*, Carello et al., 1989; Frak et al., 2001; Johnson, 2000). However, effects on response speed and accuracy are subject to alternative interpretations such as an increase of cognitive demands that would slow down performance and hamper accuracy indirectly. Our study evidenced a change in estimated grasping capability. More specifically, participants underestimated their grasping capability when squeezing a ball between their index finger and thumb. This finding goes beyond the mere observation of decreased performance in previous studies. First, the underestimation bias cannot be assigned to increased cognitive load because the precision grip did not increase response speed when squeezing a ball. On the contrary, responses of the grasping judgment were faster for the precision grip compared to the resting and bimanual grip conditions, suggesting that the activation of the effectors concerned by the judgment facilitates the judgment. Second, the underestimation bias was not due to participants adopting a more conservative strategy because we previously showed that it could be turned into an overestimation bias by asking participants to spread their fingers apart rather than to squeeze a ball (Geers et al., 2018, see Chapter 2). Third, the underestimation bias was specific to the grip implied by the grasping judgment (*i.e.*, a precision grip) as no bias was observed when the motor condition required participants to squeeze the ball using a different hand gesture (*i.e.*, a bimanual grip). Our study thus provides

unambiguous evidence that prospective grasping judgments integrate somatosensory information relative to the specific effectors required by the judged action.

The somatosensory account assumes that predicting the feasibility of an action proceeds through mental simulation that would require encoding the properties of the target object (*e.g.*, orientation, size), activating the sensorimotor representations of the effectors in their actual position, and transforming these representations according to the orientation/size of the target object (Frak et al., 2001; Johnson, 2000). While former studies focused on the way the actual hand posture may influence the starting point of the simulation (Johnson, 2000), our study assessed the influence of hand posture on the final state estimates of grasping capability. The results evidenced a biased comparison between object size and represented grip aperture, but they do not tell whether this mechanism is accompanied or followed by the mental simulation of the action. Another unexpected result, which has been rarely discussed within the framework of motor simulation, relates to the integration of somatosensory information about the current body state in the prospective action plan even when it is a potential source of error. In principle, the current grip aperture does not predict the general capability to grasp objects and should thus not be taken into account when predicting this capability. It is possible that the cognitive system requires some somatosensory input because it cannot represent grasping capability out of nothing. An alternative explanation is that, even if it is not relevant for the present task, somatosensory information is integrated by default to the prospective plan because it has played a significant role in the process by which the knowledge of grasping capability emerged during development.

Results showed that grasping estimates were bound to the perceived size rather than to the veridical size of objects. The so-called Ebbinghaus illusion is

known to affect perceptual judgments leading participants to consider the central circle as smaller *vs.* larger when surrounded by large *vs.* small circles. We have shown that the illusion effect extends to action judgments: participants underestimate their grasping capability when the circle is surrounded by small circles and overestimate their grasping capability when it is surrounded by large circles. Grasping judgments are thus influenced, on the one hand, by the somatosensory information about the current grip aperture and, on the other hand, by the visual information about the context. The weight given to these different sources of information is unclear. In Experiment 1, their effects were additive, but in a previous experiment, they were found to interact with each other so that underestimation was particularly marked when the target circle was perceived as larger than it actually was (Geers et al., 2018, see Chapter 2). In any case, the joint influence of grip aperture and the visual context implies a departure from the view that action prediction exclusively relies on the cognitive processes involved in motor planning and action execution. As we argued elsewhere (Geers et al., 2018, see Chapter 2), this finding is best explained by perceptual and sensorimotor processes working in concert to support action prediction.

Finally, our study leads to the original finding that the grip reduction caused by the action of squeezing interferes with the discrimination of large numbers in numerical magnitude comparison. Several studies have reported semantic-to-motor interactions such as numbers influencing the kinematics of action (*e.g.,* Andres et al., 2004; Andres, Ostry, Nicol & Paus, 2008; Lindemann et al., 2007; Moretto & di Pellegrino, 2008). The finding of the reverse interaction, from motor control to semantic processing, has been restricted to action observation so far (Badets et al., 2012; Badets & Pesenti, 2010; 2011; Grade et al., 2017). The present results show that the execution of a grasping movement may directly interfere with number magnitude processing, even though the movement is unrelated to the numerical task.

This provides direct evidence for the existence of motor-to-semantic interactions linking action and numerical comparison. We assume that the conflict between the processing of large numbers and the somatosensory input relative to grip closure originates in a shared magnitude representation housed in the parietal cortex (Badets et al., 2012; Badets & Pesenti, 2010; Castiello, 2005; Pesenti, Thioux, Seron & De Volder, 2000; Simon, Mangin, Cohen, Le Bihan & Dehaene, 2002; Walsh, 2003). However, it is worth noting that the precision grip did not elicit any interference in the number comparison task, while this grip had been linked to number magnitude in several other studies. In contrast with previous studies, we did not study the crosstalk between motor and semantic processes from stimulus-response compatibility effects but measured its direct consequences on the ability to compare numbers. The amount of motor interference was matched across conditions since we asked participants to adopt a precision grip with each hand or to position both hands in opposition to perform a bilateral grip. Other processes that are specific to the bilateral grip condition might thus be involved in the interference of grip closure with number processing. Further research is necessary to elucidate this issue. The dissociated effects of precision grip in action judgments and of bimanual grip in numerical judgments indicate that the somatosensory information relative to hand posture influences action prediction independently of the semantic information relative to numerical magnitude.

In conclusion, our results provide firm evidence that action prediction is unavoidably tied to the state of the perceptual and sensorimotor system at the time the mental representation of one's motor capability is formed. Perceptual information about the visual environment and somatosensory information about the current hand posture were both integrated into the prospective plan even though irrelevant or detrimental for judging one's ability to grasp objects. Moreover, our results bring the first evidence that the execution of an unrelated grasping action can

influence number processing, providing direct evidence for the existence of motor-to-semantic interactions, hence further supporting the view that these two functions share cognitive processes for magnitude representation.

Chapter 4

Visual illusion modulates the integration of somatosensory information in the prospective action plans

1. Introduction

How is it that one's actions rarely miss their target? The success of an action partly relies on one's capability to anticipate its feasibility and eventually adapt the motor plan (Jeannerod, 1994; Johnson, 2000). We showed in Chapter 2 that predicting one's capability to grasp an object between finger and thumb entails the integration of visual information about the perceived object size, as well as somatosensory information about the current grip aperture. The prediction of success correlated negatively with perceived object size, which was manipulated with the size-contrast Ebbinghaus illusion, and correlated positively with current grip aperture, which was manipulated with concurrent hand motor tasks. In particular, participants underestimated their capability to grasp the central circle of the Ebbinghaus illusion when their current grip aperture was reduced because squeezing a ball between finger and thumb, and they overestimated this capability when grip aperture was enlarged because spreading finger and thumb apart. The effect of the size-contrast illusion has already been evidenced repeatedly in both the context of perception and action (Franz, et al., 2000; Franz & Gegenfurtner, 2008; Massaro & Anderson, 1971; Pavani et al., 1999; Vishton et al., 1999) and was thus expected. On the contrary, the effect of the current hand posture was unexpected given that

maximal grasping capability remains identical whether the hand is open or closed at the time of the judgment. It is true that some other studies have evidenced an effect of body-related information on action judgements, but which concerned the body state in which the judgment would have been done (Carello et al., 1989; Rochat & Wraga, 1997). The question we address here is why the state of the body, and in particular of the hand, at the time of the grasping judgment exerts such a pervasive influence on grasping judgments, even when it is not relevant and even detrimental for judging our general capability of making an action.

Chapter 3 suggested that the effect of the concurrent motor task on grasping judgments truly reflects integration of the available somatosensory information about the index finger and thumb in the prospective action plan, by excluding an effect of semantic information about the magnitude associated with the grip. In a follow-up experiment where prospective action judgements were measured out of any illusion context, we noticed that the concurrent motor task no longer had any effect. Hence, a potential explanation is that reliance on somatosensory information emerged as a consequence of the presence of the illusion.

The present study tested more systematically whether somatosensory integration depends on the presence of the illusion by including two groups of participants: one group that made grasping judgments on a target circle surrounded by peripheral circles inducing the Ebbinghaus illusion (*i.e.*, with illusion), and another group that made grasping judgments on the target circle alone, without surrounding circles (*i.e.*, without illusion). We manipulated somatosensory information about the grip by asking participants of both groups to perform alternatively two concurrent motor tasks (squeezing *vs.* spreading fingers). Under the hypothesis that somatosensory integration depends on the presence of the illusion, we expected grasping judgements to be affected by the concurrent motor

tasks when the target circles are embedded within the Ebbinghaus displays but not, or to a lesser extent, when they are presented alone. More precisely, the group of participants confronted to the illusion should underestimate their grasping capability when their current grip aperture is decreased because squeezing a ball compared to when their current grip aperture is enlarged because spreading their fingers apart. In contrast, the adopted grip aperture should have little influence on the judgments of the participants performing the task on circles devoid of illusory context. To test the hypothesis that participants relied on somatosensory information because exposure to the visual illusion decreased their confidence in the judgment (Desender, Boldt & Yeung, 2018), we also asked them to express, after each trial, their level of certainty in the given response. This hypothesis predicts that increased reliance on somatosensory information should be associated with lower confidence ratings in the group experiencing visual illusions.

2. Method

2.1 Participants

Forty healthy volunteers (10 males, mean age and SD: 22 ± 2 years) participated in this experiment. They had normal or corrected-to-normal vision and were unaware of the hypotheses tested. They all gave their informed consent prior to the experiment, and all the procedures were in accordance with the ethical standards of the Declaration of Helsinki. Half of the participants were randomly assigned to the group with illusion and the other half to the group without illusion. We determined the sample size by conducting a power analysis based on the effect sizes obtained in our previous experiments using the same concurrent motor tasks. Sample size analysis indicated that at least 16 participants were required to observe a true effect of the concurrent motor tasks in the context of the illusion (d = 0.69)

with an 80% power using a one-tailed pairwise comparison ($p < 0.05$). The research plan was pre-registered (https://osf.io/xy3mz).

2.2 Apparatus and stimuli

Participants sat at a viewing distance of 75 cm from a vertical screen. A chin rest was used to keep their head in a fixed position and align their gaze with the screen centre (Figure 1A). A voice key was fixed on the chin rest to record RLs. A projector (MP7740, 3M, United States) placed behind the screen displayed the stimuli with a 1280 x 1024-pixel resolution, with 1 pixel corresponding to 0.19 cm and 1 cm corresponding to 0.76°. Stimuli creation was programmed with Psychopy2 (Peirce, 2009) and stimuli presentation and data recording were handled using E-prime2 (Schneider et al., 2002).

The stimuli consisted of target circles whose size was -5, -3, -2, -1, +0, +1, +2, +3 and +5 cm relative to participant's MGA, as measured prior to the experiment using a set of wooden bars ranging from 9 to 20 cm with 1-cm increments. The MGA was given by the longest bar the participant was able to hold comfortably between the tips of the index finger and thumb of the dominant hand. The mean size (±SD) of the participants' MGA was 12.2 ± 1.0 cm for the group without illusion (n = 20) and 12.0 ± 1.2 cm for the group with illusion (n = 20), $t(39) = 0.58$, $p = .562$. In the group with illusion, the apparent size of the target was manipulated by a surrounding annulus consisting of circles that were either larger or smaller than the target, making the latter appear smaller or larger, respectively (referred hereafter as "small" and "large" illusory display). The large surrounding circles were twice as large as the target, and the small surrounding circles were twice as small as the target. An additional display with contextual circles of the same size than the target was used as a control not inducing any illusion (Figure 1B). The gap between the target and

the surrounding circles was always equal to the size of the target so that illusion effects could not be ascribed to obstacle avoidance mechanisms (Haffenden & Goodale, 2000; but see also Franz et al., 2003).

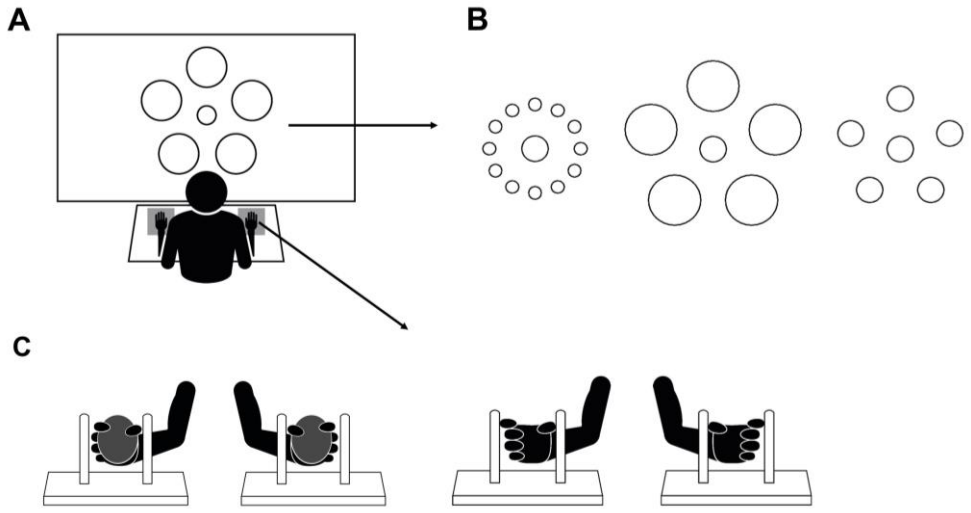

Figure 1. *Experimental set-up. (A) The participants sat in front of a wide screen onto which the stimuli were projected from behind. They held their hands below cardboard surfaces that kept hands out of sight. (B) The Ebbinghaus displays included, on the left, a display with small surrounding circles making the central circle appear larger (i.e., large display), at the centre, a display with large surrounding circles making the central circle appear smaller (i.e., small display) and, on the right, a display with surrounding circles of the same size than the central circle (i.e., neutral display). (C) The concurrent motor tasks: Participants performed grasping judgments while squeezing a foam ball between the index finger and thumb of each hand (left) or while keeping the index finger and thumb spread at 110% of their MGA (right).*

2.3 Tasks and procedure

The task required participants to estimate whether they would be able to grasp the central circle between their index finger and thumb, without moving, and then indicate their confidence in the given response. One group of participants made

the grasping judgments on central circles surrounded by peripheral circles inducing the Ebbinghaus illusion (*i.e.*, group with illusion); the second group made the grasping judgments on central circles presented alone, without surrounding circles (*i.e.*, group without illusion).

Each trial started with the presentation of a fixation cross at the screen centre for 500 ms, immediately followed by the target circle. The participants were asked to judge whether they considered the target as graspable by saying "yes" or "no" and to indicate their level of confidence by adding "certain" or "uncertain". They had to respond as quickly and faithfully as possible, and their responses were encoded on-line by the experimenter. The image disappeared as soon as the response was given, and the next trial began 1500 ms later. During one half of the experiment, participants made their judgments while squeezing a 7-cm foam ball between the index finger and thumb of each hand, with constant pressure, so that their grip on the ball filled the 8cm-gap between two vertical iron bars placed next to each hand (Figure 1C). During the other half of the experiment, they made their judgments while spreading their index finger and thumb wide apart so that the nails were constantly in contact with two vertical iron bars separated by a distance corresponding to 110% of the MGA (Figure 1C). The participants were asked to maintain this hand posture throughout the block of trials, and a webcam was used to monitor their performance on-line. The participants performed 27 practice trials before taking 2 blocks of 81 trials for each motor task (spread *vs.* squeeze). In the blocks performed by the group with illusion, the 9 target sizes were presented 3 times for each of the 3 illusory displays (small, neutral *vs.* large). In the blocks performed by the group without illusion, the 9 target sizes were repeated 9 times – with no illusory display – in order to obtain the same number of trials across groups. The different stimulus configurations were randomly mixed within each block, and

starting with the squeezing or spreading motor task was counterbalanced across participants.

2.4 Data analysis

2.4.1 Response latencies

Trials in which RLs were shorter than 100 ms (0.82% of the dataset) were discarded from any further analysis as rapid stimulus offset compromised judgment accuracy. We also discarded from the RL analysis the trials in which the voice key failed to trigger (8.43%) and the data of one participant for whom we could not record RLs. The RLs were analyzed with a GLMM including the GROUP (with *vs.* without illusion) as a fixed factor and the differences between participants as random effects.

2.4.2 Grasping judgment

As a prerequisite, we tested that participants who made grasping judgments on target circles embedded in Ebbinghaus displays were indeed sensitive to the illusion. To do so, the probability of affirmative responses in the group with illusion was modelled using a GLMM including the ILLUSION (small, neutral *vs.* large display), the MOTOR TASK (squeeze *vs.* spread), and their interaction as fixed factors and the differences between participants as random effects.

Then, to assess differences in somatosensory integration between the two groups, we restrained the analysis to the neutral trials (*i.e.*, free of size distortion) of the group with illusion and a sample of one-third of the trials (*i.e.*, hereunder the experimental trials) of the group without illusion. The rationale was to consider the trials corresponding to the “small” and “large” displays as fillers and use them only to ascertain that the participants from the first group were sensitive to the illusion.

Along the same lines, two-third of the trials performed by the group without illusion was considered as fillers and used only to ensure that the two groups performed the same number of judgments throughout the experiment. We used a GLMM to model the responses to the neutral trials of the group with illusion and the experimental trials of the group without illusion. The GROUP (with *vs.* without illusion), the MOTOR TASK (squeeze *vs.* spread), the SIZE of the target (-5, -3, -2, -1, 0, +1, +2, +3 *vs.* +5 cm relative to MGA) and their interactions were included as fixed effects and the differences between participants as random effects.

2.4.3 Subjective confidence

In order to compare the level of subjective confidence across the two groups, we entered the confidence ratings (*i.e.*, "certain" or "uncertain") in a GLMM including the SIZE of the target (-5, -3, -2, -1, 0, +1, +2, +3 *vs.* +5 cm relative to MGA), the GROUP (with *vs.* without illusion) and their interaction as fixed effects, and the differences between participants as random effects. This analysis was performed on the neutral trials of the group with illusion and on the experimental trials of the group without illusion.

3. Results

3.1 Response latencies

No difference in RLs was observed between the group with illusion (1099 ± 57 ms) and the group without illusion (1151 ± 59 ms), $F(1,12100) = 0.39$, $p = .533$.

3.2 Grasping judgment

The GLMM on the reponses to the grasping judgments made by the group with illusion revealed a main effect of the ILLUSION, $F(2, 6761) = 54.60$, $p < .001$. Post-hoc pairwise contrasts indicated that, compared to the neutral display (.51 ± .04), the rate of affirmative responses was smaller for the large display (.47 ± .04), $t(6761) = 2.72$, $p = .007$, difference (D) = 0.04, *95% CI* = [.01, .07], and larger for the small display (.63 ± .04), $t(6761) = -7.41$, $p < .001$, $D = -0.12$, *95% CI* = [-.15, -.08]. There was also a main effect of the MOTOR TASK, $F(1, 6761) = 37.10$, $p < .001$, indicating that the rate of affirmative responses was smaller for the squeezing (.50 ± .04) than for the spreading task (.58 ± .04), $D = .08$, *95% CI* = [-.10, -.05] . There was no ILLUSION X MOTOR TASK interaction, $F(2, 6761) = 54.60$, $p < .649$.

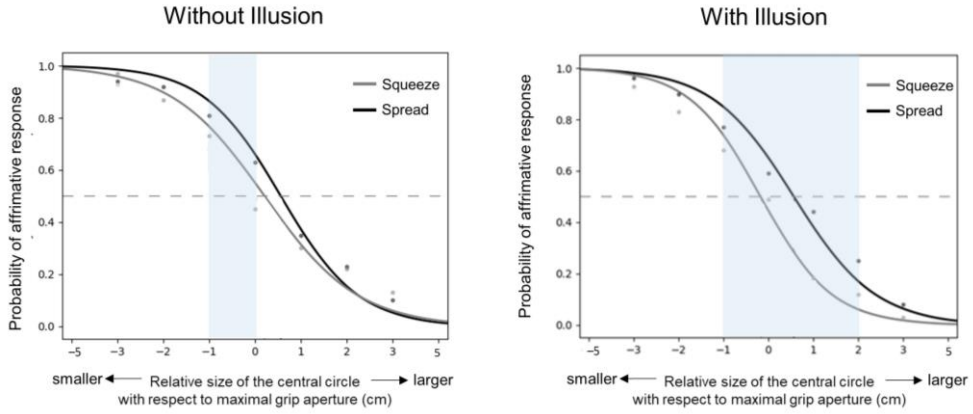

Figure 2. *Fitted curves from cumulative data showing the motor interference on grasping judgments performed by participants from the group with and without illusion. The dots represent the average rate of affirmative responses (y-axis) as a function of the difference between the actual size of the central circle and the MGA of the participant (x-axis). Solid lines represent the predicted values obtained by means of logistic regression. The range of sizes for which the difference between the squeezing and spreading motor task is significant is highlighted in light blue.*

The GLMM that aimed to compare the groups with and without illusion showed a main effect of SIZE, $F(1, 4382) = 917.06$, $p < .001$, indicating that the rate of affirmative responses decreased as the size of the circle increased. There was also a main effect of the MOTOR TASK, $F(1, 4382) = 45.96$, $p < .001$, with participants giving less positive responses when squeezing (.48 ± .09) than when spreading fingers (.67 ± .08), $D = -.19$, $95\%\ CI = [-.25, -.13]$. There were also a significant MOTOR TASK x GROUP interaction, $F(1, 4382) = 7.36$, $p = .007$ and a GROUP X MOTOR TASK X SIZE interaction, $F(1, 4382) = 4.32$, $p = .038$. Post-hoc pairwise contrasts indicated that the difference between the squeezing and spreading tasks was significant for sizes from -1 to +2 cm for the group with illusion and for sizes from -1 to +0 cm for the group without illusion (Figure 2).

3.3 Subjective confidence

The GLMM of the confidence ratings showed that the main effect of SIZE fitted a quadratic function, $F(4, 312) = 32.33$, $p < .001$, indicating that confidence was the highest when the target size was at the extremities of the range used (*i.e.*, -5 and + 5 cm relative to MGA), and the lowest when target size was close to MGA (Figure 3). There was no main effect of the GROUP, $F(1, 38) = 0.37$, $p = .544$, and no SIZE X GROUP interaction, $F(4, 312) = 0.27$, $p = .89$.

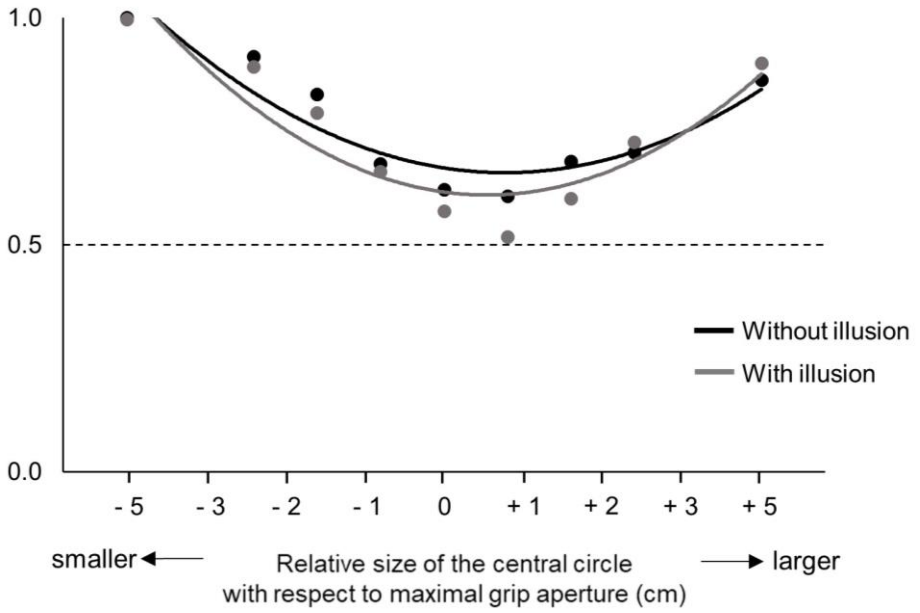

Figure 3. *Fitted curves from cumulative data showing the certainty ratings for each group. The dots represent the average rate of "certain" responses (y-axis) as a function of the difference between the actual size of the central circle and participants' MGA (x-axis). Solid lines represent predicted values obtained by estimation of the quadratic function.*

4. Discussion

The present study investigated whether the reliance on somatosensory information during grasping judgments depended on the presence of the Ebbinghaus illusion. First, we showed that participants performing grasping judgments on the Ebbinghaus displays were indeed sensitive to the illusion: they underestimated *vs.* overestimated their capability to grasp the central circle when it was surrounded by smaller *vs.* larger circles. Second, we showed that participants from both the group with and without illusion underestimated their grasping capability while they were squeezing a ball compared to when spreading fingers apart. Third, we found that

such motor interference was a function of the illusory context. In the group performing the task on circles without illusory context, the adopted hand posture influenced the judgment of circles whose size was at the limit of grip aperture. In contrast, the group exposed to illusory size distortions showed a motor bias for all circles between -1 and +2 cm relative to the MGA.

The present results converge with our previous observations that grasping judgments were influenced not only by the visual context, manipulated through the Ebbinghaus illusion but also by hand posture, manipulated through concurrent motor tasks (Geers et al., 2018, see Chapter 2). Chapter 3 further suggested that the effect of the motor task is not a mere semantic bias but reflects the integration of somatosensory information about the effectors of the judged action in the prospective plan. The present findings add on the previous ones by showing that the amount of somatosensory integration is contingent on the presence of the size-contrast illusion. Judgments of graspability on the very small and large circles indicate that, when the difference between circle size and one's MGA is salient, somatosensory feedback from the hand grip is not integrated into the comparison process, whether visual context is provided or not. However, somatosensory information comes into play when target size is close to the MGA, and the judgment is difficult to make. Such difficulty was evidenced by behavioural performance (*i.e.*, the rate of "yes" responses fell at the chance level), and by subjective reports (*i.e.*, participants' confidence in their response dropped off). The association between increased somatosensory integration and decreased confidence in one's performance supports the idea that subjective confidence might play a role in seeking information to secure a decision (Desender et al., 2018).

Furthermore, at the task level, we found that somatosensory information received more weight when the visual context created size distortions. In the group

with illusion, the current hand posture influenced the judgments not just when the object size approached MGA, but also when it diverges from MGA by +1 or +2 cm. A difference of +2 cm led participants to judge the object as non-graspable in 80% of the cases. It is worth reminding that the difference of motor interference between the groups with and without illusion emerged from the analysis on neutral trials not inducing any illusion at the time of the judgment. It is thus well the mere exposure to the illusion that is responsible for the increased reliance on somatosensory information. This might be because size distortions induced by the illusion increase the variability of perceived size across trials, and hence, the difficulty of the task, leading to seeking of additional information just as when target size is close to the MGA. However, this was reflected neither in RLs nor subjective confidence ratings. One plausible account is that, although the illusion increased task difficulty, the group with illusion revised their subjective ratings upwards because they experienced increased reliance on somatosensory information. Because we asked participants to indicate their level of confidence after they made their judgment, we cannot exclude that the integration of somatosensory information into the comparison process might have played a role in their appreciation of response certainty.

Another potential explanation is that, as in the case of multisensory cue combination (e.g., Alais & Burr, 2004; Knill & Richards, 1996; Sheppard, Raposo & Churchland, 2013), the weight of somatosensory information increases in the context of the illusion because the latter decreases the reliability of the visual information about object size at the block level. One way the visual illusion could reduce this reliability is by delivering conflicting allocentric and egocentric representations of size. Indeed, circle size estimates differ as a function of whether size is perceived relative to the observer (and thus independently of the visual context; *i.e.,* egocentric coding) or relative to the surrounding elements (*i.e.,*

allocentric coding). Both representations could be processed simultaneously and produce an unstable percept of size. Hence, it remains to be further investigated whether task difficulty alone modulates the reliance on somatosensory information or whether the reliability of visual information also comes into play.

To sum up, while prospective judgments about one's capability to grasp an object are primarily determined by visual information, somatosensory information about grip aperture can be used to refine the judgments when object size is close to maximal grasping capability or when presented within the context of a size-contrast illusion. These results suggest that somatosensory integration depends on the difficulty of the task. The question of whether the reliability of the visual information *per se* may exacerbate somatosensory integration needs further investigation.

Chapter 5

Role of the fronto-parietal cortex in prospective action judgments

1. Introduction

The capacity to imagine the progression of an action, before it is eventually executed, is a fundamental aspect of adaptive behaviour. For example, anticipating a failure to grasp an object because it is too large or too far will enable the implementation of motor adaptations facilitating the action, such as taking a step closer or using two hands. A dominant view assumes that such prospective action judgments involve the mental simulation of the implied action(s) (Johnson, 2000). This simulation would recruit the same processes as those involved in action planning and execution, namely encoding the visual properties of the object, activating the sensorimotor representation of the effectors (*e.g.*, the hand), and computing the visuomotor transformations required to achieve the action given a set of biomechanical rules (Johnson, 2000; Bernstein, 1967, Rosembaum, 1991). Evidence for the involvement of motor simulation in prospective action judgments comes from the finding that they are indeed affected by the same biomechanical constraints than the actual execution of the corresponding action(s) (Carello et al., 1989; Frak et al., 2001; Johnson, 2000; Mark et al., 1997). For instance, the time required to define the grip one would use to grasp a cylinder increases as a function of the angular distance of the wrist rotation along the most biologically plausible path rather than along the shortest path (Johnson, 2000). However, an effect of biomechanical constraints on hand motor judgments has also been reported in

individuals who lack the relevant somatosensory and motor representations due to a congenital absence of upper limbs (Funk & Brugger, 2008; Vannuscorps & Caramazza, 2015; 2016a; 2016b; Vannuscorps et al., 2012). Hence, the observation that behavioural performance is modulated by biomechanical constraints cannot be considered as a signature of motor imagery being involved in the task.

Brain imaging provides another line of evidence for attesting the role of motor simulation in prospective action judgments. Available fMRI data suggest that prospective action judgments involve dorsal fronto-parietal regions associated with the explicit simulation or execution of actions (*e.g.*, IPL and SPL, including areas around the anterior part of the IPS [AIP], ventral and dorsal premotor cortex, DLPF; Coello et al., 2008; Bartolo et al., 2014; Decety et al., 1994; Gerardin et al., 2000; Johnson et al., 2002). However, the precise overlap between prospective action judgments and motor imagery is unknown as they have never been directly compared. Moreover, some regions within the fronto-parietal cortex have been associated with magnitude processing in non-motor tasks, such as length, size or number comparison (Dormal & Pesenti, 2009; Fias et al., 2003; Pinel et al., 2004). The calibration of object-directed actions requires the computation of magnitude estimates, such as grip aperture or reaching distance, but existing studies have left out the possibility that the fronto-parietal cortex might actually play a role in magnitude processing (Walsh, 2003). When considering the primary somatosensory (S1) or motor (M1) cortices, an increase of the blood-oxygen-level-dependent (BOLD) signal has been occasionally reported during explicit simulation of an action but not during prospective action judgments. A close look at the available data indicates that explicit motor imagery only induces a 50-70% rise in BOLD signal compared to action execution, which may explain why it has remained undetected in many studies (Gerardin et al., 2000; Lotze et al., 1999; Nair, Purcott, Fuchs, Steinberg & Kelso, 2003; Porro et al., 1996).

TMS offers an alternative to capture subtle changes in corticospinal excitability (CSE) of hand muscles during motor imagery. Single-pulse TMS over M1 allows an instantaneous measure of CSE through the recording of motor-evoked potentials (MEPs) in the contralateral hand (Parkin, Ekhtiari & Walsh, 2015). MEPs provide a sensitive output measure of fronto-parietal activity during motor imagery, as CSE changes may be caused by M1 or any frontal or parietal area remotely connected to M1 (Bestmann & Duque, 2016). When TMS is used to excite pools of corticospinal cells projecting onto different muscles, it is further possible to show that CSE changes are specific to the muscles involved in the imagined movement (*e.g.*, Fadiga et al., 1999).

The present study capitalises on the respective advantages of fMRI and TMS to test whether or not prospective action judgments involve motor simulation in the fronto-parietal cortex. In a first experiment, we used fMRI to map neural activity in the whole brain while participants were making judgments about their capability to grasp rectangles of various lengths between their index finger and thumb (*i.e.*, grasping judgments) or while they were explicitly imaging themselves grasping various objects (*i.e.*, motor imagery). In order to differentiate the brain areas involved in action processing from those involved in magnitude processing, a control task required participants to judge whether rectangles were larger than a perceptual reference (*i.e.*, length judgments). Under the motor simulation hypothesis, grasping judgments and motor imagery should share activity within the fronto-parietal areas. The comparison with activations found during length judgments allows removing from this shared network the part dedicated to magnitude processing. In a second experiment, we directly measured motor excitability changes in a set of hand muscles using TMS-induced MEPs. Under the motor simulation hypothesis, grasping judgments should be associated with a selective increase of MEPs in the first dorsal interosseus (FDI) and the abductor pollicis brevis (APB), which both

contribute to adjusting the precision grip, but not in the abductor digiti minimi (ADM), which is not relevant for thumb-index pinch movements.

2. Method

2.1 fMRI Experiment

2.1.1 Participants

Thirty-two healthy volunteers (21 females, mean age and standard error (SE): 23 ± 0.41 years) participated in this fMRI experiment. They were all right-handed according to the Edinburgh inventory questionnaire (Oldfield, 1971), had no history of neurological or psychiatric disorders, had normal or corrected-to-normal vision, and were unaware of the purpose of the study. They gave their written informed consent prior to the experiment. The study was non-invasive, performed in accordance with the ethical standards of the Declaration of Helsinki, and approved by the Biomedical Ethical Committee of the Université catholique de Louvain.

2.1.2 Tasks and Stimuli

The fMRI experiment included a prospective grasping judgment, a motor imagery task, a perceptual length judgment and their reference tasks (Figure 1A). The grasping judgment (GJ) required participants to judge whether they would be able to grasp a rectangle lengthways between their index finger and thumb, without actually moving their fingers. To minimise head motion, participants had to respond "yes" aloud only when they judged the rectangle as graspable but stay silent when they judged it as ungraspable. The stimuli consisted of seven black rectangles with a height of 1 cm and a length equal to participant's MGA ± 0, 1, 2, or 5 cm. The reference task was a detection task in which the participant was required to say "yes" aloud each time a 3x1 cm rectangular shape appeared on the screen. The motor

imagery task (MI) required participants to imagine themselves grasping an object displayed on the screen as if they were about to use it. The stimuli consisted of coloured pictures of 40 everyday objects (see Supplementary Material 1). The reference task consisted of the display of the same pictures scrambled in such a way that objects could no longer be identified. The length judgment (LJ) required participants to judge whether a rectangle was longer or not than a standard shown just before the beginning of the acquisition run. Participants had to respond "yes" aloud when the bar was longer than the standard and stay silent when the response was "no". The stimuli and the reference task were the same as those used for the grasping judgment performed by the participant, except that the stimulus length was computed from the MGA of another participant ± 0, 1, 2, or 5 cm, so that the references used for length and grasping judgments were different for each participant but equal across participants (mean ± SE: 12 ± 0.18 cm).

2.1.3 Procedure

To optimise the signal-to-noise ratio while controlling for speech-related head motion artefacts (Birn, Cox & Bandettini, 2004), we used a block-design paradigm, with 10 blocks lasting 20,000 ms each, alternating an experimental task and its reference interleaved with 10,000 ms fixation periods (Figure 1B). Within each block and trial, each stimulus was projected on a screen, in the rear of the scanner, and viewed by the participant via a tilted mirror mounted on the head coil for 2000 ms, with a 500-ms inter-trial interval. For the grasping and length judgments, each block consisted of 8 trials including 3 rectangles smaller than the participant's MGA/standard, 3 rectangles larger than their MGA/standard and 2 of the length of their MGA/standard, presented in random order. For the reference (detection) task, each block consisted of 4 to 5 stimuli presented with a random inter-trial interval. For the motor imagery, each experimental block included 8 objects and

each control block 8 scrambled objects. Each pair of experimental and control tasks was used in two fMRI acquisition runs, resulting in 6 runs which order was pseudo-randomly counterbalanced across participants such that the grasping judgment was always performed before the motor imagery task in order to keep mental simulation implicit during the grasping judgment (*i.e.*, LJ – GJ – MI, GJ – LJ – MI and GJ – MI – LJ). Verbal responses were conveyed by a plastic tube to a digital recorder placed in an anechoic box outside the scanner room (Andres, Pelgrims, Michaux, Olivier & Pesenti, 2011).

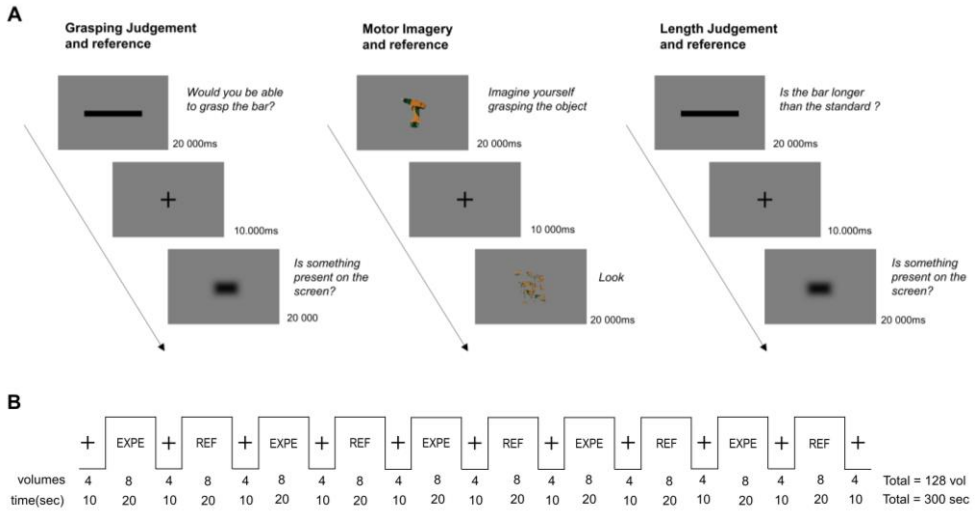

Figure 1. *Schematic representation of the time course of the fMRI experiment. Part A represents the experimental tasks and their reference with an example of the stimuli used, and part B an example of acquisition run structure. Each run consisted of 20s-periods of one of the experimental task or its reference alternating with 10s-periods of fixation.*

2.1.4 Imaging data acquisition

For each participant, a high-resolution anatomical image was first acquired with a 3.0 Tesla magnetic resonance imager (Achieva, Philips Medical Systems) and an 32-channel phased array head coil using a T1-weighted 3D turbo fast field-echo

sequence with an inversion recovery prepulse (time to echo [TE] = 4.6 ms, time for repetition [TR] = 9.1 ms, flip angle [FA] = 8°, field of view [FOV] = 220x197 mm², 150 contiguous axial slices of 1 mm, voxel size = 0.76x0.64x1 mm³, SENSE factor = 1.4). Functional images were then acquired as series of blood-oxygen-sensitive T2*-weighted echo-planar volumes (GRE-EPI) with the following parameters: TE = 32 ms, TR = 2500 ms, FA = 90°, FOV = 220 x 220 mm², 36 contiguous axial slices acquired in an ascending sequence, slice thickness = 3.5 mm with no interslice gap, voxel size = 1.96x1.96x3.5 mm³, SENSE factor (parallel imaging) = 2.5. Each acquisition run comprised 124 volumes, resulting in 80 volumes per experimental/reference task.

2.1.5 Data analysis

A GLMM was used to analyse yes/no responses in a subset of 20 participants. The other participants were excluded from this analysis due to technical issues affecting the recording of their verbal responses. Because instructions associated small rectangles with a "yes" response in grasping judgments but with a "no" response in length judgments, we coded the responses so that the length effect could be interpreted consistently in the two tasks. The "yes" response was coded 1 for the grasping judgment and 0 for the length judgment (*i.e.*, the rectangle was perceived as "graspable" and "small"), whereas the "no" response was coded 0 for the grasping judgment and 1 for the length judgment (*i.e.*, the rectangle was perceived as "non-graspable" and "large"). The GLMM included the type of JUDGMENT (GJ *vs.* LJ), the LENGTH of the rectangle relative to MGA/standard (-5, -2, -1, +0, +1, +2 *vs.* +5 cm), and their interaction as fixed effects and the differences between participants as random effects. Bonferroni correction was applied to the post-hoc comparisons where relevant.

Brain imaging data were processed using Statistical Parametric Mapping (SPM12, Welcome Department of Imaging Neuroscience, London UK; Penny, Friston, Ashburner, Kiebel & Nichols, 2011). All functional volumes were (1) realigned to the first volume of the respective run (closest to the anatomical scan) to correct for within- and between-run motion, (2) co-registered with the anatomical image, (3) corrected for slice acquisition delays, (4) normalised to the standard MNI template using a Trilinear interpolation and a voxel size of 2x2x2 mm^3, and (5) smoothed with a 5-mm FWHM Gaussian kernel. During realignment, drifts in the translation or rotation (*i.e.*, roll, pitch, yaw) were checked for each participant and run. The data of one participant were excluded because of drifts superior to 5 mm in translation; all other data showed drifts inferior to 5 mm in translation and to 3 degrees in rotation; the data of another participant were also excluded because unusually strong susceptibility artefacts were visible at the level of the frontal cortex. Condition-related changes in brain activity were estimated for the 30 remaining participants by a whole-volume voxel-wise analysis using a general linear model on which the responses evoked by each condition of interest were modelled by a standard hemodynamic response function. The contrasts computed at the individual level corresponded to each task contrasted with its reference (GJ – refGJ, MI – refMI, and LJ – refLJ). We then examined the critical contrasts at the group level. In order to reveal the brain areas commonly activated in GJ and MI, the contrasts computed at the group level were entered in a conjunction analysis ([GJ – refGJ] AND [MI – refMI]). Contrary to the cognitive subtraction approach that consists in revealing the neural substrate of the processing component of interest by contrasting a task that engages this component and a reference task that does not, the conjunction approach does so by comparing the activations of two pairs of tasks where the component of interest is the only common processing difference across task pairs. The main advantage of conjunction designs is that one has to control neither for all

but the component of interest nor for the interaction terms that might be included in these components (Price & Friston, 1997; Price, Moore & Friston, 1997). In this case, by using respectively images of objects and rectangles in MI and GJ, we could exclude that the areas commonly involved in the two tasks underlie the processing of object function or identity. Because GJ required a verbal answer and MI required no answer, we could also exclude the contribution of the shared network is linked to response production. Rather, the contribution of the shared network should be attributed to processes commonly involved in the solving of MI and GJ. In order to identify brain areas of this common network that were specific to the context of action, the areas found in the contrast of the length judgment and its reference were removed from the conjunction using a mask ([GJ – refGJ] AND [MI – refMI] masked exclusively by [LJ – refLJ]). We also sought for differences between tasks by computing the following subtractions: [GJ – refGJ] – [MI – refMI], [MI – refMI] – [GJ – refGJ], [GJ – refGJ] – [LJ – refLJ] and [LJ – refLJ] – [GJ – refGJ]. We reported only activations surviving a statistical threshold of $p < 0.05$ corrected for *Family Wise Error* and extending to at least 10 contiguous voxels.

2.2 TMS Experiment

2.2.1 Participants

Nine healthy volunteers (7 females, $M_{age} = 24 \pm 0.94$ years) participated in this experiment. They were right-handed according to the Edinburgh inventory questionnaire (Oldfield, 1971), had no history of neurological or psychiatric disorders, had normal or corrected-to-normal vision, and had not participated in the fMRI experiment. All were screened for TMS contraindications, including recent use of alcohol, caffeine and drug (Rossi, Hallett, Rossini & Pascual-Leone, 2009). They gave their written informed consent before the experiment and were unaware

of the purpose of the study. The study was non-invasive, performed in accordance with the ethical standards of the Declaration of Helsinki.

2.2.2 Tasks and Stimuli

Participants were required to perform prospective grasping judgments and length judgments similar to those of the fMRI experiment, with two main changes. First, in order to disentangle the veridical size of the graspable stimuli from their perceived size relative to the visual context, judgments were performed on a horizontal line ended by arrows pointing inwards or outwards. Typically, when the line is ended by inwards pointing arrows (> <), it appears to be longer, while it appears smaller it is ended by outwards pointing arrows (< >), corresponding to the Müller-Lyer illusion configuration. We also used an additional figure with vertical lines (| |) displayed at each end of the horizontal line as a control, not inducing any illusion. Previous studies showed that the size distortion is striking in perceptual length judgments, but its effect on grip aperture during grasping movement toward the horizontal line was significantly smaller, most probably because action is more object-centred and less influenced by the visual context than perception (*e.g.*, Daprati & Gentullici, 1997; Dewar & Carey, 2006; van Doorn et al., 2007). Second, in order to get a finer behavioural measure, we added two intermediate lengths for the horizontal line resulting in -5, -3, -2, -1, 0, +1, +2, +3, + 5 cm, with respect to the standard (length judgment) or MGA (grasping judgment). Mean stimuli length was 11 ± 0.41 cm for both the grasping and length judgments.

2.2.3 Experimental procedure

The grasping and length judgments were performed on distinct sessions scheduled on two different days at a one-week interval. The order of the two judgments was counterbalanced between participants. During each session, the

participants sat at 60 cm of a computer screen with both hands resting on a table, palms down and arms semiflexed. Each trial started with the presentation of a fixation cross for 500 ms, followed by a Müller-Lyer figure. The participants responded "yes" or "no" aloud to indicate whether they judged the horizontal line as graspable or not (grasping judgments) or as larger than the standard or not (length judgments). The instructions emphasised the need to respond as quickly and accurately as possible, and responses were noted by the experimenter. After the response, the figure disappeared, and a blank screen was displayed for a time randomly set between 3000 and 5000 ms before a new trial started. For each judgment, all possible combinations of length (*i.e.*, 9 values), illusion (*i.e.*, 3 displays) and TMS timing (*i.e.*, 3 delays, see below) were repeated three times, in random order, giving rise to 243 trials divided into 2 sub-blocks.

2.2.4 TMS protocol

Single-pulse TMS was applied with a 70 mm figure-of-eight coil connected to a Magstim 200 magnetic stimulator (Magstim, Whitland, Dyfed, UK). The coil was placed over the left M1, tangentially to the skull, with the handle pointing backwards and laterally at a 45° angle away from the sagittal axis, approximately perpendicular to the central sulcus (Grandjean et al., 2018; Labruna et al., 2019). MEPs were recorded following each TMS pulse with surface electromyography (EMG) electrodes disposed on the FDI, APB and ADM muscles of the right hand. EMG data were collected for 1000 ms spanning the range of 500 ms before to 500 ms after the pulse. The EMG signals were amplified (x 1000), bandpass filtered on-line (10–500 Hz; NeuroloLog; Digitimer), and digitalised at 2000 Hz for offline analysis.

In each participant, we first located the optimal spot for eliciting MEPs in the FDI muscle (*i.e.*, the "hotspot"). This site was marked on a cap fitted on the

participant's head to provide a reference point of M1 throughout the experimental session (Derosiere, Vassiliadis, Demaret, Zénon & Duque, 2017). The resting motor threshold (rMT) was defined as the lowest stimulation intensity allowing the generation of MEPs of at least 50 μV peak-to-peak on 5 out of 10 consecutive trials in the FDI muscle. Across participants, the rMT was 43 % (± 7.4) of maximum stimulator output. The TMS intensity used during the experimental session was set at 115 % of the rMT (Bestmann and Duque, 2015). At this intensity, a single TMS pulse delivered with a figure-of-eight coil, which stimulates a zone of about 10 mm of diameter, eliciting MEPs simultaneously in adjacent hand muscles (*i.e.*, in the FDI, APB and ADM muscles) as corticospinal neurons projecting to different muscles of a given limb strongly overlap within M1 (Brasil-Neto et al., 1992; Derosiere et al., 2017; Thielscher and Kammer, 2002; Willett et al., 2019). To probe the putative changes in CSE occurring during grasping and length judgments, we delivered a pulse at one out of three possible timings in the two tasks: (1) 150 ms or (2) 300 ms after stimulus onset, and (3) between 3000 and 5000 ms after response onset during the inter-trial interval (ITI). A total of 81 MEPs was recorded at each timing in each task, with three MEPs for each possible combination of object size and illusion display. In addition, we recorded 20 MEPs, before each sub-block started, to obtain a baseline measure of MEP amplitude throughout the experiment.

2.2.5 Data analysis

A GLMM was used to model the probability of yes/no responses with the type of JUDGMENT (grasping *vs.* length), the MLI figure (short, neutral *vs*. long), the TIMING (150 ms,300 ms *vs.* ITI), the LENGTH of the line relative to MGA/standard (-5, -3, -2, -1, 0, +1, +2, +3 *vs.* +5 cm), and their interactions as fixed effects, and the differences between participants as random effects. In the MEP analysis, trials with background EMG activity (root mean square computed from -250 to -50 ms

before the TMS pulse) exceeding 2.5 SD above the mean were discarded (2.22% removal). This was done to prevent contamination of the MEP measurements by significant fluctuations in background EMG (Derosiere et al., 2013; Grandjean et al., 2018). We then extracted the MEP peak-to-peak amplitude for each trial. MEP amplitudes were averaged separately for each TMS timing, each muscle, each task and each subject. MEPs with an amplitude exceeding 2.5 SD around the mean of the condition were discarded (73 ± 4 trials remaining per condition). A GLMM was then used to model the MEP amplitude in each muscle, separately, with JUDGMENT (length *vs.* grasping), TIMING (baseline, 150 ms, 300 ms *vs.* ITI) and their interaction as fixed effects, and the differences between participants as random effects. Bonferroni correction was applied to post-hoc comparisons where relevant.

3. Results

3.1 fMRI Experiment

3.1.1 Behavioural data

The GLMM analysis showed that LENGTH significantly predicted participants' responses, $F(1, 3195) = 609.28$, $p < .001$, with the rate of affirmative responses decreasing/increasing for the grasping/length judgment as the length of the rectangle increased. The analysis also revealed an effect of the JUDGMENT, $F(1, 3195) = 29.77$, $p < .001$, indicating that participants gave less positive responses for the grasping (mean ± *SE* = 0.53 ± 0.08) than for the length judgment (0.67 ± 0.08). There was also a significant JUDGMENT x LENGTH interaction, $F(1, 3195) = 32.48$, $p < .001$, indicating that the slope was steeper for the length judgment than for the grasping judgment (Figure 2).

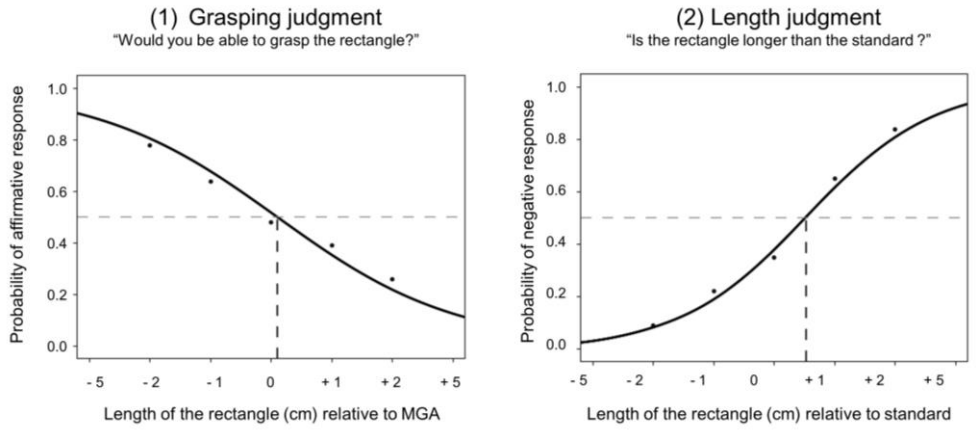

Figure 2. *Fitted curves from cumulative data of size on grasping and length judgments of the fMRI experiment. The dots represent the average rate of affirmative responses (y-axis) as a function of the length of the rectangle (x-axis) with respect to (1) the MGA or (2) the size of the standard. The solid lines represent the predicted values obtained by means of logistic regression.*

3.1.2 Brain imaging data

Grasping Judgments. Contrasting the grasping judgment task with its reference revealed brain activations bilaterally in the IPL and along the anterior-posterior axis of the IPS, including AIP (MNI coordinates x, y, z: 42, -49, 47 and -45, -37, 44). Parietal activations in the right hemisphere included the angular gyrus and extended to the precuneus. Activations in the frontal cortices were almost restricted to the right hemisphere, including the supplementary motor area (SMA) bilaterally, the right middle and anterior cingulate cortex and the superior and middle frontal gyri. Activations were also registered within the pars opercularis, orbitalis and triangularis of the right inferior frontal gyrus, which partly corresponded to DLPF and the rostral part of the PMv. In the occipital areas, clusters of activation were found around the right calcarine sulcus, in the left and right inferior occipital gyri, and in the right middle occipital gyrus, corresponding to the primary (V1) and

secondary (V2) visual areas. Other clusters of activations were found in the left posterior lobe of the cerebellum (VII, crus I and II), and in the left and right insula (Table 1a and Figure 3A).

Motor imagery. Contrasting the motor imagery task with its reference revealed a large left-lateralised fronto-parietal network. Parietal activations concerned the left IPL and SPL, along the anterior-posterior axis of the IPS (including AIP; -45, -34, 41), and both the left and right supramarginal gyri. Activations in the frontal cortices included the SMA bilaterally and the left precentral gyrus, in particular PMd and caudal PMv, the left superior and middle frontal gyri, and the pars triangularis and opercularis of the left inferior frontal gyrus, partly corresponding to DLPF and rostral PMv. In the right hemisphere, frontal activations were restricted to the middle and anterior cingulate cortex and the pars opercularis part of the inferior frontal gyrus. There were also activation foci in both the left and right associative visual cortex of the inferior occipital gyrus, the middle occipital gyrus, fusiform area and inferior temporal gyrus. Finally, there were clusters of activation in the left posterior lobe of the cerebellum (VI and crus I of VII) and the putamen (Table 1b and Figure 3B).

Length Judgments. The contrast between length judgment and its reference revealed foci of activations bilaterally in the IPL, along the anterior-posterior axis of the IPS (including AIP; 39, -43, 44 and -45, 40, 44). Parietal activations in the right hemisphere included the angular and supramarginal gyri and extended to the precuneus. Frontal activations included bilaterally the precentral gyrus, namely the caudal PMv, and the middle frontal gyrus. In the right hemisphere, activations were also found in the middle and anterior cingulate cortex and the pars opercularis, orbitalis and triangularis of the inferior frontal gyrus, partly corresponding to the DLPFC and rostral PMv. In the occipital cortices, cluster of activations included both the right and left middle occipital gyri and the left inferior occipital gyrus

around the calcarine sulcus, corresponding to V1, V2 and the associative visual areas. Activations were also found bilaterally in the insula and the left posterior lobe of the cerebellum (VII, crus I and II; Table 1c and Figure 3C).

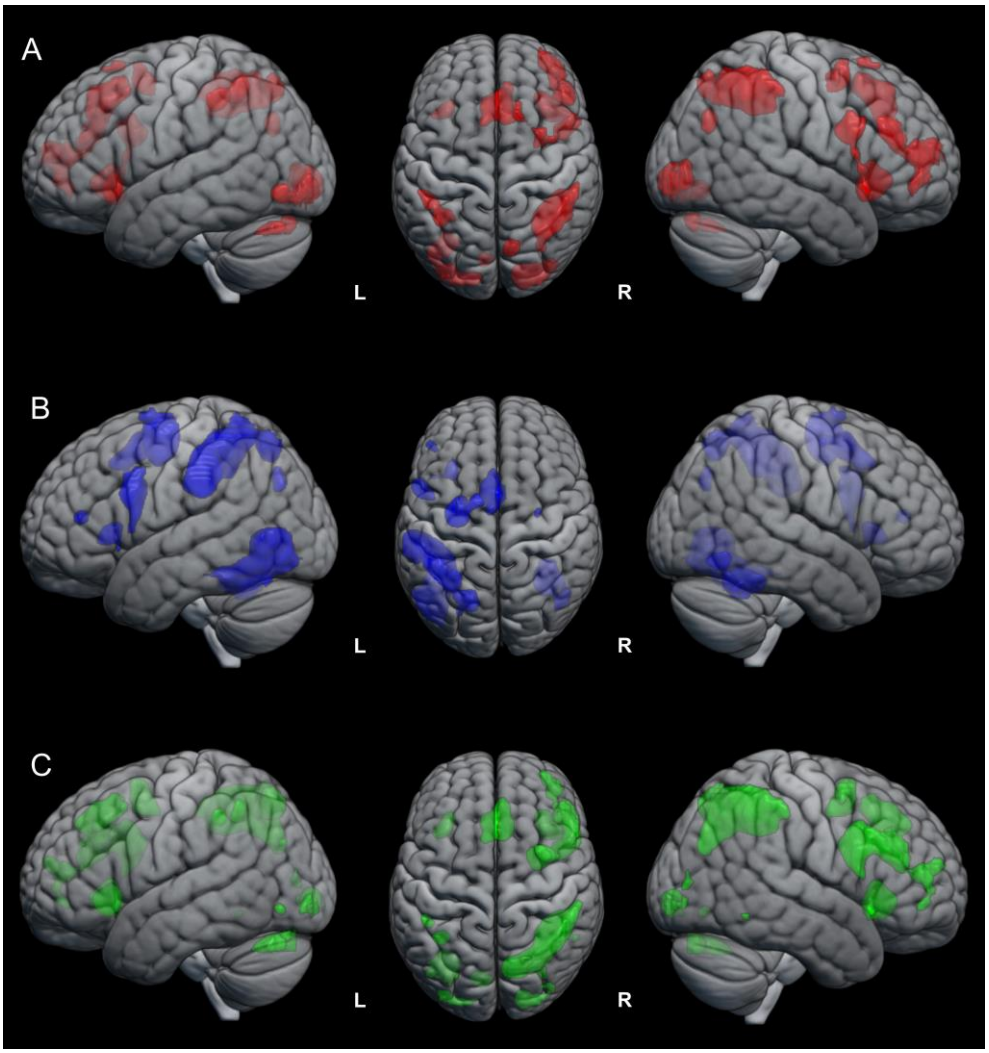

Figure 3. *Rendering of the statistical maps showing the brain areas activated in (A) the grasping judgment task vs. its reference, (B) the motor imagery task vs. its reference and (C) the length judgment task vs. its reference, surviving at a statistical threshold of* $p_{FWE} < 0.05$ *corrected for multiple comparisons and extending to k = at least 10 contiguous voxels.*

Grasping judgments and motor imagery. The conjunction of grasping judgment and motor imagery, each contrasted to its own reference ([GJ – refGJ] AND [MI – refMI]), revealed the areas commonly involved in both grasping judgment and motor imagery tasks. These mainly corresponded to a fronto-parietal network including the left IPL, AIP (-45, -37, 44), the part of the right precentral gyrus corresponding to the caudal PMv, the left and right SMAs and the right pars opercularis. Activations were also found in the associative areas of the left inferior occipital gyrus and in both the left and right insula (Table 2a and Figure 4). In order to identify which of these brain areas are specific to the context of action, the same conjunction was masked exclusively by the contrast between the length judgment and its reference ([GJ – refGJ] AND [MI – refMI] masked exclusively by [LJ – refLJ]). This analysis did not reveal any significant cluster either at corrected or uncorrected thresholds ($p < .001$).

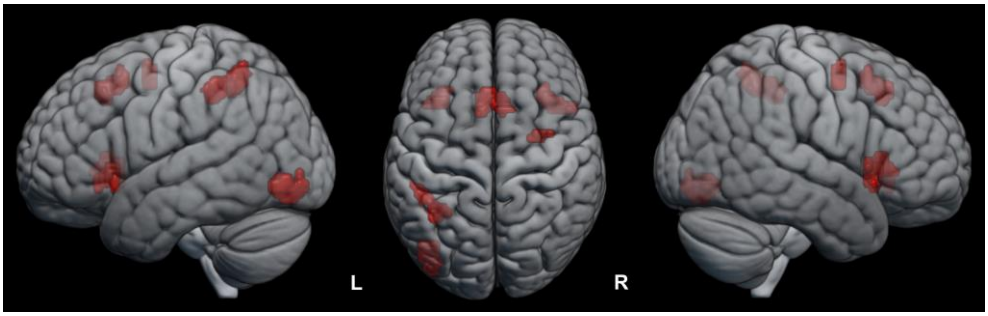

Figure 4. *Rendering of the brain areas commonly activated in the grasping judgment and the motor imagery task, surviving a statistical threshold of pFWE < 0.05 corrected for multiple comparisons and extending to k = at least 10 contiguous voxels.*

The picture emerging from the preceding task contrasts (see renders in Figure 3) suggests that grasping and length judgments involved the same right-lateralised fronto-parietal network, while motor imagery involved a similar but left-lateralised network. To investigate further this issue, we contrasted grasping

judgments to motor imagery and length judgments, and conversely. The subtraction of the activations found during grasping judgments from those during motor imagery, each contrasted to its own reference ([MI – refMI] – [GJ – refGJ]), revealed that motor imagery was mainly associated with greater activation in parietal and frontal areas of the left hemisphere. In the parietal cortex, activation foci were found in the supramarginal gyrus and along the intraparietal sulcus, extending to the medial part of the precuneus. Greater activation for motor imagery was also found in the left somatosensory cortex of the postcentral gyrus. In the frontal cortex, activation foci were found in the part of the left precentral gyrus corresponding to M1 and PMd. Additional activation foci were found in left middle frontal gyrus, both left and right SMA, and the pars opercularis and triangularis of the left inferior frontal gyrus, including the rolandic operculum. This included activation of the rostral PMv and DLPFC. Large clusters of activations were also found bilaterally in the cerebellum (lobules IV, V and VI). Temporal activations were found in both hemispheres including the fusiform gyrus, the left inferior, middle and superior temporal gyri. Clusters of activations were also found in the left inferior occipital gyrus, the right cuneus, the putamen and the insula (Table 2b). The reverse contrast ([GJ – refGJ] – [MI – refMI]) revealed that grasping judgments were associated with greater activation in right occipital and parietal areas, alongside the IPS, in the precuneus and in the inferior occipital gyri bilaterally, including V1 and V2 (Table 2c). The direct comparisons between grasping and length judgments ([GJ – refGJ] – [LJ – refLJ] and [LJ – refLJ] – [GJ – refGJ]) did not reveal any difference between the brain activations elicited by the two tasks, except in the right posterior parietal cortex showing increased activity during length judgment (uncorrected $p < .01$; Table 2d).

Table 1. *Brain regions showing significant activations for (a) grasping judgments, (b) motor imagery and (c) length judgments compared to their own reference task. k = cluster size (number of voxels); x,y,z = MNI coordinates of peak activation at the cluster level; T = t-Statistic; **p-values < 0.001 FWE corrected for multiple comparisons; * p-values < 0.05 FWE corrected for multiple comparisons.*

	Anatomical Regions	*k*	*x*	*y*	*z*	T
a	[GJ – refGJ]					
	Right calcarine sulcus, inferior and middle occipital gyri,	208	18	-91	-1	11.31**
	Right middle and anterior cingulate gyri, bilateral supplementary motor area	250	6	26	38	10.54**
	Left inferior occipital gyrus	184	-24	-94	-10	10.29**
	Right insula, opercular part of the inferior frontal gyrus	302	39	20	-7	10.02**
	Right angular gyrus, inferior parietal lobule, intraparietal sulcus, middle occipital gyrus	480	36	-55	47	9.46**
	Right middle and superior frontal gyri, orbital and triangular parts of the inferior frontal gyrus	266	42	50	11	8.54**
	Right precuneus	47	9	-70	50	7.18**
	Left inferior parietal lobule, intraparietal sulcus	111	-45	-37	44	7.97**
	Right supplementary motor area, middle frontal gyrus	94	15	20	65	7.57**
	Left cerebellar lobule VII (Crus I)	61	-33	-64	-31	7.46**
	Left insula	59	-33	20	-1	7.21**
	Left cerebellar lobule VII (Crus II)	28	-6	-79	-28	7.12**
b	[MI – refMI]					
	Right cerebellar lobule VI and VII (Crus I), inferior occipital gyrus, fusiform gyrus, inferior temporal gyrus	589	33	-52	-28	16.15**
	Left inferior occipital gyrus, cerebellar lobule VI, fusiform gyrus, inferior temporal gyrus	882	-45	-73	-7	15.94**
	Left precentral gyrus, middle and anterior, cingulate gyrus, bilateral supplementary motor area, left superior and middle frontal gyrus, triangular and opercular part of the inferior frontal gyrus, insula, pallidum	2028	-27	-10	56	14.46**
	Left inferior and superior parietal lobules, intraparietal sulcus, supramarginal gyrus, middle occipital gyrus	1330	-45	-34	41	14.14**
	Left precentral gyrus	88	-27	-7	53	8.09**
	Right insula, opercular part of the inferior frontal gyrus	109	36	20	5	7.31**
	Right supramarginal	11	36	-37	47	5.51*
c	[LJ – refLJ]					
	Right middle and anterior cingulate gyrus	448	6	26	38	12.30**
	Right inferior parietal lobule, intraparietal sulcus, angular gyrus, supramarginal gyrus, precuneus, inferior and middle occipital gyrus, calcarine sulcus, inferior temporal gyrus	1519	42	-43	44	12.27**
	Right insula, orbital, opercular and triangular parts of the inferior frontal gyrus, middle frontal gyrus, precentral gyrus	1527	39	20	-7	11.85**
	Left cerebellar lobule VII (Crus I and II), inferior occipital gyrus, middle occipital gyrus, calcarine sulcus	595	-33	-67	-28	11.25**
	Left insula	140	-36	17	-1	9.56**
	Left inferior parietal lobule, intraparietal sulcus, middle occipital gyrus	246	-45	-40	44	8.79**
	Left middle occipital gyrus	34	-27	-76	29	7.27**
	Left middle frontal gyrus	19	-30	53	17	6.79**
	Left precentral gyrus	34	-42	2	32	6.74**

Table 2. *Brain regions showing activation in (a) the conjunction of the grasping and motor imagery task, (b) the contrast between grasping judgments and motor imagery, (c) the contrast between motor imagery and grasping judgments and (d) the conjunction of the grasping and length judgments, each experimental task first being contrasted to its reference. k = cluster size (number of voxels); x,y,z = MNI coordinates of peak activation at the cluster level; T = t-Statistic; **P-values < 0.001 FWE corrected for multiple comparisons; * P-values < 0.05 FWE corrected for multiple comparisons.*

	Anatomical Regions	*k*	*x*	*y*	*z*	T
a	[GJ – refGJ]					
	Right calcarine sulcus, inferior and middle occipital gyri,	208	18	-91	-1	11.31**
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b	[MI – refMI]					
	Right cerebellar lobule VI and VII (Crus I), inferior occipital gyrus, fusiform gyrus, inferior temporal gyrus	589	33	-52	-28	16.15**
	Left inferior occipital gyrus, cerebellar lobule VI, fusiform gyrus, inferior temporal gyrus	882	-45	-73	-7	15.94**
	Left precentral gyrus, middle and anterior, cingulate gyrus, bilateral supplementary motor area, left superior and middle frontal gyrus, triangular and opercular part of the inferior frontal gyrus, insula, pallidum	2028	-27	-10	56	14.46**
	Left inferior and superior parietal lobules, intraparietal sulcus, supramarginal gyrus, middle occipital gyrus	1330	-45	-34	41	14.14**
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	Right insula, opercular part of the inferior frontal gyrus	109	36	20	5	7.31**
	Right supramarginal	11	36	-37	47	5.51*
c	[LJ – refLJ]					
	Right middle and anterior cingulate gyrus	448	6	26	38	12.30**
	Right inferior parietal lobule, intraparietal sulcus, angular gyrus, supramarginal gyrus, precuneus, inferior and middle occipital gyrus, calcarine sulcus, inferior temporal gyrus	1519	42	-43	44	12.27**
	Right insula, orbital, opercular and triangular parts of the inferior frontal gyrus, middle frontal gyrus, precentral gyrus	1527	39	20	-7	11.85**
	Left cerebellar lobule VII (Crus I and II), inferior occipital gyrus, middle occipital gyrus, calcarine sulcus	595	-33	-67	-28	11.25**
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	Left middle occipital gyrus	34	-27	-76	29	7.27**
	Left middle frontal gyrus	19	-30	53	17	6.79**
	Left precentral gyrus	34	-42	2	32	6.74**

3.2 TMS Experiment

3.2.1 Behavioural data

The GLMM analysis revealed a significant effect of LENGTH, $F(1, 4346) = 798.43$, $p < .001$, indicating that the rate of affirmative responses decreased for the grasping judgment and increase for the length judgment as the length of the horizontal line increased. There was also a significant effect of MLI figure, $F(2, 4346) = 186.58$, $p < .001$, indicating that, compared to the neutral figure (0.73 ± 0.10), participants gave less affirmative responses to the long figure (0.15 ± 0.07), $t(4355) = 9.62$, $p < .001$, and more affirmative responses to the short figure (0.91 ± 0.04), $t(4355) = -3.15$, $p = .002$. The analysis also revealed an effect of JUDGMENT, $F(1, 4346) = 205.88$, $p < .001$, indicating that participants gave less positive responses for the grasping (mean ± *SE*: 0.34 ± 0.01) than for the length judgments (0.85 ± 0.08). There was also a significant MLI x JUDGMENT, $F(2, 4346) = 12.30$, $p < .001$, and LENGTH x MLI x JUDGMENT interaction, $F(4, 4346) = 7.10$, $p < .001$, indicating that the effect of the illusion was weaker on grasping than on length judgments (Figure 5).

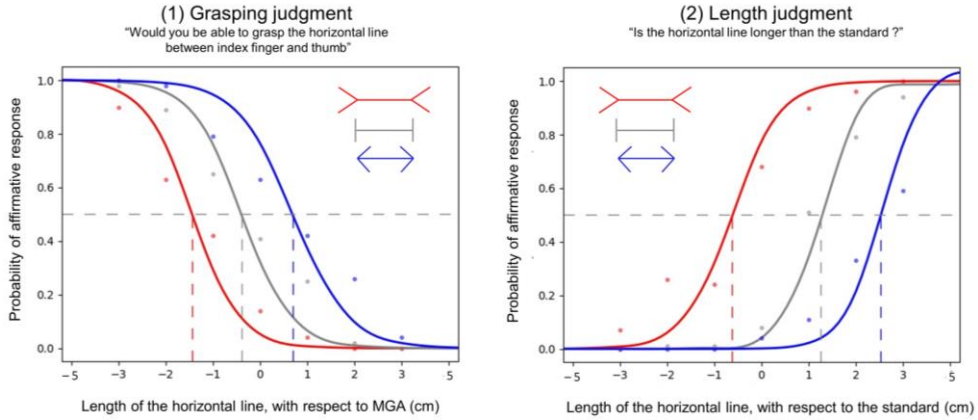

Figure 5. *Fitted curves from cumulative data showing the effect of the Müller-Lyer illusion on grasping and length judgments of the TMS experiment. The dots represent the average rate of affirmative responses (y-axis) as a function of the length of the rectangle (x-axis) with respect to (1) the MGA or (2) the length of the standard. The solid lines represent the predicted values obtained by means of logistic regression.*

3.2.2 Electrophysiological data

FDI. The GLMM analysis on the amplitude of the MEPs recorded from the FDI showed a main effect of JUDGMENT, $F(1,4979) = 447.69$, $p < .001$, a main effect of TIMING, $F(3, 4979) = 4.76$, $p = .003$, and a significant interaction between the two factors, $F(3, 4979) = 2.97$, $p = .031$. For the grasping judgment, post-hoc pairwise contrasts indicated that, compared to the baseline (0.91 ± 0.15 mV), the MEPs were significantly larger during the ITI (1.10 ± 0.16 mV), $t(4979) = -3.72$, $p = .001$. For the perceptual judgment, post-hoc pairwise contrasts did not show any significant difference between TMS conditions (Figure 6A).

APB. The GLMM analysis on the amplitude of the MEPs recorded from the APB showed a significant effect of JUDGMENT, $F(1,5076) = 565.15$, $p < .001$, of TIMING, $F(3, 5076) = 19.29$, $p < .001$, and a significant interaction between the two factors, $F(3, 5076) = 4.16$, $p = .006$. For the grasping judgment, post-hoc pairwise

contrasts indicated that, compared to the baseline (0.47 ± 0.10 mV), the MEPs were significantly larger at 150 ms (0.56 ± 0.12 mV), $t(5076) = -3.33$, $p = .004$, 300 ms (0.51 ± 0.11 mV), $t(5076) = -1.97$, $p = .049$, and during ITI (0.62 ± 0.14 mV), $t(5076) = -3.92$, $p = .001$. For the perceptual judgment, post-hoc pairwise contrasts did not show any significant difference between the timings (Figure 6B).

ADM. The GLMM analysis on the amplitude of the MEPs recorded from the ADM showed a significant effect of JUDGMENT, $F(1,4784) = 239.11$, $p < .001$, indicating that MEPs were larger during the grasping judgment (0.39 ± 0.07 mV) than during the length judgment (0.29 ± 0.05 mV). There was a main effect of TIMING, suggesting an increase of MEP amplitude at 300 ms and during ITI, but pairwise contrasts with the baseline showed no significant differences (p-values > 0.1). There was no significant JUDGMENT X TIMING interaction, $F(3, 4784) = 1.07$, $p = .362$ (Figure 6C).

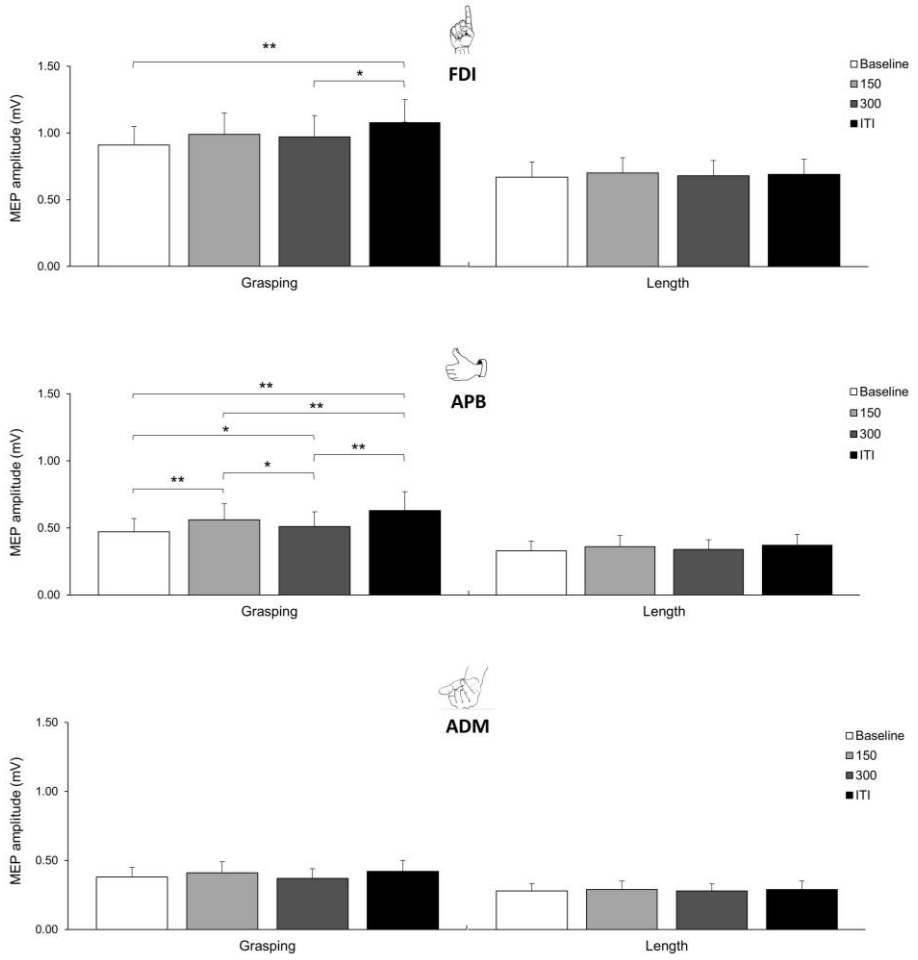

Figure 6. *Mean MEP amplitude (mV) recorded from the right FDI, APB and ADM following TMS over left M1. MEPs are shown for the baseline out, 150 ms, 300 ms and ITI in both the grasping (left side) and length (right side) judgment. Error bar represent standard errors; * p-value < .05; ** p-value < .01.*

4. Discussion

Previous studies suggest that predicting the outcome of an action implies the mental simulation of the related action. The brain circuits supporting such prospective action judgments and motor imagery are thus expected to overlap in the parietal and frontal cortices. However, the existence and precise nature of their neural overlap have never been addressed directly by comparing the brain activations elicited by the two tasks. Moreover, part of the neural network involved in prospective action judgments was also found involved in spatial cognition tasks not related to action leaving the existence and nature of a shared network between motor imagery and prospective action judgments unknown. The fMRI experiment assessed the possible neural overlap of prospective action judgments and explicit imagery of grasping and tested its specificity relative to the neural correlates of perceptual length judgments. The TMS experiment tracked motor excitability changes in hand muscles through the comparison of the MEPs during grasping and length judgments.

The behavioural data indicate that participants made accurate judgments and did not confound perceptual and motor strategies. In both experiments, the instructions for the grasping and length judgment tasks were formulated differently in order to prevent participants from adopting a similar strategy in both tasks. While participants had to judge whether a rectangle was small enough to be grasped between finger and thumb in the grasping judgment task, they had to decide whether a rectangle was larger than a memorised reference in the length judgment task. Hence, grasping judgments required a “yes” response to small rectangles, whereas length judgments required a “no” response to small rectangles. Moreover, the perceptual reference used in the length judgment task was of a different length than the MGA in each participant. Behavioural results showed that the regression of

participants' responses on rectangle size had a negative slope in grasping judgments and a positive slope in length judgments, meaning that participants answered each task differently as required by the instructions. In the TMS experiment, the Müller-Lyer illusion was introduced as an additional means to differentiate the processing of relative and veridical object size estimates in perceptual and grasping judgments. We observed that grasping judgments were less affected by the Müller-Lyer illusion than perceptual judgments, in line with the idea that object-directed actions rely on a different spatial reference frame that insulates the object from the visual context. Both judgments thus integrate information relative to the visual context, but the reduced effect of Müller-Lyer illusion in grasping judgments suggests the involvement of concurrent mechanisms that refined object size estimates for action calibration. This observation goes against a strict independency of the processes underlying visual perception and object-driven action. Still, it fits with the idea that the visual context matters less when the object size is matched with grip aperture rather than with a perceptual template (Milner & Goodale, 1995).

The brain imaging data showed that explicit motor imagery engaged the left IPL and SPL, the left PMv and PMd, as well as the left M1 and S1, in line with previous studies (for a meta-analysis, see Hétu et al., 2013). In the right hemisphere, the IPL, the rostral PMv and the SMA were also involved, though to a lesser extent. The larger involvement of the left hemisphere is consistent with the dominant role of this hemisphere in motor functions. Left hemispheric lesions typically result in stronger motor deficits than right hemispheric lesions (Haaland & Harrington, 1989; 1994; Kimura, 1977; Sabaté, Gonzàlez & Rodrĭguez, 2004). This asymmetry was replicated in neuroimaging studies with healthy participants, especially for PMv and S1, with larger activity in the left compared to the right hemisphere during both action execution and motor imagery (Beisteiner, Höllinger, Lindinger, Lang & Berthoz, 1995; Kim et al., 1993; Porro, Cettolo, Francescato & Baraldi, 2000). While

lesion studies indicated that the right IPS might contribute to hand shaping independently of its left homologue (Glover et al., 2005; Davare, Andres, Clerget, Thonnard & Olivier, 2007; Tunik et al., 2005), the SPL is found to be more activated in the left hemisphere during both simulated and actual actions (Beisteiner et al., 1995: Moll et al., 2000). It is worth noting that the left-lateralised network of frontal, parietal, and temporo-occipital areas observed during motor imagery has already been reported in previous studies that included a condition consisting in the mere viewing of tools or graspable objects with a specific function, with no instruction to simulate a movement towards these objects. It has been proposed that objects with a functional use automatically elicit the activation of the related action(s) (Creem-Regehr and Lee, 2005; Grezes & Decety, 2002; Vingerhoets, 2008; Wadsworth & Kana, 2011). A similar network is also involved in tool-use pantomiming (Choi et al., 2001; Vingerhoets et al., 2011). The reported left-lateralised network might thus encompass not only the neural substrate for the mental simulation of grasping movements but also the brain areas representing the object to be grasped and the associated functional knowledge (*e.g.*, object function(s), appropriate hand position(s) necessary for the functional use of the object; Andres, Pelgrims & Olivier, 2013; Andres, Pelgrims, Oliver & Vannuscorps, 2017).

In contrast, grasping judgment was associated with increased activity in the right parietal and frontal cortices. The conjunction analysis with the motor imagery task revealed overlap in the right caudal PMv and the bilateral superior frontal gyrus extending medially to the SMA. In the left hemisphere, only a small portion of the left AIP, extending to the superior part of the IPL, also contributed to grasping judgments. Moreover, none of these regions was specific to action processing, as they were also involved in perceptual length judgment. This unexpected right-hemisphere lateralisation is best explained by the involvement of spatial processes shared with length judgment (for a review, see Vogel, Bower & Vogel, 2003). It has

been proposed that any magnitude would be processed within a generalised system located in the IPL (*i.e.*, a theory of magnitude; Walsh, 2003). Areas around the right IPS, in particular, are activated whenever two magnitudes presented visually (*e.g.*, sizes, lengths or orientations) have to be compared (Dormal & Pesenti, 2009; Faillenot et al., 1999; Fias et al., 2003; Pinel et al., 2004). The generalised magnitude system housed in the horizontal part of the right IPS would have evolved as a key component of the sensorimotor transformations achieved by the parietal cortex (Gallistel & Gelman, 2000; Walsh, 2003), such as matching grip aperture with object size (Faillenot, Toni, Decety, Grégoire & Jeannerod, 1997). This close connection between magnitude and action processing might also explain the involvement of some frontal areas contributing to grasping and length judgments. Previous studies indicated that the right premotor cortex, including PMv and PMd, is activated whenever spatial distances are compared (Dormal & Pesenti, 2009; Fias et al., 2003), or held in short-term memory (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; D'Esposito, Postle, Ballard, & Lease, 1999; Scherf, Sweeney & Luna, 2006). We propose that overlapping activations within the right fronto-parietal cortex during grasping and length judgments underly the computation of object size estimates and the comparison to a reference maintained in short-term memory.

While the fMRI experiment revealed no increase of the BOLD signal in M1, the TMS experiment revealed consistent changes in the CSE of hand muscles during grasping – but not length – judgments. This finding highlights the advantage of using TMS, in addition to fMRI, to probe the state of the motor system in the covert stages of action. In motor imagery tasks, the BOLD signal reflecting M1 activity is indeed cut down by 30-50%, which makes it difficult to detect (Gerardin et al., 2000; Lotze et al., 1999; Nair, Purcott, Fuchs, Steinberg & Kelso, 2003; Porro et al., 1996). Using TMS over the left M1, we showed that grasping judgments induced a selective increase of MEP amplitude in the FDI and APB – but not ADM – muscles of the

right hand. Such an increase can be viewed as the signature of the sensorimotor representation of the precision grip, which requires index and thumb – but not pinkie – movement. However, note that the absence of effect in the ADM might result from the difficulty to elicit consistent MEPs in this muscle due to the use of a single hotspot primarily defined to elicit MEPs in the FDI muscle. More importantly, the timing of CSE changes in FDI and APB was not locked to the resolution of the grasping judgment. Compared to baseline, the MEP amplitude increased not only during the trials, *i.e.* 150 and 300 ms after stimulus onset, but also in-between trials, *i.e.* more than 3000 ms after response onset, and this increase was actually larger in the latter condition. Such modulation of MEP amplitude was not observed in perceptual length judgments, which were fully matched with grasping judgments, except that they did not require activating the grip representation. We, therefore, propose that participants covertly activated the motor representation of their precision grip (or hand) in advance to every new grasping judgment, as evidenced by the particular enhancement of motor excitability in-between trials, and maintained this representation active during the judgment, as evidenced by the lower but significant enhancement of motor excitability during each trial. This pattern of results deviates from what has been previously observed in motor imagery tasks, where CSE changes are strictly bound to the progression of the imagined movement (Stinear & Byblow, 2003). This discrepancy adds to the finding that prospective grasping judgments did not replicate the extended left hemisphere activations associated with the full-blown mental simulation of the movement during explicit imagery of grasping. Obviously, the steady increase of hand motor excitability during grasping judgments is best taken into account by the maintenance in working memory of the information relative to MGA for further comparison with object size.

A noticeable difference between grasping and length judgments is that the comparison of object size indeed requests the contribution of different modalities,

i.e., the visual representation of the reference and the sensorimotor representation of the grip. The specific involvement of sensorimotor representations is further supported by our previous finding that a concurrent hand motor task interfered with grasping judgments while leaving size judgments unaffected (Geers et al., 2018, see Chapter 2). More precisely, squeezing *vs.* spreading fingers led participants to under *vs.* over-estimate their grasping capability, suggesting that actual hand posture biased the comparison between hand representation and object size. The question arises how the internal magnitude system adjusts the comparison metrics to the visual template representation or to the hand sensorimotor representation used as a reference for length or grasping judgments, respectively. At the behavioural level, our finding that length judgments are more affected than grasping judgments by Müller-Lyer illusion suggests that visual and sensorimotor information have a different weight indeed in the two judgments. At the neural level, the direct comparison between length and grasping judgments reveals increased activity in the right posterior parietal cortex. This region might deal with the specific requirements of length comparison, as a previous study showed that neural activity in the right posterior parietal cortex is modulated by the effect of Müller-Lyer illusion on perceived object size (Weidner & Fink, 2006). Although our fMRI experiment did not identify any region specifically involved in the integration of the motor input during grasping judgments, we found increased hand motor excitability revealing the activation of the sensorimotor representation of the precision grip. We believe AIP could play a role in driving this activation because of its proximity with the hand sensorimotor cortex and its tight connectivity with grasp-related areas (Lewis & Van Essen, 2000; Simon et al., 2002). An offline TMS study showed that the transient perturbation of AIP tunes down the PMv-M1 connection driving the activity of muscles specifically involved in the precision grip (Davare, Rothwell & Lemon, 2010). Future studies should exploit the respective advantages of fMRI and TMS to

delineate further the parietal areas specifically involved in the computation of object size and grip aperture estimates.

To conclude, our results indicate that perceptual and grasping judgments share common processes for the computation of size estimates in the right fronto-parietal cortex, with a possible gradient of activation from posterior to anterior IPS subregions according to the weight of visual and sensorimotor information in the estimation process. The right hemisphere contribution to grasping judgments contrasts with the left hemisphere contribution to explicit motor imagery and challenges the idea that action prediction is analogue to the mental simulation of an action. Our brain imaging and electrophysiological data converge to suggest that the motor system is activated covertly, at a subthreshold level, to refresh the short-term memory of one's MGA and facilitate its comparison with object size in subsequent judgments. Overall, the study demonstrates how neurophysiological measurements obtained with non-invasive brain stimulation may bridge the gap between cognitive and brain imaging research and thereby renew functional hypotheses about action prediction.

5. Supplementary material

Stimuli used in the motor imagery task: 40 colour images of graspable objects.

Chapter 6

Integration of the visual context relies on the parvocellular pathway

1. Introduction

As seen in the general introduction of this thesis, the idea of two visual streams dates back to the 80s where the anatomical subdivision between the ventral and the dorsal streams was already put forward to account for the functional dissociation observed in primates' vision. The two streams were initially distinguished according to their specialisation for the processing of specific visual properties: the ventral stream was assumed to process object identity, while the dorsal stream was assumed to process object location (Ungerleider & Mishkin, 1982). Since then, this anatomical subdivision has been retained, but the definition of its function has evolved to emphasise differences in terms of output rather than input. The current dominant view assumes that the ventral and dorsal streams distinguish not so much according to the visual properties they process than the transformations they apply to these inputs to serve different purposes, namely perception and goal-directed action. The TVS model assumes that the perceptual system of the ventral stream computes the object coordinates relative to its surroundings, *i.e.*, in a scene-based reference frame. On the contrary, the motor system of the dorsal stream would estimate the exact metrics of the object and compute them in an egocentric reference frame without being influenced by the visual context.

The results of Chapter 2 challenge this claim by showing that both perceptual and grasping judgments are sensitive to the Ebbinghaus illusion and thus integrate the visual context when computing object size. While the results indicate that perception and action do not process size differently, they do neither indicate whether the ventral and dorsal streams contribute differently to the size estimation process nor if their contribution depends on the aim pursued by the observer. The fMRI experiment of Chapter 5 indicates that both ventral (*e.g.*, LOC) and dorsal (*e.g.*, IPS) areas are involved in perceptual and grasping judgments. Nevertheless, the correlative nature of these data prevents determining whether the relative contribution of each stream varies according to the judgment made. Moreover, the absence of visual context in this experiment makes it impossible to draw any conclusion about the stream(s) responsible for context integration. Given the existence of cross-talk between the two streams, the size-contrast illusion might either emerge on the ventral stream with the resulting relative size estimate being transmitted to the dorsal stream or be duplicated along the two streams. Hence, my results, so far, do not preclude the ventral and dorsal streams are differently involved according to the output requirement or compute different estimates of size that are later integrated into the perceptual and motor outputs.

In the present Chapter, we took advantage of the respective physiological properties of the parvo- and magnocellular pathways to bias visual information either towards the ventral or dorsal stream in order to probe their respective contribution to size estimates for perceptual and grasping judgments. As a reminder, after visual information hits the retina, it is conveyed to the visual cortex mainly along two subcortical pathways: the parvo- and magnocellular pathways. The neurons of the parvocellular pathway have a high spatial but low temporal resolution and most of them are selective to colour contrast due to colour-opponency (Derrington & Lennie, 1984; Hubel & Livingstone, 1990; Schiller & Malpeli, 1978).

They are generally more efficient at high luminance contrast but mediate contrast sensitivity over a broad range of spatial frequencies (Legge, 1978; Tolhurst, 1975). On the contrary, the neurons of the magnocellular pathway have a low spatial but high temporal resolution and most of them are not selective to colour (Derrington & Lennie, 1984; Hubel & Livingstone, 1990; Schiller & Malpeli, 1978). In addition, they are more efficient at low luminance contrast, at least when spatial frequency is low (Legge, 1978; Tolhurst, 1975). Before these two pathways run into the ventral and dorsal streams, they partly combine at the level of the visual cortex (for a review, see Sincich & Horton, 2009) so that the ventral stream receives almost as much parvo- than magnocellular information, and the dorsal stream receives predominantly, but not exclusively, magnocellular information (Merigan & Maunsell, 1993; Sawatari & Callaway, 1996). We used the specific physiological properties of the parvo- and magnocellular pathways to bias the processing of an Ebbinghaus illusion display towards one or the other pathway and investigated the impact on perceptual and grasping judgments.

In the first two experiments, participants were required to make either grasping (Experiment 1) or perceptual (Experiment 2) judgments on equiluminant stimuli that could only be discriminated from the background by their colour. These equiluminant stimuli elicit a specific response of the colour-opponent neurons. Most of the colour-opponent cells being part of the parvocellular pathway, the equiluminant stimuli should mainly be processed along the ventral stream and much less along the dorsal stream (Livingstone & Hubel, 1987a; 1988). Under the assumption perceptual judgments require the ventral stream and grasping judgments the dorsal stream, perceiving the size of equiluminant stimuli should be less affected than comparing them with grip aperture since perceptual judgments would be provided with more (parvocellular) information than grasping judgments. In the last two experiments, participants made either grasping (Experiment 3) or perceptual

(Experiment 4) judgments on stimuli presented at low contrast, high temporal and low spatial frequency. With these parameters, the stimulus should elicit a preferential response of the magnocellular neurons, and thus be processed along both streams. However, the preferential activation of the magnocellular neurons being at the expense of the parvocellular neurons, the ventral stream should suffer a more significant loss of information than the dorsal stream (Livingstone & Hubel, 1987a; 1988; Skottun & Skoyles, 2011). Stimuli biased to the magnocellular pathway should thus affect more significantly perceptual than grasping judgments. Concerning the illusion, if the integration of the visual context takes place in the ventral stream, it should be more affected when biased towards the magnocellular pathway (Experiment 3 and 4) than when biased towards the parvocellular pathway (Experiment 1 and 2). Hence, this study will inform us about the respective contribution of the ventral and dorsal streams to perception and action, but also how these streams serve the integration of the visual context with respect to perception and action.

2. Experiment 1

2.1 Method

2.1.1 Participants

Twenty students (5 males, mean age ± SD: 22 ± 4 years) from the Université catholique de Louvain participated in this experiment. They all gave their written informed consent prior to their inclusion, had a normal or corrected-to-normal acuity, declared themselves as right-handed and were unaware of the purpose of the experiment. The study was non-invasive and performed in accordance with the ethical standards of the Declaration of Helsinki.

2.1.2 Apparatus and stimuli

Participants were seated in a dark room at 60 cm in front of a 27-inch PC monitor (refresh rate: 60Hz; resolution: 1920 x 1080 pixels; graphic board: AMD Radeon R5 350X). The values of the three guns in the display were linearised by gamma correction (Pelli & Zhang, 1991). A chin rest aligned with the body midline was used to keep head-screen distance constant throughout the experiment. Hands were held under a cardboard surface mounted above the surface of the table, in the horizontal plane, rendering the hands invisible to the participant. The participant wore glasses with frosted lenses in order to prevent the magnocellular neurons from responding to colour borders (Schiller & Colby, 1983). Stimulus generation and presentation, as well as data recording, were programmed using Psychopy2 (Peirce et al., 2019). A luminance meter LS-100 (Konica Minolta Business Technologies, Inc., Tokyo, Japon) was used for photometric measurement of the stimuli.

The stimuli consisted of three configurations of the Ebbinghaus illusion. The configurations varied in two aspects: the size of the central circle and the size of the surrounding circles. The sizes used for the central circle were 2, 2.5, 2.75, 3, 3.25, 3.5, 3.75, 4 and 4.5 cm, subtending 1.91 to 3.80° of visual angle. The apparent size of the central circle (*i.e.*, the target) was manipulated by a surrounding annulus consisted of circles that were either twice as small or twice as large as the target, making the latter appear, respectively, larger or smaller (referred hereafter as the "large" and "small" illusory displays). An additional display with surrounding circles of the same size than the central circle was used as a control inducing no distortion (referred hereafter as "neutral" illusory display). The gap between the target and the annulus was always twice as small as the target diameter to avoid obstacle avoidance mechanisms being responsible for the illusion effect on grasping judgments (Haffenden & Goodale, 2000, but see also Franz et al., 2003). The entire

Ebbinghaus display covered 4 to 15.75 cm, thereby subtending 3.8° to 15.04° of visual angle. The stimuli were displayed in red, with three possible luminance values defined individually before the experiment, on a uniform green background (10.30 cd/m²). In the *equiluminant* condition, the luminance of the stimulus was equiluminant to the background as defined by the heterochromatic flicker fusion method (see below); in the *dark* condition, the luminance of the stimulus was 5.60 cd/m² darker than the equiluminance setting; in the *bright* condition, the luminance of the stimulus was 5.60 cd/m² brighter than the equiluminance setting (Figure 1).

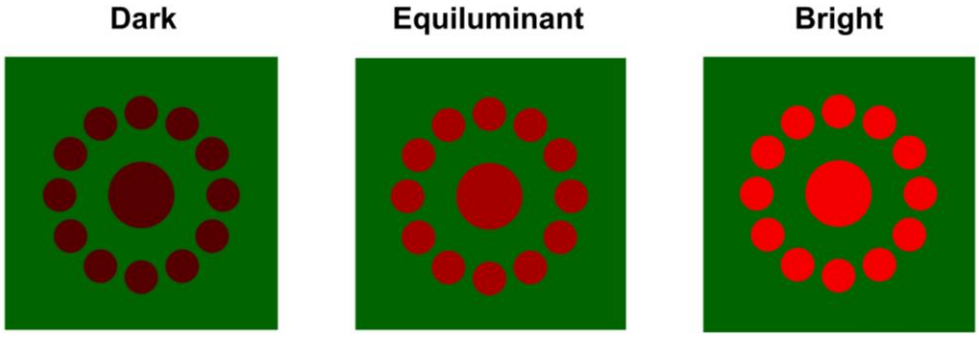

Figure 1. *Example of stimuli of the three luminance conditions used in Experiment 1 and 2. The green background was kept constant across conditions. The luminance of the red stimulus was: defined by the heterochromatic flicker fusion method in the equiluminant condition, 5.60 cd/m² darker than the equiluminance setting in the dark condition and 5.60 cd/m² brighter than the equiluminance setting in the bright condition.*

2.1.3 Tasks and procedure

Participants were required to judge whether they would be able to grasp the central circle of an Ebbinghaus display between their index finger and thumb without spreading them any wider than their actual aperture, which was maintained at 3.25 cm throughout the experiment. The experiment was divided into two sessions scheduled on different days. Each session started with the estimation of the

equiluminance point, separately for each illusory display. Then, the participant performed a few practice trials followed by three blocks of grasping judgments corresponding to the three luminance conditions (dark, equiluminant, and bright) whose order was counterbalanced across participants.

The equiluminance point was defined by means of the heterochromatic flicker fusion method. The stimulus alternated between the green used for the background (*i.e.*, 10.30 cd/m²) and a red of 6.45 cd/m² with a modulation frequency of 30Hz. Parvocellular neurons are not able to follow the chromatic alternation at this temporal frequency, generating colour fusion, which results in the perception of a brownish colour. As the red and green have different luminance, the magnocellular neurons still give rise to a sensation of luminance flickering, *i.e.*, perception of alternations between light and dark yellow/brown. Participants were then required to increase or decrease the luminance of the red channel by steps of 0.35 cd/m² by pressing the right or left arrow, respectively. They were encouraged to explore the entire range of red luminance (6.45 to 17.30 cd/m²) to choose the level at which the stimulus appeared the most stationery reflecting the fact that the magnocellular neurons were not responding anymore, as there is no perceived difference in luminance between the red and green (*i.e.*, they are equiluminant). Indeed, chromatic modulation without any luminance change elicits a selective response of the colour-opponent neurons, which are not able to follow the alternation and give rise to an impression of stationary state (Hubel & Livingstone, 1987; for an animated example of the heterochromatic flicker fusion, see https://michaelbach.de/ot/col-flicker/). This procedure was repeated three times for each illusory display. We computed separately for each display, the median value of the red stimuli identified as equiluminant. These medians were then used to create the stimuli of the three experimental conditions. The mean (±SD) luminance for the equiluminance point across participants was 10.80 ± 0.47 cd/m² for the small illusory display, 10.58 ±

0.54 cd/m² for the neutral display and 10.45 ± 0.61 cd/m² for the large illusory display.

Each trial of the grasping judgment task started with the presentation of a fixation cross at the centre of the screen for 500 ms, followed by an Ebbinghaus display. The participant responded by "yes" or "no" to indicate as quickly and accurately as possible whether they judge the target as graspable or not without spreading their index finger and thumb any wider than their actual aperture. Instructions emphasised the need to actually spread the index finger and thumb of each hand so that they encompass two iron bars and form a 3.25cm-aperture during the entire experiment. The stimulus disappeared as soon as the participant responded. The response was encoded on-line by the experimenter; the next trial started 1,000 ms later. The participant performed 6 practice trials before taking, for each luminance condition, one block of 135 trials consisting of the 9 possible sizes of the target, repeated 5 times with each of the 3 Ebbinghaus displays. The different combinations of target size and Ebbinghaus display were randomly mixed within each block, while the luminance condition was varied across blocks.

2.1.4 Data analysis

Participants' responses ("yes" or "no" coded as 1 and 0) were modelled with a GLMM with the SIZE of the target (logistic function), the ILLUSION display (small, neutral *vs*. large), the LUMINANCE condition (equiluminant, dark *vs.* bright) and their interaction as fixed effects and the differences between participants as random effects. The Bonferroni correction was applied when multiple comparisons were conducted.

2.2 Results

The GLMM analysis revealed a significant effect of SIZE, $F(1, 16182) = 3{,}278$, $p < .001$, indicating that the rate of affirmative responses decreased when the size of the target increased. The analysis also showed a main effect of the ILLUSION, $F(2, 16182) = 27.43$, $p < .001$. Post-hoc pairwise contrasts indicated that, compared to the neutral display (mean ± SE = 0.75 ± 0.10), participants gave more affirmative responses when judging the small illusory display (0.0.93 ± 0.03), $t(16182) = -2.64$, $p < .008$, and less affirmative responses when judging the large illusory display (0.52 ± 0.14), $t(16182) = 6.09$, $p < .001$ (Figure 2B). There was also an ILLUSION by SIZE interaction, $F(2, 16182) = 35.65$, $p = .004$, indicating that the slope for the small illusory display was less steep than for the neutral and large displays (Figure 2A). There was also a significant main effect of LUMINANCE, $F(2,16182) = 5.94$, $p = .003$, integrated in a LUMINANCE by SIZE interaction, $F(2,17397) = 5.67$, $p = .003$, pointing to an increase of affirmative responses to target sizes that are larger than the actual grip aperture in the equiluminant condition compared to the two other luminance conditions (Figure 2C). Post-hoc pairwise contrasts indicated that the rate of affirmative responses was significantly larger for the equiluminant compared to the dark condition (0.54 ± 0.14), $t(16182) = 2.87$, $p = .013$, when the target size was 3.5 cm (0.59 ± 0.13), and than both the dark (0.29 ± 0.11), $t(16182) = 3.16$, $p = .005$ and bright (0.31 ± 0.12) conditions, $t(16182) = 2.39$, $p = .034$, when target size was 3.75 cm (0.36 ± 0.12; Figure 2D). For all other sizes, there was no difference between luminance conditions (all p-values > 0.05). The interaction between luminance condition and illusion was not significant, $F(4, 16182) = 0.66$, $p = .619$.

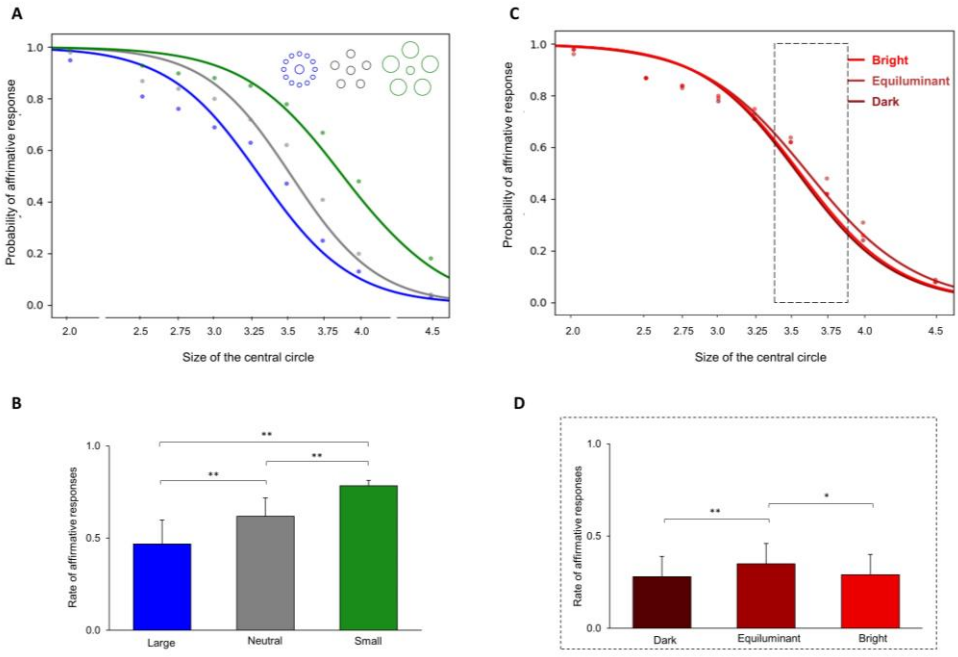

Figure 2. *Effect of the Ebbinghaus illusion (A & B) and luminance condition (C & D) on grasping judgments in Experiment 1. The two graphs in the upper part of the figure represent the fitted curves from cumulative data showing the effect of the illusion (left side) and of the luminance condition (right side). The dots represent the average rate of affirmative responses (y-axis) as a function of the size of the central circle (x-axis). Solid lines represent the predicted values obtained by means of logistic regression. The two graphs in the lower part of the figure represent the mean rate of affirmative responses according to the illusion (left side) and the luminance condition (right side; displayed for targets of 3.75 cm). No significant difference was observed at mean size. Error bars represent standard errors; **p-values < .001 corrected for multiple comparisons; * p-values < .05 corrected for multiple comparisons.*

3. Experiment 2

3.1 Method

3.1.1 Participants

A new sample of 19 participants students (5 males, age: 21 ± 2 years) from the Université catholique de Louvain participated in this experiment. They all gave their written informed consent prior to their inclusion, had a normal or corrected-to-normal acuity, declared themselves as right-handed and were unaware of the purpose of the experiment. The study was non-invasive and was performed in accordance with the ethical standards of the Declaration of Helsinki.

3.1.2 Apparatus and stimuli

We used the same apparatus and stimuli as in Experiment 1 but added a reference circle, consisting of a single white circle with a diameter of 3.25 cm, corresponding to 3.10° of visual angle, and luminance of 78.00 cd/m², for the perceptual comparison task. The equiluminant red value was defined using the same heterochromatic flicker fusion task as in Experiment 1. The mean (±SD) luminance for the equiluminance point across participants was 10.80 ± 0.31, 10.61 ± 0.37 and 10.64 ± 0.43 cd/m² for the small, neutral and large displays, respectively.

3.1.3 Tasks, procedure and data analysis

Experiment 2 followed the same procedure as Experiment 1, except that the instructions required participants to judge whether the central circle of the Ebbinghaus illusion was larger or not than a reference circle (instead of graspable in Experiment 1). Participants practised the task until they had memorised the size of the reference. The practice was performed just before the perceptual comparison

task: the reference circle was displayed for 20 sec and then replaced by a succession of central target circles (*i.e.*, without illusion) that participants were asked to judge as larger or not than the reference. The same sizes as in the experimental task were used. The participant received feedback after each trial, and the training ended when the participant reached 95% correct responses for 27 trials in a row. This was done to ensure participants had correctly memorised the size of the reference circle before performing the experimental task. The reference was further presented before each block of the experimental task as a reminder. Finally, in this experiment, hands were kept flat under the cardboard surface. The data analysis was the same as in Experiment 1.

3.2 Results

The GLMM analysis revealed a significant effect of SIZE, $F(1, 15236) = 3{,}155$, $p < .001$, indicating that the rate of affirmative responses increased with target size. The analysis also showed a main effect of the ILLUSION, $F(2, 15236) = 19.35$, $p < .001$. Post-hoc pairwise contrasts indicated that, compared to the neutral display (0.13 ± 0.03), participants gave less affirmative responses when judging the small illusory display (0.05 ± 0.01), $t(15236) = 3.92$, $p < .001$, and more affirmative responses when judging the large illusory display (0.38 ± 0.07), $t(15236) = -6.61$, $p < .001$ (Figure 3B). The analysis also revealed an ILLUSION by SIZE interaction, $F(2, 15236) = 35.65$, $p < .001$, indicating that the slope was less steep for the small illusory display than for the neutral and large displays (Figure 3A). There was also a significant main effect of the LUMINANCE condition, $F(2,15236) = 19.52$, $p < .001$ (Figure 3C). Post-hoc pairwise contrasts indicated that compared to the equiluminant condition (0.15 ± 0.04), participants gave less affirmative responses in the dark condition (0.10 ± 0.02), $t(15236) = 3.22$, $p = .003$, but more affirmative responses in the bright condition, $t(15236) = -2.80$, $p = .005$. The difference between the dark and

bright conditions was also significant, $t(15236) = -4.18$, $p < .001$ (Figure 3D). Finally, there was a LUMINANCE by SIZE interaction, $F(2,15236) = 5.67$, $p = .003$. Post-hoc pairwise contrasts indicated that the effect of luminance was linear (darker < equiluminant < brighter) for sizes ranging from 2 to 3.5 cm. For larger sizes, however, the equiluminant condition gave rise to more affirmative responses than the two other luminance conditions. When the target size was as large as 4 and 4.5 cm, the equiluminant condition ($mean_4 = 0.87 \pm 0.03$; $mean_{4.5} = 0.99$) was significantly different from both the dark ($mean_4 = 0.80 \pm 0.05$; $mean_{4.5} = 0.97$), $t_4(15236) = 3.54$, $p_4 = .001$, $t_{4.5}(15236) = 2.34$, $p_{4.5} = .039$,and bright conditions ($mean_4 = 0.83 \pm 0.04$; $mean_{4.5} = 0.97$), $t_4(15236) = 2.80$, $p_4 = .010$, $t_{4.5}(15236) = 2.76$, $p_{4.5} = .018$ (Figure 3E). When the size was 3.75 cm, a significant difference was found between the equiluminant (0.68 ± 0.07) and dark conditions only (0.55 ± 0.07), $t(15236) = 5.65$, $p < .001$). There was no interaction between the illusion and the luminance condition, $F(4, 15236) = 0.86$, $p = .482$.

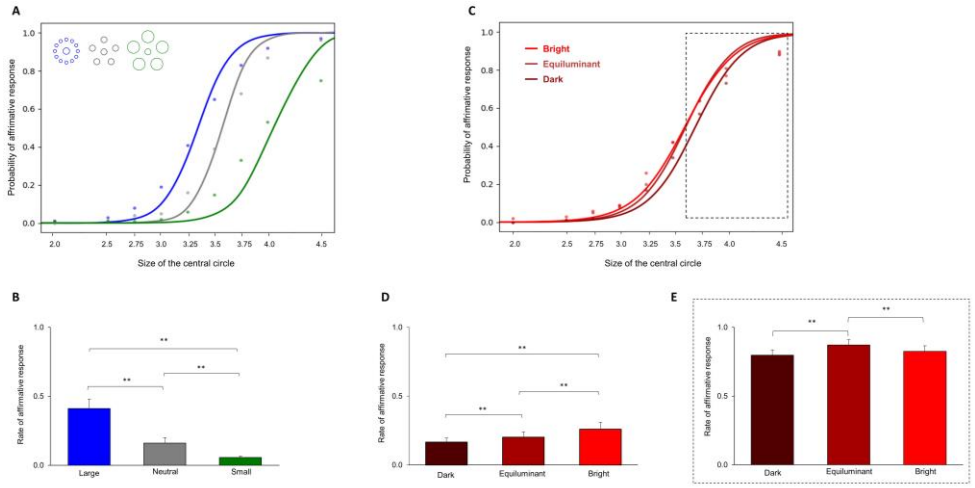

Figure 3. *Effect of the Ebbinghaus illusion (A & B) and luminance condition (C - E) on perceptual judgments in Experiment 1. The two graphs in the upper part of the figure represent the fitted curves from cumulative data showing the effect of the illusion (left side) and luminance conditions (right side). The dots represent the average rate of affirmative responses (y-axis) as a function of the size of the central circle (x-axis). Solid lines represent the predicted values obtained by means of logistic regression. The three graphs in the lower part of the figure represent the mean rate of affirmative responses according to the illusion (left side) and the luminance condition (middle: means displayed for mean target size; right side: means displayed for targets of 4cm). No significant difference was observed at mean size. Error bars represent standard errors; **p-values < .001 corrected for multiple comparisons; * p-values < .05 corrected for multiple comparisons.*

4. Experiment 3

4.1 Method

4.1.1 Participants

A new sample of 20 participants students (1 male, age: 22 ± 2 years) from the Université catholique de Louvain participated in this experiment. They all gave their written informed consent prior to their inclusion, had a normal or corrected-to-normal acuity, declared themselves as right-handed and were unaware of the purpose of the experiment. The study was non-invasive and was performed in accordance with the ethical standards of the Declaration of Helsinki.

4.1.2 Apparatus and stimuli

The same set up as in Experiment 1 was used, but with a 34-inch PC monitor (refresh rate: 100Hz; resolution: 3440 x 1440 pixels; graphic board: GeForce GTX 180). The same Ebbinghaus configurations and sizes as in Experiment 1 and 2 were used. However, they were displayed in two different conditions. In the first condition, stimuli were displayed at a low foreground-background luminance contrast (3%), high temporal frequency (25Hz), and low spatial frequency (1.25 c/deg) in order to bias their processing to the magnocellular pathway (*i.e.*, M-biased condition). In the second condition that serves a control, stimuli were displayed with high contrast, low temporal frequency (stationary) and high spatial frequency (12.5 c/deg). In both conditions, the stimulus was black (0.30 cd/m²). The background was white (78 cd/m²) in the control condition, providing a standard contrast for the measurement of Ebbinghaus illusion. In the M-biased condition, the background was dark grey (0.31 cd/m²), so that the stimuli could only be discriminated from the perception of subtle differences in luminance (Figure 4).

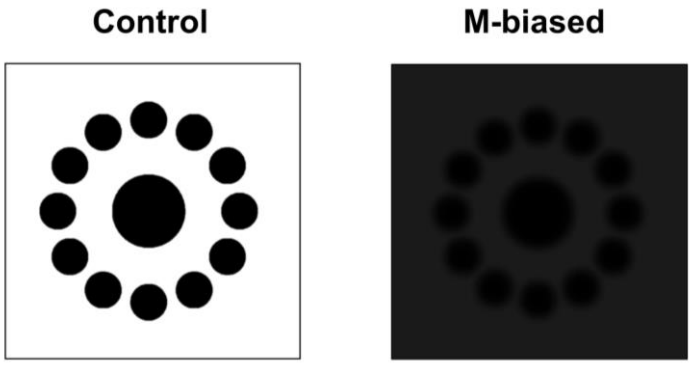

Figure 4. *Example of the stimuli of the two visual conditions used in Experiment 3 & 4. The stimuli were always black. In the control condition, the stimuli were stationary and displayed on a white background at high contrast and spatial frequency. In the M-biased condition, the stimuli were displayed on a dark grey background at low contrast (3%), low spatial frequency (1.25 c/deg) and were flickering at 25 Hz.*

4.1.3 Tasks and procedure

We used the same grasping judgment task and procedure as in Experiment 1, except that the conditions were not defined as a function of equiluminance but as a function of the contrast detection threshold estimated through a staircase procedure. In each trial of the staircase procedure, we presented either a black circle (diameter: 3.25 cm) or ellipse (width: 3.00 cm; height; 3.25 cm) on a grey background. The task required participants to identify the shape (circle = left arrow; ellipse = right arrow). If their response was correct, the luminance of the background decreased, whereas it increased when they made an error. The contrast threshold was defined as the mean of the eight last reversal points. All participants had a contrast threshold below 3% (1.46 ± 0.99 %). Since the ellipse differed from the circle only by being 0.25 cm less wide, this indicates that all participants were able to detect subtle differences of sizes with the contrast values used in the experimental task.

4.1.4 Data analysis

We performed a GLMM analysis with the response ("yes" or "no" coded 1 and 0) as dependent variable, the SIZE of the target (logistic function), the ILLUSION display (small, neutral *vs*. large), the VISUAL CONDITION (M-biased *vs.* control) and their interaction as fixed effects and the differences between participants as random effects. The Bonferroni correction was applied when multiple comparisons were conducted.

4.2 Results

The GLMM analysis reavaled a significant effect of SIZE, $F(1, 10788) = 2{,}287.05$, $p < .001$, indicating that the rate of affirmative responses decreased when the size of the target increased. There was also a main effect of the ILLUSION, $F(2, 10788) = 9.84$, $p < .001$, indicating that, compared to the neutral display (0.63 ± 0.12), the rate of affirmative responses to the small illusory display (0.85 ± 0.07) was smaller, $t(10{,}788) = -3.81$, $p < .001$, and the rate of affirmative responses to the large illusory display (0.54 ± 0.13) was larger, $t(10{,}788) = 4.15$, $p < .001$. The ILLUSION by SIZE interaction was also significant, $F(2, 10788) = 18.39$, $p < .001$, indicating that the slope was less steep for the small illusory display than for the neutral and large displays. The analysis also revealed a significant VISUAL CONDITION by SIZE interaction, $F(1, 10788) = 3.96$, $p < .047$. Post-hoc pairwise contrasts indicated that the rate of affirmative responses was higher in the M-biased condition than in the control condition for target sizes ranging from 2.75 to 3.75 cm, all p-values < .05. More importantly, we found a significant ILLUSION by VISUAL CONDITION interaction, $F(2{,}10788) = 3.21$, $p = .040$. Post-hoc pairwise contrasts indicated that the illusion was present in the control condition, with both the small (0.75 ± 0.10) and large (0.25 ± 0.10) illusory displays being significantly different

from the neutral display (0.47 ± 0.13), $t(10,788) = 6.82$, $p < .001$ and $t(10,788) = -5.15$, $p < .001$. In the M-biased condition, the illusion was reduced with only the small illusory display (0.91 ± 0.04) being significantly different from the neutral display (0.77 ± 0.09), $t(10,788) = 2.65$, $p = .024$. No difference was observed between the large (0.80 ± 0.09) and the neutral display, $t(10,788) = 1.21$, $p = .225$ (Figure 5). When computing the illusion effect by substracting the rate of affirmative responses for the small display by the rate of affirmative responses for the large display, a post-hoc pairwise contrast indicated that the illusion effect is significantly smaller in the M-biased (0.09 ± 0.03) than in the control condition (0.18 ± 0.03), $t(358) = -3.51$, $p = .001$.

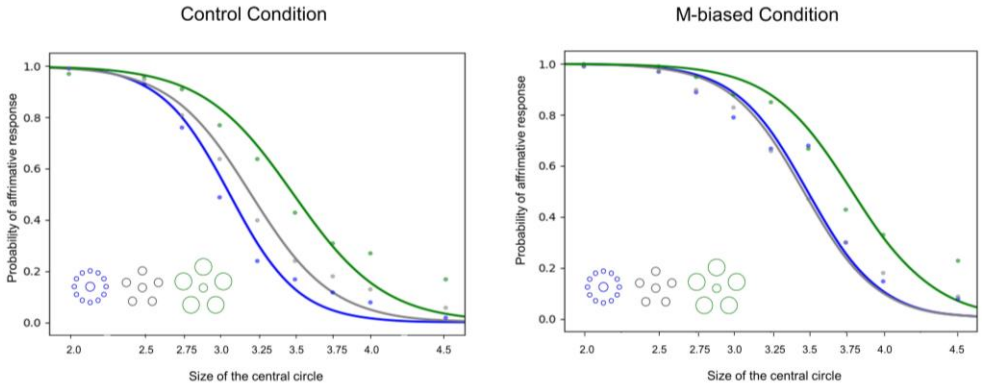

Figure 5. *Fitted curves from the cumulative data showing the effect of the Ebbinghaus illusion on grasping judgments in the control condition (left side) and M-biased condition (right side) of Experiment 3. The dots represent the average rate of affirmative responses (y-axis) as a function of the size of the central circle (x-axis). Solid lines represent the predicted values obtained by means of logistic regression.*

5. Experiment 4

5.1 Methods

5.1.1 Participants

A new sample of 20 participants students (2 males, age: 21 ± 1 years) from the Université catholique de Louvain participated in this experiment. They all gave their written informed consent prior to their inclusion, had normal or corrected-to-normal acuity, declared themselves as right-handed and were unaware of the purpose of the experiment. The study was non-invasive and was performed in accordance with the ethical standards of the Declaration of Helsinki.

5.1.2 Apparatus, stimuli, tasks, procedure and data analysis

We used the same apparatus and stimuli as in Experiment 3 but asked participants to perform the perceptual judgment task used in Experiment 2 instead of the grasping judgment task. The contrast detection threshold was defined via the same procedure as in Experiment 3. All participants had a threshold below 3% (mean ± SD = 1.43 ± 0.78 %), indicating that all participants were able to detect subtle differences of sizes with the contrast values used in the experimental task. The data analysis was the same as in Experiment 3.

5.2 Results

The GLMM analysis revealed a significant effect of SIZE, $F(1, 10788) = 2{,}121.88$, $p < .001$, indicating that the rate of affirmative responses increased with target size. There was also a main effect of the ILLUSION, $F(2, 10788) = 6.08$, $p = .002$, indicating that, compared to the neutral display (0.09 ± 0.02), the rate of affirmative responses to the small illusory display (0.03 ± 0.01) was smaller,

$t(10,788) = 4.00$, $p < .001$, and the rate of affirmative responses to the large illusory display (0.17 ± 0.03) was larger, $t(10,788) = -4.43$, $p < .001$. There was also an ILLUSION by SIZE interaction, $F(2, 10788) = 18.39$, $p < .001$, indicating that the slope was less steep for the small illusory display than for the neutral and large displays. The analysis also revealed an effect of the VISUAL CONDITION, $F(1, 10788) = 4.25$, $p < .039$, with the M-biased condition (0.04 ± 0.01) giving rise to less affirmative responses than the control condition (0.14 ± 0.03). More importantly, the ILLUSION by VISUAL CONDITION interaction was significant, $F(2,10788) = 5.23$, $p = .005$. Post-hoc pairwise indicated that the illusion was present in the control condition, with both the small (0.05 ± 0.01) and large (0.35 ± 0.06) illusory displays being significantly different from the neutral display (0.11 ± 0.02), $t(10,788) = -3.24$, $p = .001$ and $t(10,788) = -6.51$, $p < .001$. In the M-biased condition, the illusion was reduced with only the small illusory display (0.02 ± 0.01) being significantly different from the neutral display (0.07 ± 0.02), $\underline{t}(10,788) = -3.55$, $p = .001$. No difference was observed between the large (0.78 ± 0.02) and the neutral displays, $\underline{t}(10,788) = 0.62$, $p = .533$ (Figure 6). After having computed the illusion effect by substracting the rate of affirmative responses for the large illusory display by the rate of affirmative responses for the small illusory display, a pairwise contrast indicated that the illusion effect is significantly smaller in the M-biased (0.13 ± 0.03) than in the control condition (0.24 ± 0.03), $t(358) = -3.51$, $p = .001$.

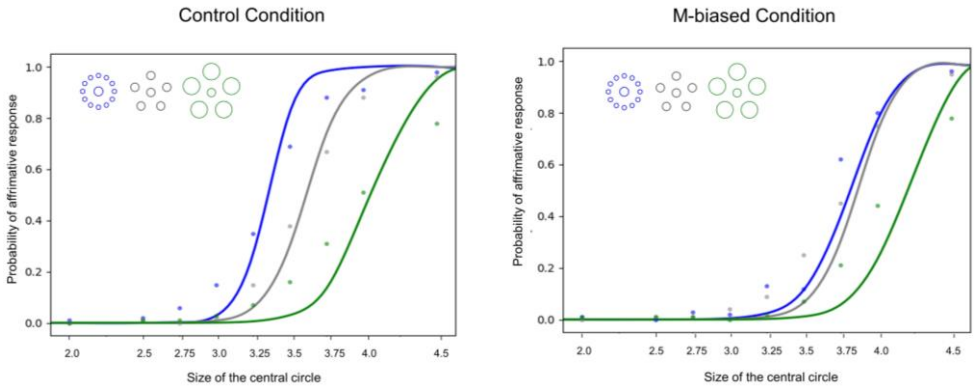

Figure 6. *Fitted curves from the cumulative data showing the effect of the Ebbinghaus illusion on perceptual judgments in the control condition (left) and M-biased condition (right) of Experiment 4. The dots represent the average rate of affirmative responses (y-axis) as a function of the size of the central circle (x-axis). Solid lines represent the predicted values obtained by means of logistic regression.*

6. Discussion

The present Chapter investigated whether the ventral and dorsal streams contributed differently to perceptual and grasping judgments and the integration of the visual context during these judgments. To do so, we used the respective physiological properties of the parvo- and magnocellular neurons to bias the processing of equiluminant stimuli towards the parvocellular pathway and thus the ventral stream, and bias the processing of low contrast stimuli presented at high temporal but low spatial frequency towards the magnocellular pathway and thus predominantly to the dorsal stream.

Experiment 1 showed that grasping judgments were affected when performed on equiluminant stimuli. Compared to the control conditions, participants responded more frequently that they would be able to grasp the equiluminant target when it was actually larger than their current grip aperture. Equiluminance thus decreased participants' capability to match object size with their grip. This is further

supported by the observation that the slope between predicted graspability and target size was less steep in the equiluminant condition than in the two control conditions. Experiment 2 revealed an effect of luminance on perceptual judgments whereby the darkest the stimuli, the smallest it was perceived. However, equiluminance affected the perceptual judgments made on large targets, over and beyond the effect of luminance, by bringing size estimates closer to real size. Together, the results of Experiment 1 and 2 suggest that the magnocellular information is involved in both grasping and perceptual judgments. However, its contribution differs according to the judgment since the lack of magnocellular response hampered grasping judgments but improved perceptual judgments. Finally, we replicated our previous finding that the Ebbinghaus illusion affected both perceptual and grasping judgments, regardless of stimulus luminance, suggesting that the illusion emerged outside the magnocellular pathway.

Experiment 3 and 4 showed that, when the Ebbinghaus illusion was presented with the low contrast, high temporal and low spatial frequency of the M-biased stimuli, its influence was reduced both on perceptual and grasping judgments. This finding suggests that the parvocellular information is critical for the processing of the visual context. In addition, compared to the control condition, M-biased stimuli increased the probability to judge the object as smaller or as graspable. This finding suggests that, in addition to its role in the processing of visual context, the parvocellular pathway contributes, together with the magnocellular pathway, to estimate object size since relying on the sole magnocellular pathway resulted in underestimation whatever the output requirements.

It is worth noting that biasing the processing of the visual information towards one or the other retinocortical pathway had only a moderate effect on perceptual and grasping judgments. In all experiments and conditions, participants

remained sensitive to the actual variations of target size and performed the task correctly. This might be due to the difficulty to completely isolate a pathway. For example, it is difficult to ensure equiluminance at eccentricities that are distant from the fixation point due to inhomogeneities in the parvo- and magnocellular distribution across the retina (Smith, Lee, Pokorny, Martin, and Valberg, 1992; Lee & Sun, 2009). Moreover, some magnocellular neurons do respond to colour stimuli, especially when these stimuli are large (Kruger, 1979). The stimuli used in this study covered a large area of the retina (*i.e.*, 3.8° to 15.04° of visual angle), and they probably failed to completely abolish the response of the magnocellular neurons. However, participants reported the entire stimulus to be stationary during heterochromatic flicker fusion, indicating that the response of the magnocellular neurons was sufficiently reduced to impair the perception of colour alternations across the attended visual field. In addition, the observation that equiluminance specifically affected responses to the largest stimuli goes against the idea that we failed to ensure equiluminance due to stimulus size. The selective effect of equiluminance on large sizes might be better explained by the density of magnocellular neurons, and thereby the effect of silencing them, increasing from the fovea to the periphery of the retina (Azzopardi, Kirstie & Cowey, 1999). Silencing the parvocellular pathway is not an easier task. For instance, parvocellular neurons are sensitive to luminance contrast over a broad range of spatial frequencies (Legge, 1978; Tolhurst, 1975). However, psychophysiological studies in humans showed that the combination of low contrast, high temporal frequency and low spatial frequency was found to produce activations that were tightly restricted to the magnocellular pathway (Kulikowski & Tolhurst, 1973; Legge, 1978; Skottun & Skoyles, 2008; 2011).

The moderate effect of our manipulations might rather be due to some redundancy in the contribution of the parvocellular and magnocellular pathways,

with each pathway carrying sufficient information to support perceptual or grasping judgments on its own. Indeed, when the magnocellular pathway was tuned down, participants remained able to perform both grasping and perceptual judgments, suggesting that the input provided by the parvocellular pathway can be used efficiently to derive object size estimates for perceptual as well as grasping judgments. As the dorsal stream predominantly receives magnocellular information, this suggests that grasping judgments can be performed on information processed outside the dorsal stream. However, it should be noted that even if grasping judgments could be made without magnocellular input, the observation that equiluminance slightly hampered grasping judgments but improved perceptual judgments suggests that magnocellular input carries some information that is critical for grasping but nor perceptual judgments. Similarly, perceptual and grasping judgments remained sensitive to actual size variations when the visual information was biased towards the magnocellular pathways. This suggests that the input provided by the magnocellular pathway is sufficient to support the processing of actual size for perceptual as well as grasping judgments. Nevertheless, we observed an overall underestimation of the actual size of the target when it was biased to the magnocellular pathway. Yet, this effect might simply reflect the fact that stimuli without sharply-defined edges are perceived as smaller. This can already be noticed in Figure 4. The critical finding is that there was no specific impairment of perceptual judgments or specific gain for grasping judgments when visual information was biased to the magnocellular pathway, suggesting that the parvocellular input and thus the ventral stream is not bound specifically to perceptual judgments. Altogether, these results question the assumption that output requirements define which stream is at hand.

The observation that stimuli biased towards the parvocellular pathway do not affect the illusion effect suggests that the dorsal stream is not required to

integrate the visual context. On the contrary, the observation that the illusion decreased when it is biased towards the magnocellular pathway suggests that integration of the visual context is supported by the parvocellular input and thus mainly by the ventral stream. Importantly, this was true for both perceptual and grasping judgments. Together with the finding that perceptual judgments are still possible when visual context processing is decreased, this challenges the assumption that the perception of size is unavoidably tied to the context, while the motor system relies on sizes estimates that are independent of the context.

In conclusion, our study provides the first demonstration that the parvocellular pathway is causally involved in the integration of the visual context, as measured through a size-contrast illusion, regardless of the judgment at hand. These original data thus suggest that the parvo- and magnocellular pathways convey different information, at least with respect to the visual context, but that they cannot be considered as the hallmark of perception and action. In addition, our results suggest that parvocellular and magnocellular pathways can support perceptual and grasping judgments independently of the contribution of the other pathway. Our results thus question the long-standing idea that the functional dissociation between perception and action is relevant to account for the anatomical division of the visual system in a parvocellular-dominant ventral stream and a magnocellular-dominant dorsal stream.

Chapter 7

General Discussion

This thesis aimed to investigate and compare the representations and processes underlying perception and action to test the long-standing idea of their independence and assess the respective contribution of the ventral and dorsal streams in these processes. In Chapter 1, I described the current dominant model that assumes vision for perception and vision for action rely on distinct anatomical streams to deal with the very specific demands of these two aspects of processing the visual world. In particular, the model states that the ventral stream encodes an object relative to its environment to give rise to an integrated representation of the visual world, while the dorsal stream encodes the real metrics of the object without being influenced by the context to calibrate the amplitude of reaching movements and the size of the grip for optimal hand-object interactions. After reviewing the available data, I argued there is no conclusive evidence for perception and action to perform different computations on the incoming visual information, and that there is a lack of knowledge about the nature of the representations used by the sensorimotor system to prepare of actions. This is mainly because actions are typically assessed during their overt stages when the additional sensory information provided by the acting hand causes an imbalance with the information uniquely available for perception and blurs the contribution of the underlying representations. I suggested these issues could be overcome by using prospective action judgments that involve the covert stages of action, without any actual movement, and thereby allow the representations and processes underlying action to be directly investigated and compared to perception. These advantages were used not only to study the influence of the visual

context on perceptual and motor behaviours, but also to investigate how these behaviours integrate visual, sensorimotor and semantic information, and what is the contribution of the ventral and dorsal streams.

Chapter 2 tested, in a series of experiments, whether the computation of object size for action, unlike perception, is centred on the target object independently of its visual context by looking at the effect of a size-contrast illusion on prospective grasping judgments. In addition, I tested whether grasping judgments specifically involved the sensorimotor representations of the hand by adding concurrent motor tasks. I showed that the illusion affected both perceptual and grasping judgments, while the motor tasks affected only grasping judgments. These results thus suggest that grasping judgments rely on the sensorimotor representations of the hand and integrate the visual context.

Chapter 3 excluded that the effect of the motor task observed in the previous chapter is mediated by semantic information about the magnitude associated with the grip (*e.g.,* smallness). I showed that, among two grip squeezing tasks (*i.e.*, precision *vs.* bimanual grip), only the one involving the same grip as in the judged action (*i.e.*, the precision grip) caused an underestimation of grasping capability. I further excluded that the selective effect of the precision grip was due to a more consistent association with the concept of "smallness" compared to the bimanual grip, by showing that the bimanual – but not the precision – grip slowed down the processing of numbers categorized as larger than a reference in a number comparison task. This suggests that grasping judgments truly integrate the available somatosensory information from the concerned effectors in the prospective action plan, independently of semantic biases.

Chapter 4 investigated the potential interaction between the size-contrast illusion and somatosensory information during grasping judgments. The results

showed that the effect of a concurrent motor task on grasping judgments was enhanced when the target was embedded within the Ebbinghaus illusion. These results suggest that the integration of the somatosensory information about the concerned effectors is modulated by task difficulty and potentially by the reliability of the visual information of object size.

Chapter 5 investigated the neural correlates of perceptual and grasping judgments. Using fMRI, I showed that these judgments involve the same neural network, which includes brain areas from both the ventral and dorsal streams. I argued that the network shared by perceptual and grasping judgments underlies a common need to compute object size and compare it to a reference maintained in short-term memory. However, the MEPs recorded in hand muscles during a TMS experiment revealed that grasping judgments, unlike perceptual judgments, were associated with a steady increase of CSE, in particular between the trials. I proposed that this reflects the specific involvement of the hand sensorimotor representations when required to compare object size with MGA, in contrast to when required to compare object size to a visual reference.

Finally, Chapter 6 probed the respective contribution of the ventral and dorsal streams in perceptual and grasping judgments, and especially with regard to the integration of the visual context. To do so, I used the physiological properties of the parvo- and magnocellular pathways to bias the processing of the visual information towards the ventral or dorsal stream. Results showed that both grasping and perceptual judgments can be efficiently performed when the information is biased towards either stream, suggesting that each stream carries sufficient information to support on its own perceptual and grasping judgments. Moreover, the effect of the size-contrast Ebbinghaus illusion on perceptual and grasping judgments was decreased when biased towards the dorsal stream, suggesting that

visual context integration requires the parvocellular input of the ventral stream, regardless of the judgment at stake.

In this general discussion, I will adopt a broader perspective than in previous chapters and discuss the new insights of my findings with respect to two issues identified as central in the general introduction. First, I will take stock of what prospective action judgments can tell us about the representations underlying action. Second, I will discuss the implications of the results obtained with grasping and perceptual judgments for the TVS model. I will then provide an alternative view where the ventral and dorsal streams are proposed to work together to provide size estimates serving both perception and action. Finally, I will conclude by discussing some limitations and future perspectives.

1. Representations underlying prospective grasping judgments

One of the key aspects of this thesis was to use prospective action judgments to understand better the representations underlying the covert stages of action. There is evidence in the literature for the involvement of the same representations in prospective action judgments and actual action. Prospective action judgments were found extremely consistent with the outcome, the run time and the biomechanical constraints associated with the actual execution of the judged action (Frak et al., 2001; Johnson, 2000). Moreover, they were associated with activity within frontal and parietal areas typically considered as part of the "motor system" (Bartolo et al., 2014; Johnson et al., 2002). In line with these observations, Johnson (2000) proposed that prospective action judgments activate the sensorimotor representations of the effectors concerned by the judged action and then transform them into the orientation and size required by the response options.

This thesis provides further support for the idea that the representations of the effectors are involved in grasping judgments. Indeed, Chapter 2 to 4 showed that a concurrent hand motor task affected grasping, but not perceptual judgments. Interestingly, the effect went beyond a mere interference effect as it was specific to the current posture of the concerned effector, *i.e.*, the precision grip, adopted at the time of the judgment, with a small *vs.* large grip aperture leading participants to underestimate *vs.* overestimate their grasping capability. These results suggest that, rather than relying on a memory representation of the MGA to compare it to object size, an on-line representation exploiting somatosensory information about the current posture of the effectors is built. It is worth noting that the incoming somatosensory information needs, however, to be integrated into the stored somatosensory representations of one's body to be interpreted correctly (Head & Holmes, 1991). The observation grasping judgments call upon the current grip aperture is very intriguing since potential grasping capability is not bound to the current state of the hand. The particular enhancement of the CSE in advance to a grasping judgment relative to the significant but smaller CSE observed during the judgment (Chapter 5) suggests that one relies on the somatosensory information of the index finger and thumb to allow the re-enactment and the maintenance of the representation of maximum grip size in short-term memory throughout the task. It is reasonable to assume that this motor strategy is especially needed as task difficulty is high. This may account for the finding that reliance on somatosensory information increased when object size was embedded in a size-contrast illusion or close to maximum grasping capability (Chapter 4). Together, these results may suggest that one continuously monitors available somatosensory information to help the comparison of the grip representation with object size. Alternatively, the somatosensory information might constantly shape the stored representation of the body. In line with this, it has been shown that spreading the fingers apart increases

the representation of hand size compare to when fingers are pressed together (Longo, 2015). It is plausible that the concurrent motor tasks used in the present experiments have induced enduring modifications of one's representation of the grip size, which might, in turn, have biased its comparison with object size. However, the modulation of motor interference by the illusory context (Chapter 4) is difficult to explain in this view, as there is *a priori* no reason why the stored representation of one's MGA would be more malleable in difficult or unreliable situations. This remains to be further investigated, for instance, by studying somatosensory integration and modifications of grip size representation over time. Whether the present results reflect reliance on somatosensory information to maintain grip representation in memory or the extreme plasticity of this representation to incoming somatosensory information, they do indicate that the sensorimotor representations of the index finger and thumb are involved in grasping judgments.

Importantly, the present results do not support the idea that the sensorimotor representations are spatially manipulated. According to Johnson (2000), prospective grasping judgments would be accompanied by the activation of hand representation in its current position and the mental simulation of an opening or closing movement adjusting current hand position to object size. The neural counterpart of this proposal is that grasping judgments and explicit simulation of a grasping movement would induce activity within a common neural network responsible for motor simulation. I showed that they do indeed share activity within a fronto-parietal network, but that this network does not underlie motor simulation. Indeed, all areas of this common network were also activated when two lengths had to be compared in perceptual judgments (Chapter 5). These and other related findings suggest that the parietal component of the common network underlies the processing of object magnitude and its comparison to any other magnitude (*e.g.*, Dormal & Pesenti, 2009; Faillenot et al., 1997; 1999; Fias et al., 2003; Pinel et al., 2004; Walsh, 2003), while the frontal

component underlies the maintenance of a reference in short-term memory (*e.g.*, Courtney et al., 1998; D'Esposito et al., 1999; Scherf, Sweeney & Luna, 2006). In contrast, motor imagery showed additional activation within the left fronto-parietal areas compared to grasping and perceptual judgments, suggesting that the left hemisphere is a key component for representing the object to be grasped and the associated functional knowledge and/or to simulate a movement towards this object. The pattern of hand CSE observed during grasping judgments in the TMS experiment further challenges the motor simulation hypothesis. During motor imagery, CSE changes are typically bound to the progression of the imagined movement (*e.g.*, Stinear & Byblow, 2003), but I showed that CSE was steadily increased during grasping judgments and in particular during the inter-trial interval. These results are at odds with the assumption that the grip representation is evoked to support a time-bound simulation of hand-object interactions.

These results do not preclude that the perceptual representations of the body are involved in prospective action judgments in addition to the sensorimotor representations. Several studies suggest that the perceptual system is also endowed with a representation of the human body that takes into account information about the range of movement allowed by the body parts (Kourtzi & Shiffrar, 1999; Marr & Vaina, 1982; Shiffrar & Freyd, 1993; Vannuscorps et al., 2012). However, these representations do not specifically refer to one's own body, and thus provide only a gross estimation of what a human is capable to grasp. Nevertheless, they might be used when the judgment does not specifically depend on one's own body capability (*e.g.*, judging the type of grasp required for a certain object) or when the sensorimotor representations are lacking or are transiently disrupted. They might also contribute to narrow down the range of achievable grip apertures by providing a range of sizes that any normally-limbed human should be able to grasp and another

range that no one should be able to grasp. The involvement, necessity and sufficiency of these perceptual representations remain, however, to be further investigated.

To conclude, I collected reasonable evidence that grasping judgments rely on the sensorimotor representations of the index finger and thumb in the dorsal stream. However, their role is restricted to the comparison with object size, without necessarily implying the grasping movement to be simulated from the current state of the grip to the opening required by object size. In my view, current hand posture rather contributes to maintain active or refine the stored representation of one's MGA. Prospective action judgments thus allow investigating the sensorimotor system, distinguishing its contribution from the one of the perceptual system, and informing about the representations underlying action in its very early stages. Chapter 4 underlined that the contribution of the sensorimotor system is particularly obvious when object size is displayed within the context of the Ebbinghaus illusion or close to one's grasping limits. Because all my experiments – except the fMRI one – used a size-contrast illusion, it is not surprising that I repeatedly evidenced the involvement of the sensorimotor system in grasping judgments. As a general conclusion, I would like to acknowledge, however, that the insights provided by prospective action judgments concern only one step of the process that leads to the implementation of action and that no conclusion on the specification and on-line control of the kinematics parameters can be drawn without extending the present research to real action.

2. Challenging issues for the TVS model

Another main objective of the thesis was to test the TVS model. In this section, I will discuss how my results challenge the claims that (1) perception and action apply different transformations to the visual information used to estimate object size and (2) rely on distinct anatomical streams to deal with these competing demands. I will also discuss (3) how the model inappropriately distinguishes the inputs of the ventral and dorsal streams, and (4) fails to account for multisensory integration during action.

2.1 Object size in perception and action

The major claim that perception needs to compute object attributes in relation with the visual environment, contrary to action that needs veridical size estimates independent of the visual environment, has been supported by the observation that size-contrast illusions affected perception but not action (*e.g.*, Aglioti et al., 1995; Haffenden & Goodale, 1998). However, evidence has accumulated over the past decade to suggest that the difference between perception and action arose because of an imbalance between the way they were assessed (Franz & Gegenfurtner, 2008). I argued that the main challenging issue persisting in the literature is a discrepancy in the quantity of available sensory information and the level of awareness.

Indeed, the behavioural results of Chapter 2, 3, 4 and 6 indicate that grasping judgments, which do not benefit from additional visual and proprioceptive feedback of the acting hand and imply verbal responses, are similarly affected by the Ebbinghaus illusion than matched perceptual judgments. When the central circle of the illusion was surrounded by larger circles, participants perceived it as smaller but also overestimated their capability to grasp it. Conversely, when the circle was

surrounded by smaller circles, it appeared larger, and participants underestimated their capability to grasp it. These results thus indicate that both perception and the covert stages of action do compute object size relative to the visual context. This consists in a shift from the view that the sensorimotor system processes object size independently of the context. These results rather support the alternative view that a common internal representation of size, influenced by the visual context, underlies both perception and action (Franz et al., 2000; Pavani et al., 1999; Vishton et al., 1999).

During the on-line control of the grasping movement, visual and proprioceptive feedback about the hand might, however, be used in comparison with the visual information about the object to correct part of the error introduced by the illusion at the very early stage of action planning (Franz & Bruno, 2008; Glover & Dixon, 2001; 2002; Prablanc et al., 1986). This could explain why some studies assessing action through MGA that typically occurs at around 70% of the movement trajectory only found a small effect of the illusion (Glover & Dixon, 2001; 2002). This also accounts for the observation that actions performed on remembered objects were more sensitive to the illusion (Westwood, Heath & Roy, 2000; Westwood & Goodale, 2003). As the visual information about the object is no more present, the comparison with the sensory information about the hand, and thus the on-line corrections, cannot take place. Nevertheless, the integration of the visual context is not devoid of interest for action and does not always have to be corrected. For instance, the relative size and distance of the various objects of a visual scene provide information about distance, which is undeniably important for visuomotor performance. Accordingly, several studies showed that visuomotor performance is improved when visual context is available (Bautista & Korienek, 1999; Coello & Iwanow, 2006; Coello & Magne, 2000; Clark, Binsted, Heath & Krigolson, 2007; Redon & Hay, 2005). Interestingly, this applies not only to action programming

(Obhi & Goodale, 2005) and prospective action judgments (Bartolo et al., 2014b; Iachini, Coello, Frassinetti & Ruggiero, 2014) but also to on-line control (Krigolson & Heath, 2004). Moreover, objects are sometimes composed of different axes such as T- or X-shapes. The different axes have then to be combined and processed relative to each other to form a composite shape that can guide action. While patient D.F. was able to grasp properly simple rods, she was impaired at grasping more complex shapes composed of different axes, suggesting that she could process one axis alone but could not put it into relation with another axis (Dijkerman, Milner & Carey, 1998; McIntosh, Dijkerman, Mon-Williams & Milner, 2004). Hence, relative size, distance and orientation are useful guides for goal-directed actions and not just by-products of the visual scene processed exclusively to answer the needs of perception.

To conclude, my and previous findings converge on suggesting that both perception and action are sensitive to the visual context, thereby ruling out the assumption that action and perception apply specific constraints to the processing of size.

2.2 Neural substrate of object size processing

Another claim of the TVS model is that perception relies on the ventral stream, while action relies on the dorsal stream. This fundamental assumption of the model has emerged from the observation that patient D.F., who showed visual agnosia after occipitotemporal damage, was unable to recognise and describe objects but was still able to grasp them, while patients with optic ataxia following parietal lesions showed the reverse pattern. This was subsequently supported by neuroimaging studies showing that the LOC is activated (Grill-Spector, 2003; Malach et al., 1995) and causally involved (Stewart, Meyer, Frith & Rothwell, 2001) in object recognition, while the IPS is activated (Culham et al., 2003) and causally

involved (Cohen, Cross, Tunik, Grafton & Culham, 2009; Davare, Andres, Clerget, Thonnard & Oliver, 2007; Rice, Tunik & Grafton, 2006; Tunik, Frey & Grafton, 2005) in grasping objects. There is thus strong evidence for object recognition to rely on the ventral stream and grasping objects on the dorsal stream. However, it is difficult from these observations to generalise the differential involvement of the ventral and dorsal streams to all perceptual and visually-guided motor behaviours. This is particularly true for the role of the ventral stream in perception. There was already evidence in the literature that perception, when it comes to size, involves the dorsal stream (Dormal & Pesenti, 2009; Faillenot et al., 1999; Fias et al., 2003; Pinel et al., 2004). The results of Chapter 5 add on the existing data by showing that perceptual judgments about length activated the dorsal stream to a great extent, including areas typically involved in grasping such as the IPS and the premotor cortex. Transient lesions of the IPS induced with TMS further indicated this area is essential to judge an object's length (Dormal et al., 2012). Importantly, the role of the IPS in action is also related to the processing of size. Chapter 5 showed that the IPS was activated when comparing object and grip size, but previous studies already showed this area was essential to shape the hand properly to object size during actual grasping. For instance, it is more activated when grasping an object than when merely reaching the same object, a movement that does not require information about object size (Culham et al., 2003). Moreover, the transitive interruption of the IPS induced with TMS perturbed the shaping of the hand to object size (Davare et al., 2007; Tunik et al., 2005). Together with related findings (Dormal & Pesenti, 2009; Fias et al., 2003; Walsh, 2003), this suggests that size is processed within the IPS for both perceptual and motor behaviours. This challenges the most fundamental principle of the model that assumes that the processing of a visual attribute such as size is processed along the ventral stream when serving perception and along the dorsal stream when serving action.

It has been proposed that the processing of size (but also space and time) evolved in the parietal cortex because of its particular interest for the sensorimotor transformations achieved by this cortex (Gallistel & Gelman, 2000; Walsh, 2003). Hence, the functional dissociation between perception and action might have shaped the organization of the visual system, with the functional modules being of closer interest for action (*e.g.*, size, movement) having developed along the dorsal stream and those for perception (*e.g.*, colour) having developed along the ventral stream. However, since the computation of size (and other magnitudes) in the dorsal stream may also be reused to serve perception, the aim pursued by a given behaviour does not provide a sufficient account for determining which stream is involved.

2.3 Contribution of the parvo- and magnocellular pathways

In this thesis, I also investigated the respective contribution of the parvo- and magnocellular pathways to perceptual and grasping judgments. Although the focus on the output requirements drove the TVS model away from the input, some predictions can be made about the parvo- and magnocellular contributions from the statements formulated by Goodale and Milner (1992). Since the parvocellular pathway feeds the ventral stream predominantly (Livingstone & Hubel, 1987a; 1988), it should be more essential to perception and relative size processing than to action. On the contrary, since the magnocellular pathway feeds the dorsal stream predominantly (Livingstone & Hubel, 1987a; 1988), it should contribute more to action than perception or relative size processing.

Results of Chapter 6 showed that grasping judgments were slightly hampered when the visual system was deprived of magnocellular input, while perceptual judgments slightly improved in this condition, suggesting that the magnocellular input is indeed more critical to the sensorimotor than perceptual system. However, perceptual and grasping judgments both demonstrated sensitivity

to the variations of the actual size of the target. The same was observed when the parvocellular pathway was silenced. The logical conclusion is that perceptual and grasping judgments can be supported by either the parvo- or the magnocellular pathway on its own. On the contrary, I showed that the effect of the illusion decreased when the parvocellular pathway was tuned down, suggesting that the integration of the visual context relies on the ventral stream. Because I found the effect of the illusion to be contingent on the parvocellular pathway in both grasping and perceptual judgments, involvement of the ventral stream might be better explained by the input characteristics than the output. Hence, the functional distinction between perception and action does account neither for the contribution of the parvo- *vs.* magnocellular pathway nor for the integration of the visual context.

To account for these results, one has to assume that the two streams communicate with each other. Indeed, since the visual context relies on the parvocellular input that is mainly comprised in the ventral stream, it has to be relayed to the dorsal stream at some point to be able to influence grasping judgments. In a later review of the model, Milner and Goodale (2008) acknowledged that the ventral and dorsal streams have to communicate with each other. They assumed that after the parallel processing of the visual information along the ventral and dorsal streams, their respective output might be transmitted to the other stream. Our results suggest that the visual information processed along one stream is itself made available to the other stream. In particular, information about the visual context is relayed from the ventral to the dorsal stream.

To conclude, the parvo- and magnocellular pathways can each support perceptual and grasping judgments independently of the contribution of the other pathway, suggesting that perceptual and grasping judgments are not bound respectively to information processed in the ventral and dorsal streams. Moreover,

the visual context that influences grasping judgments requires the parvocellular pathway to be integrated, suggesting that the ventral stream share its content with the dorsal stream.

2.4 Multisensory integration

The TVS model makes no particular assumption regarding multisensory integration, but it is congruent with the accepted view that visual information about the object and somatosensory information about the hand are integrated to guide grasping movements towards objects (Desmurget & Grafton, 2000; Mott & Sherrington, 1985; Woodworth, 1899). The parietal cortex is an important area for this multisensory integration. In monkeys, the recoding of single parietal neurons indicates that they can encode information from multiple senses. For instance, some neurons in the IPS respond to visual, vestibular and tactile stimuli (Avillac, Deneve, Olivier, Pouget & Duhamel, 2005; Chen, DeAngelis & Angelaki, 2011; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann & Bremmer, 2005). The integration within the parietal cortex of somatosensory information from the spinal cord with visual information coming from the visual cortex fits Goodale and Milner's description of the dorsal stream.

However, the results of Chapter 4 evidenced a type of multisensory integration the TVS model cannot account for. During grasping judgments, the Ebbinghaus illusion modulated the integration of somatosensory information about the hand. As I established a causal link between the illusion and the parvocellular input of the ventral stream, the former finding suggests that visual information from the ventral stream is somehow integrated with somatosensory information from the dorsal stream. While Milner and Goodale (2008) acknowledged some interaction between the two streams, these results suggest that the work of the two streams is much more integrated than hereto assumed by the TVS model. Indeed, the

interaction of the illusory effect with a concurrent motor task reveals deep integration of the visual information about the context and the somatosensory information about the current grip posture. This goes against the idea that interaction between perceptual and sensorimotor information emerges after the parallel processing of this information in the ventral and dorsal streams, respectively. It rather suggests that the two streams work together to integrate the relevant information for predicting the feasibility of an action.

To conclude, I provided evidence against the assumption that action, at least concerning its covert stages, is independent of the visual context. Thereby, my results make null and void a major theoretical argument for making a distinction between a ventral stream dedicated to perception and a dorsal stream dedicated to action. The relevance of this distinction is further challenged by accumulating evidence that perception cannot be restricted to the ventral stream. Notably, the processing of object size converges to the dorsal stream, whether the observer aims to perceive it or to act on it. Moreover, the functional dissociation between perception and action is not relevant to account for the respective contribution of the ventral and dorsal streams. Finally, the interactions between the ventral and dorsal streams proposed by Milner and Goodale in the later revisions of the model are insufficient to explain our results that imply a much more integrated and fine-grained interaction between the two streams.

3. Alternative view

The TVS model has survived previous criticisms by holding that, over and beyond the amendments required by recent research, the functional modularity of the ventral and the dorsal streams is needed to account for the dissociation between object recognition and on-line control of goal-direct action. It is worth noting that these are very specific functions that do not encompass all perceptual and visually-guided motor behaviours. More importantly, there is no conclusive evidence that these functions proceed by applying different transformations to the visual information. In this thesis, I have shown that the TVS model fails to differentiate perception and action with respect to object size processing. In this section, I will concentrate on this fundamental aspect of vision to illustrate how an alternative model, undifferentiated for perception and action, may better account for my and previous results.

3.1 Description

I propose that the retinal image gives rise to two distinct visual representations of the object, supported by two distinct pathways that converge to a generalised system for size processing located in the IPS. This system provides one single estimate of size that serves both perception and action. The resulting size estimate is then compared to sensorimotor information about the hand, in the case of grasping judgments, for example, and to visual information about the reference metrics in the case of comparative perceptual judgments. Sensorimotor information is provided via AIP, while visual information, whether it relates to the object or the reference, is provided via the posterior portion of the IPS. The contribution of sensorimotor information depends on task difficulty and the reliability of the visual information. The cognitive architecture of my proposal is depicted in Figure 1, its

neural implementation in Figure 2, and both are described with more details hereafter.

After visual information hits the eye, the various objects of the visual scene can be represented independently (*i.e.*, in distinct representations) or in an integrated way (*i.e.*, into one single representation). The present results suggest that the parvocellular pathway integrates the target object with its visual context. Importantly, it does not carry information about the visual context alone. Indeed, when visual information was biased towards this pathway, perceptual and grasping judgments were still sensitive to actual size variations of the target object, indicating that the parvocellular pathway also carries information about the target object *per se*. Hence, the parvocellular pathway would represent the object in relation to its environment. On the contrary, the magnocellular pathway would represent the target object independently of the visual context (*i.e.*, independent representation). Both pathways thus carry information about the target, which allows perceptual and grasping judgments to be performed even when either the parvo- or the magnocellular pathway is tuned down.

Size is then most probably estimated within areas around the IPS. Indeed, magnitude processing for various tasks converges to this area (*e.g.*, here, perceptual and grasping judgments, but also calibration of overt movements, line bisection, or even time comparison; Davare et al., 2007; Fink et al., 2000; 2001). Moreover, they contain neurons that respond selectively to length variations (Tudusciuc & Nieder, 2007; 2009). Size estimates for perceptual and grasping judgments were found to be sensitive to the visual context but could be computed whether or not the context was integrated. Both the independent and integrated representations of the object should thus be considered as complementary but independent inputs of the generalised system dedicated to size processing. My findings imply that the independent

representation should be transmitted to the IPS via the areas of the dorsal stream situated more posteriorly, and the integrated representation via the ventral stream. The role of the parvocellular input, and thus probably of the ventral stream, in the size estimation process is attested by the observation that it may support perceptual and grasping judgments, on its own, in the absence of magnocellular input. As I discussed earlier, the neural foundations for such interaction between the ventral stream and the IPS exist (for a review, see Cloutman, 2013; Grafton, 2010; van Polanen & Davare, 2015a). While the parvo- and magnocellular information is sufficient on its own for size to be estimated properly, the more essential role of the magnocellular input for grasping than perceptual judgments suggests their respective weight varies according to the task.

The resulting size estimate should then be compared to sensorimotor information about the MGA to allow grasping judgments or to the visual information of an external reference to allow perceptual judgments. The comparison most likely takes place in areas around the IPS too, as it is involved whenever two pieces of information have to be compared (*e.g.*, not only size but also length, luminance or orientation; Dormal & Pesenti, 2009; Fias et al., 2003; Pinel et al., 2004). However, I believe different portions of the IPS are involved according to the nature of the comparative judgment. Due to its proximity and functional connectivity with the sensorimotor cortex, the anterior part of the IPS might mediate the processing of sensorimotor information (Lewis & Van Essen, 2000; Simon et al., 2002). On the contrary, the posterior part of the IPS, due to its proximity with the posterior parietal cortex might provide visual information either about the target or reference of comparative perceptual judgments. The specific involvement of the anterior part of the IPS when comparing visual information with sensorimotor information accounts for the specific increase of the CSE observed during grasping judgments, as probed by TMS pulses over M1. Importantly, the weight of the somatosensory information

in the comparison process is calibrated according to task difficulty and possibly the reliability of the visual information. When object size is presented within the context of a visual illusion or close to maximal grasping capability, the current body state is used to refine the judgment (Figure 1). AIP has been associated with a broad range of tasks involving cross-modal integration, particularly in tasks relating vision and haptics (Grefkes, Weiss, Zilles, & Fink, 2002). It is thus likely to support the integration of somatosensory and visual information during grasping judgments. Hence, the IPS would play an important role, not only as an integrator of the parvo- and magnocellular information but also of an integrator of somatosensory and visual information.

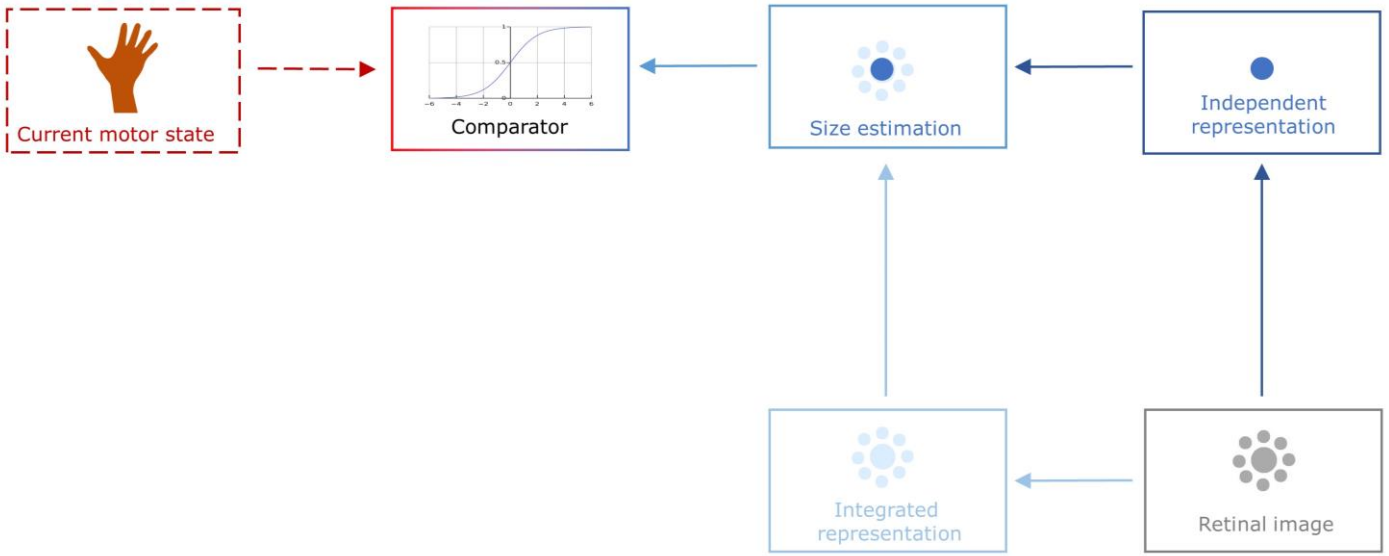

Figure 1. *Model architecture. Information about the target object is both integrated with the visual context in a single representation (integrated representation) and represented independently of the visual context (independent representation). The two representations are conveyed separately to a generalised system dedicated to size processing that integrates both representations to compute a unified size estimate. This estimate is then compared to the MGA (grasping judgment) or an external reference (perceptual judgment). In the case of grasping judgments, the reliability of the size estimate and/or task difficulty calibrate the weight of the somatosensory information about the grip aperture (dashed red line) in the comparison process.*

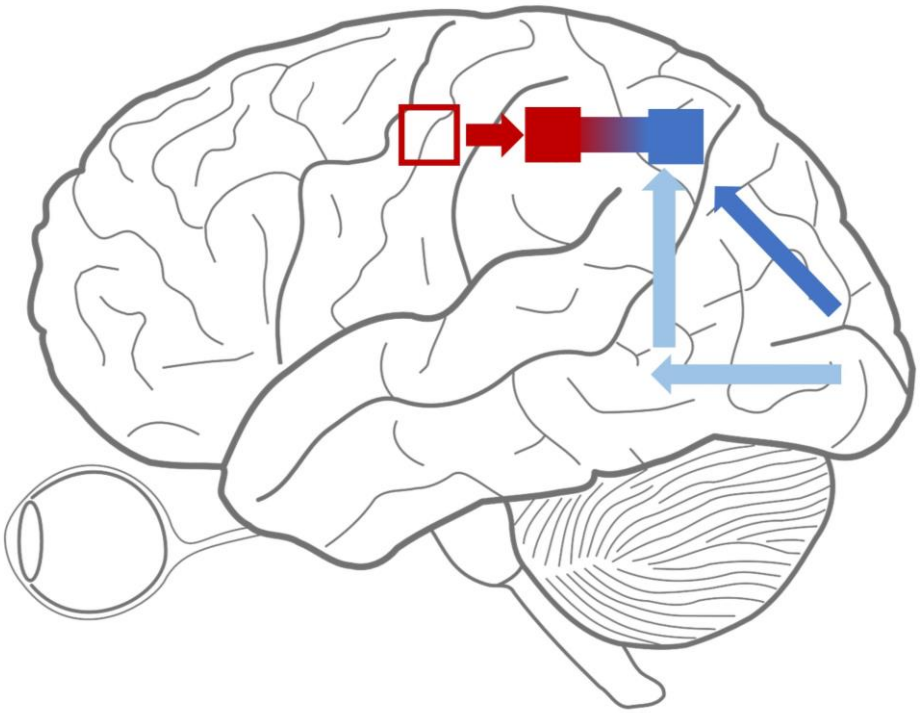

Figure 2. *Neural implementation of my proposal. The independent and integrated representations are generated, respectively, along the parvo- (light blue) and magnocellular (dark blue) pathways before being integrated within the IPS. Note that, in reality, magnocellular input also enters within the ventral stream, which might empower this stream with an additional independent representation of the target object as well. This visual information enters via the posterior extension of the IPS, while sensorimotor information (red) is provided via the anterior extension. Different portions of the IPS are thus involved when comparing object size to the representation of the grip (grasping judgment) or to a perceptual reference (perceptual judgments).*

This proposal relocates the processing of size into the dorsal stream, in opposition to object identity for which there is now good evidence that it relies on the ventral stream. My proposal, however, differs from what has been proposed by Ungerleider and Mishkin in the 80s in several ways. First, while size estimation *per*

se occurs in parietal areas lying in the continuity of the dorsal stream, it relies on information from both the ventral and dorsal streams, with the parvocellular input of the ventral stream playing an important role in the integration of the visual context. While both views predict that a lesion of the ventral stream will not disrupt the processing of size, the "what *vs.* where" model (Ungerleider & Mishkin, 1982) predicts that the size estimate would remain identical, while the present view predicts that the size estimate would be deprived of the influence of the visual context. Second, the integrative role of the parietal cortex goes even beyond the combination of the parvo- and magnocellular inputs and extends to the integration of the resulting size estimate with the current somatosensory information when the comparison deals with action calibration. So, the present model acknowledges the dominant role of the visual input but highlights the integration of size estimates from multiple visual channels and sensory modalities.

3.2 Limitations and future studies

I already discussed the limitations of each experiment in the corresponding chapter. In this section, I will discuss the various limitations of my proposal and suggest potential experimentations to overcome them.

First, relocating the processing of a spatial attribute such as size in the dorsal stream for both perception and action seems in contradiction with the neuropsychological data at the origin of the TVS model. Goodale and Milner (1992) located the processing of size for perception in the ventral stream based on the observation that patient D.F. who had important damage to the ventral stream could not discriminate or reproduce size in perceptual tasks but could use it to calibrate her grasp. However, it is worth recalling that D.F. had also suffered from damage to the posterior parietal cortex and shrinkage of cortical tissue around the IPS (James et al., 2003). This may be at the origin of her impaired perception of size. Under my

assumption that size processing is controlled by a generalised system, she should also have been impaired when using size for action. Nevertheless, this impairment might be compensated when executing the movement thanks to the additional sensory information provided by her acting hand (for a similar argument, see Schenk, 2012). Hence, the behavioural pattern observed in D.F. might reflect a general deficit for size processing resulting from damage to the IPS, which may have been partially compensated in the context of action through the available sensory information. This could be tested by investigating more systematically how the suppression or perturbation of the visual and proprioceptive information about the hand affects grasping performance in visual agnosic patients with a similar pattern than D.F.. Moreover, one could investigate the ability of these patients to process size in the context of prospective grasping judgments. In opposition to the TVS model, the present view predicts they would be impaired.

The behavioural pattern associated with optic ataxia might also be taken into account by my proposal. The preserved ability to discriminate or reproduce sizes suggests the generalised system for size estimation is efficient in patients with optic ataxia. The abnormal kinematics of their reaching and grasping movements should then reflect a deficit that is independent of the computation of size. It has already been argued elsewhere that the motor impairment in optic ataxia does not consist in a deficit for the programming of the action, but rather of the on-line visuomotor control of the action (Pisella et al., 2000; Gréa et al., 2002; Rossetti, Pisella & Vighetto, 2003; Rossetti et al., 2005). This is mainly supported by the observation that these patients had no difficulty in grasping stationary objects seen in foveal vision but were impaired when the need for on-line control increased, for instance, when the object was only shortly previewed, displaced or located in the periphery of the visual field (Gréa et al., 2002; Milner et al., 2001; Pisella et al., 2000). These observations suggest that it is not the size estimation *per se*, but the comparison with

other sensory modalities, which I situated within the anterior part of the IPS, that is impaired in these patients. While the cross-comparison of the lesions of different optic ataxia patients revealed a converging region around the IPS (Perenin & Vighetto 1988), a more fine-grained examination is required to test the anatomical prediction derived from my model. This alternative explanation of the behavioural pattern of optic ataxia thus requires to be investigated with a better spatial resolution.

Second, the attribution of visual context integration to the ventral stream and its transmission to the dorsal stream is inferred from psychophysiological data that lack spatial and temporal resolution. The neural network responsible for the integration of the visual context in size estimates might be refined with fMRI. For instance, one might record brain activations while participants perform perceptual and grasping judgments on visual targets embedded into a size-contrast illusion. This would allow to precisely identify which areas of the ventral and dorsal streams are sensitive to the strength of the illusion, how they connect to each other, and how the signal in these areas is modulated by the judgment at hand. As I assume these modulations occur at a very fine grain – voxelwise – resolution alongside the IPS, it would, however, require an fMRI scanner and/or protocol with a high spatial and/or functional resolution. Regarding the temporal properties of the parvo- and magnocellular pathways, it would be particularly interesting to refine the temporal resolution of my proposal and investigate the time course of visual context integration by using, for example, backward masking techniques. Indeed, the parvocellular pathway is slower than the magnocellular one and context might thus be integrated only when the masking allows sufficient time to encode an integrated representation of the object. This could also be assessed by applying transient TMS over the ventral stream at different timings. However, the critical ventral areas for this integration should first be identified with neuroimaging techniques.

Third, my proposal is limited to the processing of size. Obviously, size is not the only attribute of common interest for perception and action. Orientation, depth, location and shape also play an important role in object perception or manipulation. The model proposed for size could, however, inspire the study of these attributes as well. The prospect to end up with a single model generalising to different object attributes is plausible in light of the capacity of IPS neurons to encode all these properties (*e.g.*, Colby, Duhamel & Goldberg, 1993; Duhamel, Colby & Goldberg, 1992; Rizzolatti, Luppino & Mateli, 1998; Sakata, Taira, Murata & Mine, 1995) and the observation that the processing of these properties often involves both the ventral and dorsal streams (*e.g.*, Altmann, Grodd, Kourtzi, Bülthoff & Karnath, 2005; Marois, Leung & Gore, 2000; Parker, 2007; Zachariou, Klatzky & Behrmann, 2013).

Fourth, as already mentioned, my results are restricted to prospective action judgments, offering a view limited to the representations and processes underlying action in its very early stages. These results thus need to be extended to the overt execution of actions. While there is good evidence that the processing of size during grasping involves the IPS and more specifically its anterior portion (Culham et al., 2003; Davare et al., 2007 Frey, Vinton, Norlund & Grafton, 2005), the existence, nature, and relative weight of the ventral stream contribution remain to be investigated. I collected preliminary observations suggesting that the magnocellular input might be more essential to grasping than perceptual judgments. If this turns out to be confirmed, it is reasonable to assume that its weight is even greater for the execution of action, possibly at the expense of the parvocellular input. Additionally, the question of whether the integration of sensorimotor information, which is essential during visually-guided action, is also modulated by task difficulty and the reliability of the visual information remains to be tested. It is also important to keep in mind that my results are restricted to prospective judgments about the capability

to grasp an object between index finger and thumb, a hand configuration defined as the precision grip. Further research is needed before the conclusions can be extended to a broader range of grasping movements. However, a previous fMRI study suggests that the neural networks supporting precision and power grips largely overlap (Kuhtz-Buschbeck et al., 2008), and there is no a priori reason to postulate that size is processed differently when the object is grasped with either grip. I thus predict that my conclusions should extend to most grasping movements. Atypical grasping movements, which require the size of different axes to be combined and processed relative to each other (e.g., grasping a T-shape), might rely more extensively on the integrated representation of the ventral stream. This requires further investigation.

Finally, it is worth noting that my proposal is based on data from grasping judgments on 2-dimensional (2D) objects, while action is typically performed on 3-dimensional (3D) objects. This third dimension might be critical in providing the object parameters needed for the programming of grasping movements. This has been supported by the finding that dorsal areas around the IPS, and in particular the left AIP, show robust selectivity for 3D compared to 2D objects (Freud et al., 2017; Srivastava et al., 2009). However, it is essential to underline that, even if the dorsal area AIP shows selectivity for 3D information, the processing of 2D and 3D objects during grasping movements involved the very same areas (Freud et al., 2017). Grasping movements towards 2D objects are thus supported by the typical grasping network. Moreover, 3D information is also processed within the dorsal stream when it comes to perceptual discrimination (Srivastava et al., 2009; Snow et al., 2011). The contribution of the dorsal stream to perceptual and grasping judgments is thus more difficult to evaluate with 3D than with 2D objects because of its ubiquitous role in extracting 3D information. Besides 3D object representation, another important information extracted from disparity, at least when it comes to size,

concerns distance from the eye. Indeed, as described in the introduction, the estimation of object size requires information about distance that is made available mainly by binocular disparity (and/or external visual cues). In my studies, participants were always provided with binocular vision. Comparatively, under monocular vision, object size should get closer to retinal size and thus be underestimated. Finally, since disparity is a matter of the dorsal stream, it would be interesting to test whether presenting the illusion under monocular vision would produce an imbalance between the weight of the integrated representation of the ventral stream and the independent representation of the dorsal stream.

Conclusion

The aim of the present thesis was to use prospective action judgments to investigate the representations and processes underlying the covert stages of action and to test the long-standing idea of the duality of vision. I showed that grasping judgments integrated somatosensory information about the effectors and visual information about the context. I further showed that these two types of information interacted together, with the presence of visual context enhancing the reliance on somatosensory information. I also brought evidence that both the ventral and dorsal streams are involved in perceptual and grasping judgments, with the ventral stream playing a crucial role in the integration of the visual context.

Overall, the findings of this thesis bring new insights into the nature of prospective action judgments. They not only provide further evidence for the involvement of the sensorimotor representations but also suggest that these representations are not spatially manipulated contrary to what is assumed by the mental simulation hypothesis. Moreover, they reveal how multisensory integration supports the comparison between the stored sensorimotor representation of the grip and the visual information about object size: when the latter is provided with visual context or close to our body limits, the comparison process calls upon the current somatosensory information about the grip. These findings also challenge the duality of vision. In particular, they indicate that, like perception, the sensorimotor system integrates the visual context when estimating size and thereby discard the idea that perception and action are tied to different transformations of the visual input. They further show that the functional dissociation between perception and action is also not relevant to account for the respective contribution of the ventral and dorsal

streams. Finally, they suggest that the work of the two streams is much more integrated than assumed by the TVS model.

Based on these results and interpretations, I have proposed an alternative view for the processing of size during perceptual and grasping judgments where both streams provide different information to the IPS that integrates them into a unified representation of size that serves both perceptual and motor behaviours. The difference between perceptual and grasping judgments would then rely on the type of sensory information the computed size estimate has to be compared with. I have further proposed that the integration of perceptual and sensorimotor information into the comparison process is handled by different portions of the IPS along a posterior-to-anterior axis. However, the location and time course of these processes must be further specified. Moreover, my proposal is restricted to the very specific case of size processing in the context of perceptual discrimination and grasping judgments. Further research is required to expand the scope of this proposal.

After this doctoral research, I would certainly not pretend to understand the functional organization of the visual system, and I honestly believe there is still a long way to go. However, I hope my work together with many others will contribute to moving away from the duality of vision, which remains a very contaminating idea, and will pave the way towards a more integrated understanding of the visual system.

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