Implication of motor and numerical cognitive processes in the perception of external space.

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Je dédie cette thèse à mon grand-père Léon Bonhomme et à mon ami Matthieu Jacques qui, même si nous ne pouvons plus les percevoir dans nos espaces externes, resteront à jamais gravés dans nos espaces représentationnels

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CHAPTER 1: GENERAL INTRODUCTION

How the human brain represents external space is an extremely complex question that has interested both experimental psychologists and clinical neurologists for many years (Brain, 1941). The accumulation of research has shown that the brain does not appear to simply collect and process information provided by the different senses in a unitary fashion in order to represent external space, but rather uses a myriad of dynamic cognitive processes to elaborate multiple forms of 3D space representations (Previc, 1998). Among these cognitive processes, multisensory perception, body and action representations, and magnitude coding are all considered to play a role in perceiving and interacting with the surrounding world.

Support for the idea that space perception is partly derived from action and body representations comes from an understanding of action planning (Coello & Delevoye-Turrell, 2007; Gallese 2007; 2016; Jeannerod, 1997; Profitt, 2006). In order to produce an action, attention is first oriented towards a stimulus, and then a reaching action is planned based on information about the spatial location of the stimulus relative to the actor (Jeannerod, 1997). In this process, perceived space is first defined by whether the perceiver thinks being able (or not) to reach stimulus location. If the stimulus is perceived as 'reachable', the stimulus is perceived as within peripersonal space (or near space; within hand reaching range), whereas if a stimulus is perceived as 'not reachable', it is perceived to be in extrapersonal space (or far space). Space perception would benefit from action planning, where the ability to mentally simulate a reaching action to the stimulus is thought to provide the defining metric for the boundary between peri- and extra-personal spaces (Coello & Delevoye-Turrell, 2007). Support for this view has come from several studies that have shown that moderating action capabilities (e.g., by the use of tools; action adaptation paradigm; effort increase; different action expertise levels) can change the way that the reaching space boundary is perceived (Bourgeois & Coello, 2012; Longo & Lourenco, 2006; Witt & Proffitt, 2008).

Numerical magnitude processing has also been shown to interfere with spatial cognition. Space can be defined as the absolute magnitude of distance between the perceiver and the stimulus (irrespective of reach space), between different stimuli, or within a stimulus (e.g., size; the distance between the left and right sides of the object). A "theory of magnitude" (Walsh, 2003) suggests that all judgements on quantifiable dimensions could be held by a generalized magnitude apprehension system. In support of this system, research has shown behavioral interactions and neural overlaps between spatial and numerical magnitude processing (Hubbard, Piazza, Pinel & Dehaene, 2005).

Although these two perspectives define perceived space differently, recent findings show that they also interact. The presentation of action stimuli (e.g., grasping movement of the hand) can influence number processing, and vice versa, the processing of numerical stimuli can influence action execution (Andres, Davare, Pesenti, Olivier, & Seron, 2004; Badets & Pesenti, 2010, 2011; Lindemann, Abolafia, Girardi, & Bekkering, 2007; Moretto & di Pellegrino, 2008). A possible reason for these crossover effects is that the cognitive processes for action and magnitude representation take place in the same areas of the brain (i.e., fronto-parietal networks), possibly indicating shared processes.

The aim of the present thesis was to investigate and better understand the links and shared underlying mechanisms between numerical magnitude, sensorimotor processes and spatial perception. In this general introduction, I will review the literature relevant to this thesis. In Section 1.1, I start with a review of space perception. The aim of the section is to present how space that implies multisensory integration, can be subdivided into several subspaces and perceived using different reference frames. Then in Section 1.2, I will review the literature on perception and action, and their interactions, as well as how action and body representations contribute to space perception. Section 1.3 will then discuss the literature on magnitude processing, as well as the associations observed between processing numbers and space perception. Finally, in Section 1.4, I will provide a summary of the main objectives of the thesis, and the thesis content.

1.1. Space perception

1.1.1. Space, a multisensory construct

Space perception is a fascinating construct, arising from the associations of multiple sensory inputs, and engaging a huge proportion of the cerebral cortex (Previc, 1998). The nervous system combines information captured by different sensory organs to form, almost immediately, cognitive representation of the environment, enabling efficient interactions with the world (Andersen, Snyder, Bradley & Xing, 1997). A compelling example of this constructive aspect of space perception is the perceptual filling-in of the blind spot (Awater, Kerlin, Evans & Tong, 2005; Grossberg & Mingolla, 1985). The blind spot refers to a location on the retina where the optic nerve exits the eye, and where there is an absence of photoreceptors. Despite having this blind spot, a perceiver will never see black holes in the perception of the environment (even though they exist), as adaptive mechanisms will ensure the synthesis of a clear visual representation of the environment, filling in the information at the blind spot (Awater et al., 2005). A similar automatic merging of visual information occurs with binocular disparity (Gogel, 1963). Each eye has a slightly different view of the visual world due to their off-set position in the skull, but the two images projected on each retina are combined to form a homogenous vision of the external space. In these examples, the brain performs processes, unbeknown to the perceiver, so that the perceiver has a single clear view of the surrounding environment. These simple examples transfer to more complex cognitive processes. For example, in space perception, information about depth and distance is important, and this information can be automatically, unbeknown to the observer, extracted from binocular and dynamic perceptual processes of the retinal images in motion (Merleau-Ponty, 1945), and used for perceiving 3D space.

Perception and sensory-motor processing are other complex cognitive functions that rely on many automatic and integrative processes. This is somewhat supported by the different cognitive, motor and sensory functions involved, and the set of distinct areas of the brain used during perception

and action tasks. Interestingly, in this domain of research, there has been many studies that have investigated multisensory interactions that lead to the perceiver and actor to have a multimodal representation of space (for the purpose of action; Andersen et al., 1997; Gross & Graziano, 1995). In this case, various sensory modalities are involved in representing space, among which vision, but also audition, vestibular sensation and somatosensation (Andersen et al., 1997; Previc, 1998). Here, somatosensation refers to tactile sensations coming from the body, collected through different kinds of mechanoreceptors in the skin, or in the muscles and joints (Riemann & Lehpart, 2002; Rieman, Myers & Lephart, 2002; note that nociceptors and thermoreceptors also exist for the somatosensation of pain and temperature sensations, but these may have less relevance for spatial perception). Since the perceiver's visual window of the environment is dependent on the position of the eyes, head and body (Gibson, 1979; Proffitt, 2013), spatial cognitive processes must code visual information using retinotopic positions that superimpose vestibular and proprioceptive sensory information (Andersen et al., 1997). This combination of different sensory information is thought to take place mostly in the parietal cortex (PC), an associative brain area crucial for visuospatial functions (Bender & Teuber, 1949; Brain, 1941; Gross & Graziano, 1995; Holmes, 1918; Mountcastle, 1975).

The critical role of PC for visuospatial functions has been demonstrated by neuropsychological investigations of brain damaged patients. For example, lesions of the PC lead to deficits in walking and obstacle avoidance, judgements of size and distance, target fixation and pursuit, reaching and pointing movements, navigation and path learning (Holmes, 1918, Ting et al., 2011). In the case of unilateral lesion of the PC, the patient may present unilateral spatial neglect, characterized by a failure to report, respond to or orient towards stimuli presented in the contra-lesional side of space, without underlying sensory or motor deficits (Brain, 1941; Heilman, 1979). Due to the unilateral brain damage, patients show spatial neglect towards the contralateral hemifield of space (Ringman et al., 2004). Interestingly, a wide variety of symptoms have been described among unilateral neglect patients, with proposals of many different types that can co-occur (Plummer, Morris & Dunai, 2003; Ting et al., 2011). For example, various varieties of neglect

can occur depending on the modality impacted by the lesion, with distinctions between sensory (or input), motor (or output) and representational (internal) forms of neglect. *Sensory neglect* (also sometimes referred to as *attentional neglect*) is characterized by the unawareness of stimuli presented in or on the space or body opposite to the side of the lesion, and can affect independently or conjointly the different sensory modalities (e.g., visual; auditory; somatosensory). *Motor or premotor neglect* (also referred as *intentional neglect*), is defined as a failure to produce a response or movement (or an inadequate movement; hypometria or hypokinesia; Bottini, Sterzi & Valler, 1992; Meador, Watson, Bowers & Heilmann, 1986) towards a stimulus situated in the contra-lesional side of space. Finally, *representational neglect* (also referred as *imagery neglect*) affects the generation and processing of mental images or space. For example, when asked to describe from memory a famous location (e.g., Piazza del Duomo, Milano), patients only reported the buildings on the ipsi-lesional side of space, with the report changing depending upon whether the patient imagined themselves facing towards or away from the cathedral (Bisiach & Luzzati, 1978). The emergence of the different types of unilateral neglect indicates the different complex cognitive processes involved in the perception of space. Overall, neglect disorders seem characterized by disrupted networks of external world spatial representation, rather than a specific sensory deficit or precise lesion (Ting, 2011; Bartolomeo, Thiebaut & Doricchi, 2007).

Beyond the crucial role of the parietal cortex in perceiving space and multisensory binding, it appears that areas of the premotor cortex might also contribute to this integrative elaboration of spatial representations (Fadiga, Fogassi, Gallese & Rizzolatti, 2000; Gross & Graziano, 1995; Rizzolatti, Fogassi, & Gallese, 2002). Neurophysiological studies investigating visuo-tactile integration in monkeys have proposed that some parietal neurons discharge for both tactile and visual stimulation occurring within a delimited space surrounding specific body parts (e.g., head and face, arms and hands; Leinonen et al., 1979; Mountcastle et al., 1975). This extends to research showing the existence of visuo-tactile bimodal neurons in the premotor cortex that were responsive to tactile stimulation on both the hand (or on

peribuccal regions), and also for visual stimulation near body parts (Graziano, Hu & Gross, 1997; Rizzolatti et al., 1981a). Interestingly, some neurons discharged specifically for pericutaneous visual stimulation (i.e., a few centimeters from the skin; < 10 cm), while other neurons responded for stimulations taking place further away from the skin, but within reaching distance (Rizzolatti et al., 1981b). These studies showed that the presentation of an object near a body part triggered the activation of the visuo-tactile (premotor) bimodal neurons, even when no direct contact was made between the object and the skin of the monkey. Therefore, it seems that the integration of visual information captured in external space, combined with tactile information coming from the body allows the representation of the space (Brozzoli, Ehrsson & Farnè, 2014).

A similar observation has also been made for visuomotor neurons in the ventral part of the premotor cortex of monkeys (i.e., area F5; for a review see Fadiga et al., 2000). These specific neurons, also termed canonical neurons, were shown to be responsive when the monkey grasped objects, and when the monkey simply observed 3D graspable objects (Rizzolatti et al., 1988). More specifically, the presentation of small objects caused discharged activity in neurons responsible for precision grip (i.e., finger grip formed by the index and the thumb), while the presentation of large objects caused increased activity in neurons responsible for whole-hand prehension. These visuomotor neurons suggest a sensory-motor coding (or even a "motor perception") of the space where an intended action can be directed toward an object goal (Fadiga et al., 2000). The cortical motor system is therefore not confined to the implementation and execution of action, but also represents the action as an internal representation (perhaps as a motor plan). These internal representations may in turn contribute to the representation of space between the actor and the object. In this sense, space may be represented by multiple sub-spatial maps that are partly delimited by the body and its action capabilities (Gross & Graziano, 1995; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997).

From this brief review of the literature, it may be conclude that space perception is based on more processes than that of visual modality alone.

The representation of our body and its ability to produce actions also contributes to space perception. As a result, external space may imply different cognitive processes that partition space into several subspaces depending upon the purpose of the perceived space. The visuo-tactile reference fields in primate research have provided evidence that an object visually presented in the portion of space near the body can elicit bimodal (tactile-visual) neuron activation (Graziano et al., 1997; Rizzolatti et al., 1981b). However, these bimodal neurons will not fire if the object is visually presented within a portion of space sufficiently far from the monkey's body. This suggests that space near the body is processed by the brain differently than space further away. In the next section of this introduction, I discuss the different subdivisions of space perception.

1.1.2. Subdivisions of space perception

As described in the previous section, space perception is believed to be subdivided into several distinct subspaces, delimited by and dedicated to different behavioral functions when interacting with the environment (Previc, 1998). On the basis of neurophysiological, neuropsychological and behavioral findings, various models have been proposed that attempt to describe how space perception is defined by sensory modality (e.g., vision or somatosensation), motor behavior (e.g., eye, reaching, and whole-body movements), and involved in diverse sub-realms of space (Grusser, 1983; Previc, 1993; Rizzolatti, Riggio & Sheliga, 1994). In this section of the introduction, I will review these models.

Grusser's model (1983; see Figure 1.1) highlighted strict differences between *personal* and *external spaces,* with different compartments of external space. Here, personal space (or ego space) referred to the space of the inner self, experienced by internal senses (e.g., interoception or proprioception). Grusser (1983) suggested that personal space differed from *body space,* since parts of the body could be perceived in external space. He defined external space as being outside the body, experienced by outer senses, and split into four subspaces (from closest to the body, to the infinite). The first of these sub-spaces was *grasping space,* which could be

further subdivided into oral grasping (ingestion movements; somatosensation of the peribuccal regions; gustation; olfaction), manual grasping (object prehension and manipulation; visual and tactile modality) and instrumental grasping spaces (incorporation/assimilation of tools during their use; see Osiurak, 2014 for a review). The second subspace was *near-distant space* (consisting of walking movements; visual object and pathway processing; vestibular signals), and was considered beyond reaching capabilities, but delimited by an immediate comfortable walking area (e.g., a blindfolded individual will feel unsure about his position in space after having performed 6 to 15 steps). The third sub-space was the *far-distant action space* (sense of direction; mainly visual; vestibular; slightly auditory), starting from around 6-8 meters from the body. Finally, the fourth subspace was the *visual background,* extending as far as the eye can see, and containing elements of the visual background (huge buildings; the sky; clouds; stars), not perceived in three-dimension.

Another motor-to-sensory pathway model for the construction of space perception was proposed by Rizzolatti, Gentilucci and Matelli (1985). Here, visuomotor coupling between visual stimuli and actions directed toward these stimuli would motorically constrain visual parietal neurons (Rizzolatti et al., 1997). Based on single cell recording studies (partly presented in the previous section), and philosophical writings on the phenomenology of perception (Merleau-Ponty, 1945), the model argues that space perception is not a multipurpose map, but rather implies a collection of different spatial maps (Colby & Duhamel, 1996; Gross & Graziano, 1995; Rizzolatti et al., 1994). Here, a difference is made between: (i) *personal space* related to ingestion movements and peribuccal tactile sensations, (ii) *peripersonal space* related to object reaching and grasping actions, and (iii) *far space* explored through oculomotor movements and attention orienting mechanisms (Rizzolatti & Carmada, 1987).

Previc (1998) attempted to constitute a complete model by merging different existing models, while highlighting the importance of action capabilities in the parceling of space perception. The model defined a *peripersonal space* and three different extrapersonal spaces (i.e., *focal*

extrapersonal; action extrapersonal and ambient extrapersonal; see Figure 1.1), each described as having different underlying cortical networks (Previc, 1998). Previc's peripersonal space was similar to the previously described models, and defined as the area of space where object manipulation can occur within the limit of reaching capabilities. Therefore, peripersonal space would be defined based on trunk-/shoulder-centered coordinates, determining the spatial degrees of freedom available for upper-limb movements.

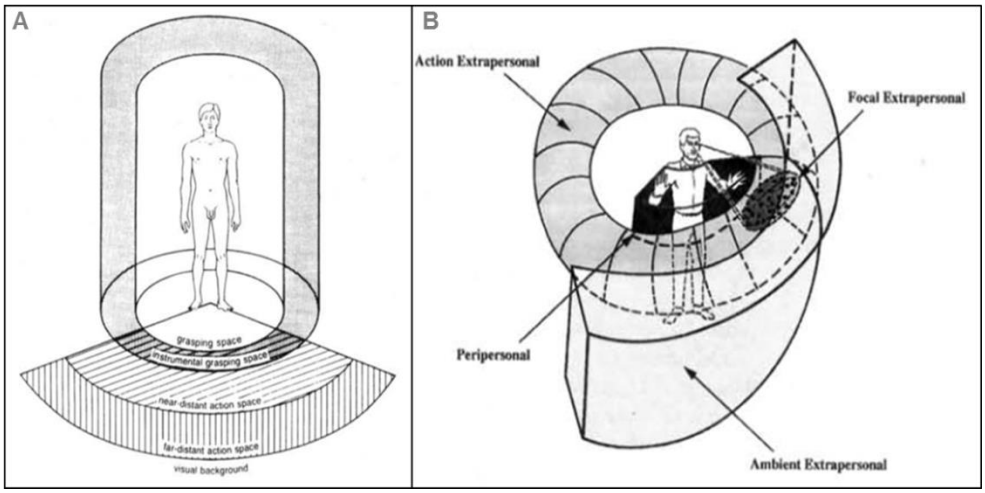

Figure 1.1: ***(A)*** *Grusser's model and* ***(B)*** *Previc's updated model of external space segmentation (adapted from Grusser, 1983 and Previc, 1998).*

Support for the differentiation of regions of space can be found in neuropsychological observations showing double dissociations between spatial processing of near and far space. These dissociations were first reported by the pioneering work of Holmes (1918), who distinguished patients with occipital and parietal lesions that had difficulties in executing goal directed reaching movements versus difficulties in walking behavior in space. More recently, findings from the investigation of unilateral neglect have shown dissociations between personal, peripersonal and extrapersonal forms of neglect (Committeri et al., 2007; Guariglia & Antonucci, 1992; Halligan & Marshall, 1991; Ting et al., 2011; Vuilleumier & Valenza, 1998). In addition, neuroimaging research has revealed different brain areas

underlying near and far spaces (Brozzoli, Gentile, & Ehrsson, 2012; Committeri et al., 2007; Weiss et al., 2000). For example, bisecting lines in near space was shown to activate dorsal visuomotor areas, while performing the same task on a more distant screen activated ventral visuoperceptual areas (Weiss et al., 2000).

These different models are not the only models of space perception however. This time focusing on the perception of depth, Cutting and Vishton (1995) proposed a model that again separated space perception into different subspaces, but this time, only as a function of distance, and independent of motor behavior (see Figure 1.2). The model described the different contributions of visual cues in the perception of distance (e.g., occlusion, visual field height, relative size, convergence and accommodation, binocular disparity, etc.), and suggested three space representations: *personal space, action space and vista space* where the different visual cues had different weights. First, personal space was defined as extending up to 2 meters from the body, and particularly benefiting from ocular and stereoscopic information (e.g., convergence, where the angle formed by two eye lines of sight is bigger for near compared to far fixated objects) and binocular disparity (i.e., slight differences between retinal images). Action space was defined as the space from the end of personal space up to 30 meters, and represented the area where one can move, throw objects and interact with conspecifics. In this space, ocular and stereoscopic information is relevant, but less useful than in personal space, and therefore have different weightings of influence. Finally, vista space starts at around 30 meters from the body, and extends as far as the eyes can see. Here, ocular and stereoscopic information are almost irrelevant, with little to no weight. Although there is a degradation of some visual information, other visual depth cues remain relevant across all spaces (e.g., occlusion, where an object occluded by another object is used to define that the occluded object is further away in space than the occluding object; relative size, where a difference in size of two identical objects in the scene indicates that the smaller object is more distant; and familiar size; relying on size-distance consistency; Palmer, 1999).

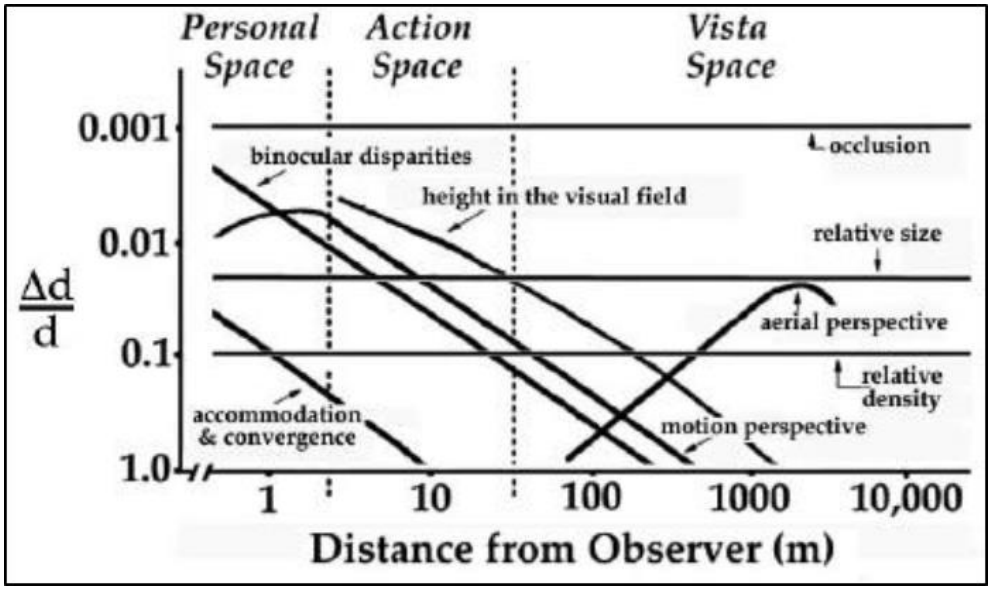

Figure 1.2: *Cutting and Vishton's (1995) model of space in distance using visual, ocular and oculomotor cue contributions.*

Support for Cutting and Vishton (1995) model can be found in patients with brain lesions in the occipito-parietal visual areas, ophthalmological disorders or in children and adolescent with "Alice in Wonderland Syndrome" (AWS; Bender & Teuber, 1949; Holmes, 1918; Liu, Liu, Liu & Liu, 2014; Schoenberg & Scott, 2011). For example, *teleopsia* refers to visual hallucinations where objects appear further away than they really are, while *pelopsia* refers to objects appearing nearer than their true position. Moreover, *micropsia* and *macropsia* denote visual distortions inducing objects to be perceived smaller or bigger respectively than their actual size. These distortions can be regrouped under the more generic term *dysmetropsia* (also commonly termed *Gulliverian illusions*), since they can occur conjointly and influence each other due to size-distance consistency. Finally, the term *metamorphopsia*, is used to refer to visual distortion affecting shapes and colors where straight lines in the environment can appear to bend. Interestingly, these hallucinations can either occur exclusively for perceived body parts appearing to change in size (Type A AWS), exclusively for external space (Type B AWS), or for both one's own body image and external space (where object but also other people appear

distorted; Type C AWS; Lanska & Lanska, 2013). This last type of AWS suggests a relation between the perception of space and body representations. Cutting and Vishton model (1995), although extremely complete concerning visual modality, might therefore not take enough in consideration the importance of represented body and its diverse capabilities, as like in the case with the other presented models of space perception (Grusser, 1983; Previc, 1998; Rizzolatti et al., 1997).

From this review of models, it seems that the representation of the space surrounding a perceiver is decomposed into distinct spatial processing cognitive systems. This partition appears to be delimited regarding the body in order to serve different types of actions and behaviors (e.g., reaching, walking, navigating, and attentional orienting; Previc, 1998). Moreover, distance from the body seems to be a significant factor in this segregation of space coding (Cutting & Vishton, 1995), similar to what can be observed with different population types of visuo-tactile neurons coding reference fields of different sizes (Graziano et al., 1997; Rizzolatti et al., 1981). However, it remains to be seen whether the perception of space is shaped for successful action, or whether action and body representations shape space perception. We will return to this discussion in Section 1.2.2., with the review of literature supporting motor coding of peripersonal space. But before discussing these points, I will introduce the different reference frames of space perception in the next section.

1.1.3. Perceiving space within different frames of references.

The last section presented findings supporting the view that when perceiving the space of the surrounding environment, the perceiver can use different processes to represent different subspaces. In all of these models, space perception seems anchored on the observer's viewpoint. However, it should also be noted that individuals have the ability to represent space from outside their own viewpoint, taking a reference frame independent of their position. For example, when evaluating the position of an object in space, the object can be perceived in reference to the observer's position (or

egocentric frame of reference) or the object can be perceived in reference to another element present in the scene (i.e., an allocentric frame of reference) (Iachini & Ruggiero, 2006; Ruggiero, Ruotolo & Iachini, 2009). Distinction between egocentric and allocentric reference frames provides two additional manners of representing space (Klatzky 1998; Paillard 1991; Meilinger & Vosgerau, 2010). In this section, I will discuss the relevance of each on space perception, and present the idea that these different but complementary reference frames participate to the representation of element location in external space (Ruggiero, Ruotolo & Iachini, 2009).

Spatial coding under an egocentric reference frame is reflected by self-to-object (or self-centered) relationships, where an object's spatial position is represented within a body centered coordinate system (Committeri et al., 2004; Galati, Pelle, Berthoz & Committeri, 2010; Meilinger & Vosgerau, 2010). This implies sensory motor parietal and premotor brain area processes. However, spatial coding under an allocentric reference frame reflects object-to-object spatial relationships, where spatial information is represented within a coordinate system centered onto an external location or object, independent of the observer's viewpoint (Meilinger & Vosgerau, 2010). This implies conceptual and memory based temporal, hippocampus and thalamus brain area processing, and can lead to different types of allocentric spatial processing, centered on any possible external element in the environment (e.g., object-, landmark- or other-centered spatial reference frames; Committeri et al., 2004; Fini, Brass & Committeri, 2015). In this sense, allocentric processing is very flexible, and can take many different subforms. Throughout the present thesis, the term *allocentric reference frame* will refer to spatial cognitive processes occurring independent from a perceiver's or an observer's viewpoint, and *allocentric distance* will refer to the distance separating two objects or landmarks in the environment. Other terms such as *altercentric spatial coding or altercentric reference frame* will be used to define allocentric processing being specifically other-centered (i.e., relative to another or third person), as these terms are often used in studies investigating how individuals adopt the perspectives of other agents within space (Becchio, Del Giudice, Dal Monte, Latini-Corazzini & Pia, 2011; Bukowski, 2014), or in studies investigating distance perception

showing distinctions between object-to-object or other-to-object relations (e.g., Fini et al., 2015).

In reference to altercentric spatial coding, research investigating perspective taking (i.e., the perspective of another person), has suggested differences between first/third person perspectives (at a phenomenal level) and ego/allo-centric reference frames (at a representational or cognitive level; Vogeley & Fink, 2003). First and third person perspective are thought to be centered on an agent's body, and imply egocentric spatial processing. The third person perspective necessitates additional translocation of the egocentric viewpoint. Allocentric spatial processing is however independent from an agent's body and viewpoint. Recent studies have adopted the term *altercentric* to specifically refer to adopting the perspective of another person (e.g., knowing what the other is seeing; Becchio et al., 2011; Bukowski & Samson, 2015). This is in contrast to the term *allocentric*, which is more generic as it can denote object, landmark or other-centered spatial referencing. However, it remains to be understood whether different neural processes are involved in allocentric versus altercentric perception.

As discussed in the previous section, neuropsychological studies investigating unilateral neglect show different manifestations of the neglect. In addition to the different types of neglect already discussed, several researchers have also demonstrated differences in neglect for egocentric and allocentric reference frames, leading to an egocentric (or viewer-centered) neglect versus an allocentric (object-centered) type of neglect (Riddoch et al., 2010; Ting et al., 2011). Here, the different reference frames modulate how spatial attention is allocated in the perception of a scene or to individual objects, and this causes the different forms of neglect. Several neuropsychological tests allow for the differentiation of these types of neglect (e.g., Bickerton et al., 2011), and an elegant study by Riddoch et al. (2010) highlighted the different roles of posterior versus anterior lesions for forms of neglect. Moreover, the temporo-parietal junction (TPJ) and the intraparietal sulcus (IPS) were crucial brain sites associated with allocentric and egocentric neglect.

Behavioral studies also investigated the differences in egocentric and allocentric special processing (Iachini & Ruggiero, 2006; Ruggiero, Ruotolo & Iachini, 2009). For example, Iachini and Ruggiero (2006) tested if proximity judgements were differentially processed under ego- or allocentric perspectives. Participants had to memorize triads of objects that remained visible for 20 seconds. After the visual presentation, they had to provide egocentric (i.e., which object was closest to you?) or allocentric (i.e., which object was closer to the cube?) proximity judgements. Results showed that egocentric judgements were faster and more accurate than allocentric ones, suggesting a primacy for egocentric coding. These different proximity judgements were then investigated in another study using functional Magnetic Resonance Imaging (fMRI) in order to identify their neural correlates (Committeri et al., 2004). While in the scanner, participants saw 3D virtual environments in which different objects were presented in the courtyard of a building. The task required the participant to evaluate which of two objects in the scene (a blue or a green rubbish bin) was the closest to themselves (viewer-centered), to another object (red ball; object-centered) or to a building (landmark-centered; see Figure 1.3, Top). A control task required that they judged which of the two rubbish bins was lying on the floor, not requiring them to process location or distance. Overall, results showed that the viewer-centered condition recruited parietal and premotor regions, whereas judgements centered on external references (object- and landmark-centered) recruited both parieto-frontal and occipito-temporal areas (see Figure 1.3, Bottom). Interestingly, findings from both neuropsychology and brain imaging suggest that the egocentric frame of reference relies on parietal sensory motor networks. In the next section, I will discuss the relations between perception and action, as well as the possible contribution of the motor system in space perception.

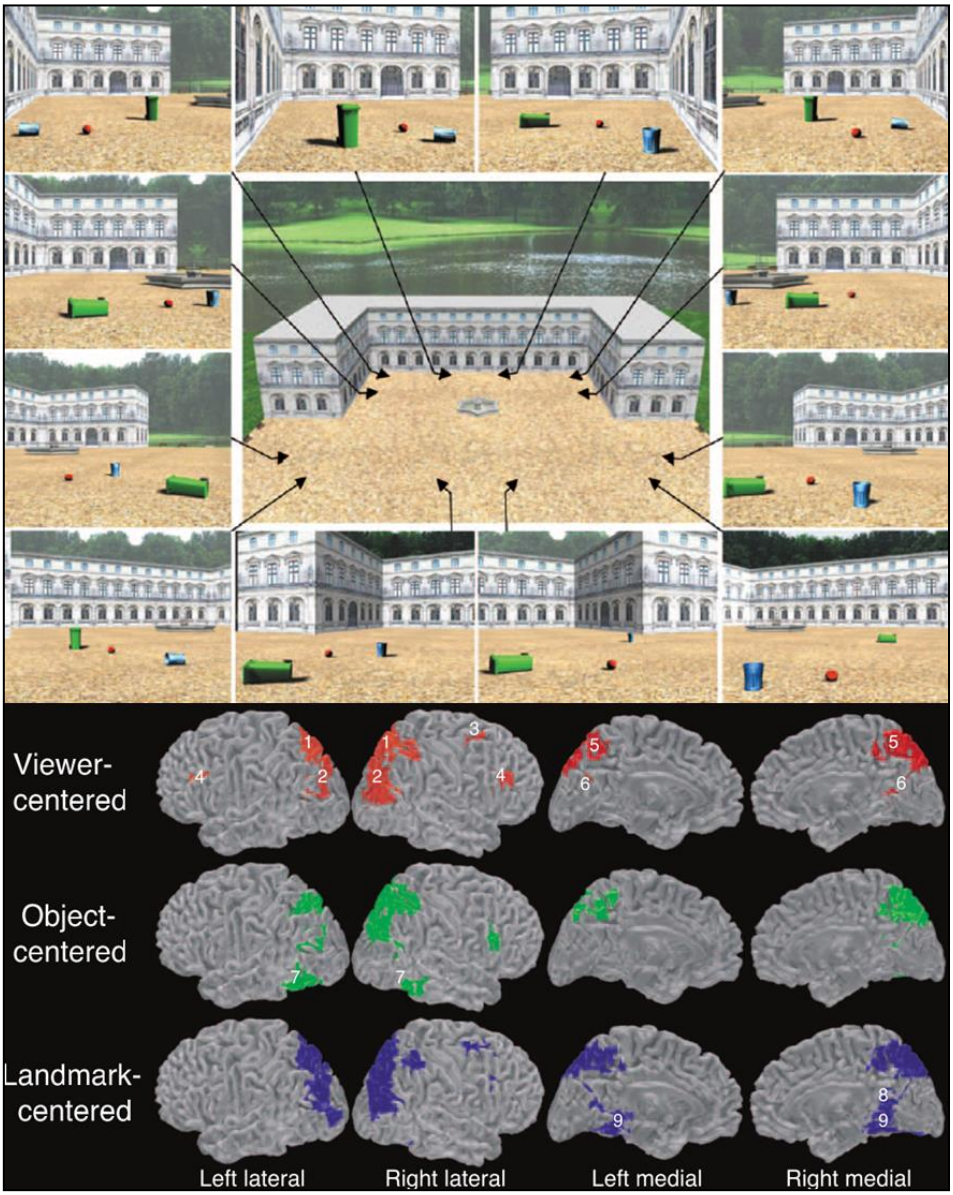

Figure 1.3: *(Top part) Stimuli used for viewer-, object- and landmark- centered proximity judgements; (Bottom part) Brain areas activated during the different proximity judgement tasks controlled with the bin orientation judgement task (adapted from Committeri et al., 2004).*

1.2. Perception and action; their privileged relationship

1.2.1. Perception-action coupling: Roots for embodied perception

1.2.1.1. Vision for action

To interact with the world, human beings permanently make a multitude of different actions. These goal-directed actions are not only crucial when interacting with the external space, but they also allow one to shape the world according to his desires and intentions. They are also vital for interacting with conspecifics, or to serve primary needs (e.g., eating). For actions to be adapted and efficient, a prior perception of the environment and the different elements must be first achieved. For example, when reaching to and grasping a glass of beer, bringing it to the mouth carefully, and delighting ourselves with this wonderful nectar, considerable information must be processed and implemented. The distance between the hand and the glass must be translated into an appropriate reaching movement that transports the hand to the exact distance of the glass, otherwise the glass will be miss-reached or worse, spilled on the floor. Also, the size (diameter) and weight of the glass must be correctly perceived to implement adequate grasping aperture and force, otherwise the glass will not be grasped, or could be dropped on the floor if not enough force is implemented (or even shatters with too much grip force). Finally, the hand must transport the glass to the mouth, calculating the distance between glass and mouth to correctly drink the beer, and not look like a fool by spilling the beverage on our clothes.

The former example nicely exposes an everyday example of an important goal directed action. Much research has been dedicated to the study of reaching and grasping actions (for reviews see Jeannerod, 1997; Jeannerod, Arbib, Rizzolatti & Sakata, 1995), shows that object directed hand actions can be decomposed into a series of movements, with the reaching sequence

being responsible for moving the hand to the object (Burnod et al., 1999), the anticipatory grip formation sequence for opening the hand in anticipation of object contact and, once contact is made with the object, a lifting phase to initiate a subsequent reaching action to move the object to a new location (Castiello, 2005; Jeannerod, 1994, 1999; Jeannerod et al., 1995).

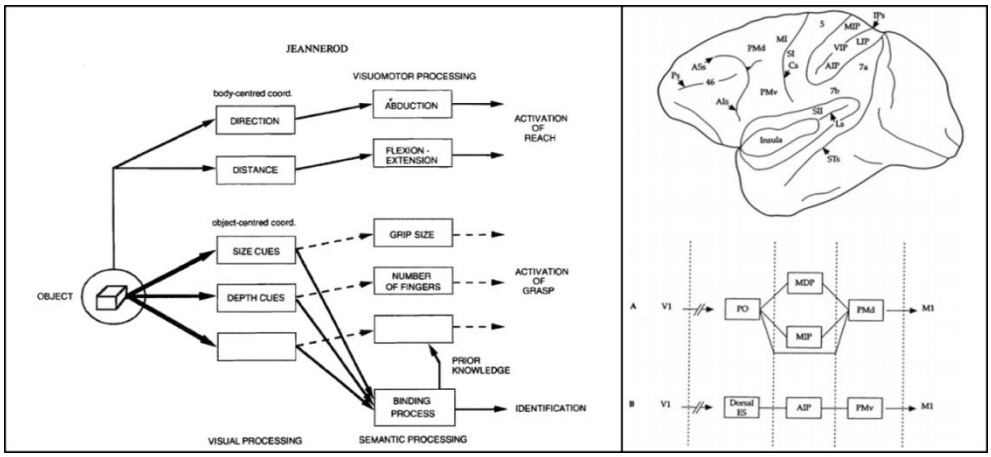

Figure 1.4: *(Left part) Schematic representation of cognitive processes involved in object directed actions (adapted from Jeannerod, 1994); (Right part) Brain areas constituting to the visuomotor channels implied in reaching (A) and grasping (B; adapted from Jeannerod, 1999).*

The cognitive mechanisms assuring a transition from the perception of the object to the implementation of an object directed action have been labeled under the term *visuomotor transformations* (Jeannerod et al., 1995), or *sensorimotor interfacing* (Freund, 2001). Neurophysiological studies on monkeys have brought evidence for the existence of neuronal circuits coding grasping movements in the inferior parietal lobule (for global coding of grasping), and the inferior premotor area (F5; for segmented/sequential coding of grasping; with hierarchies in the motoric implementation of the grasping movements; Jeannerod et al., 1995). A schematized representation of these visuomotor transformations was first proposed by Jeannerod (1994; see Figure 1.4), where a distinction between the reaching and grasping components of object directed prehension was proposed (although interactions between the two components are possible; Jeannerod, 1999;

Paulignan, Frak, Toni, & Jeannerod, 1997). More specifically, the model proposes that extrinsic properties of objects (i.e., their location in space) are coded in respect to body-centered coordinates for the appropriate implementation of reaching movements, whereas intrinsic object properties (i.e., object size or orientation), are coded in object-centered coordinates, and used for grasping movements. Evidence for this separation (among others) was put forward through the study of a patient with parieto-occipital brain damage, who was impaired in the grasping component of object prehension, but had no difficulties for locating objects in space, or for identifying the object (Jeannerod, Decety & Michel, 1994). Therefore, not only did this case study suggest a dissociation for the grasping and reaching components of object directed action, but also a dissociation between the pragmatic processing of object (where is it and how it is interacted with), and the semantic processing of object (what is it; Jeannerod, 1994; Jeannerod et al., 1995; Ungerleider & Mishkin, 1982).

Beyond the dissociation between visuomotor pathways dedicated to reaching/distance and grasping/size processing, another clear and well described dissociation in visual processing is the one between the ventral and dorsal streams. Originally, the visual processing architecture was investigated in neurophysiological studies on monkeys (Ungerleider & Mishkin, 1982) and in humans using Positron Emission Tomography (PET) (Ungerleider & Haxby, 1994). This research showed two major streams of projection from the visual cortex (V1, V2, V3). One projected towards the PC, forming the dorsal stream, and responsible for spatial vision (the 'Where' pathway; mainly magnocellular neuronal networks). The second projected towards the inferior temporal areas, forming the ventral stream, and responsible for object vision (the 'What' pathway; relying on both magnocellular and parvocellular networks roughly equally; Merigan & Maunsell, 1993; Ungerleider, Courtney & Haxby, 1998). Capitalizing on this previous work, Milner and Goodale (1995) proposed the same dissociation between the two different visual systems, but re-defined the dorsal stream as vision-for-action and the ventral stream as vision-for-perception (see Figure 1.5; Goodale, 2014; Goodale & Milner, 1992; Milner & Goodale, 1995).

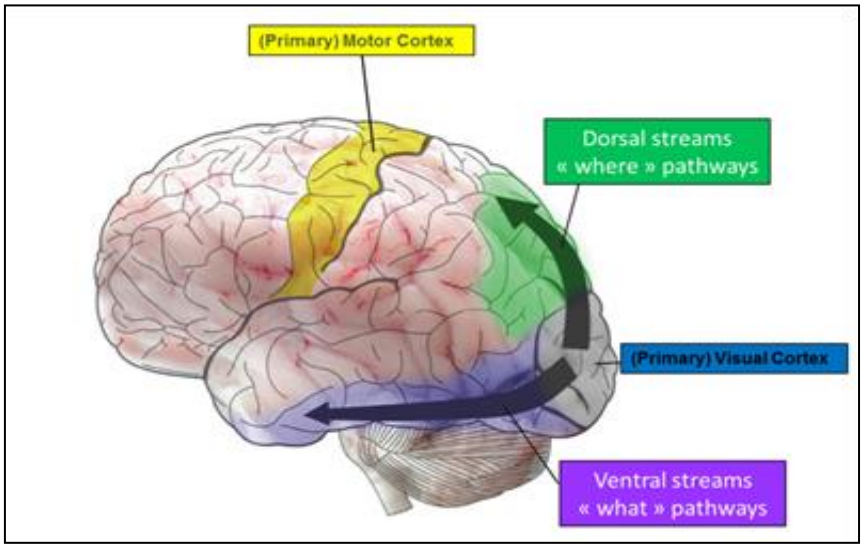

Figure 1.5: *Schematic representation of the two visual pathways involved in perceptual processing (Milner & Goodale, 1995). The dorsal stream is involved in online visual control of goal-directed actions and originates from the primary visual cortex sending projections to the parietal lobe. The ventral stream is involved in the visual identification of the elements present in the environment. Here, the early visual areas send projection to the temporal lobe.*

Evidence of distinctions between vision for action and vision for perception comes from neuropsychological and experimental research. Patients with ventral brain damage can experience visual agnosia (i.e., an inability to visually recognize objects; Bruyer, 1995; Goodale et al., 1991) and patients with dorsal brain damage can experience optic ataxia (i.e., an inability to accurately perform a goal directed action; Goodale et al., 1994). Double-dissociations between two patients, one patient presenting visual form agnosia (patient DF) and the other presenting optic ataxia (patient RV), showed differences in a perceptual shape discrimination task, where DF performed at chance level, but RV performed as well as control participants. However, dissociation was observed in an object grasping task. Now DF performed equal to control participants, making an appropriate grip to an object, whereas RV performed poorly. These findings suggested that vision for perception was not necessary for vision for action (it is not necessarily needed to "perceive" in order to "act"; Goodale et al., 1994). Other evidence for this dissociation comes from the use of visual illusions. For example,

perception and action performance was tested with the Ebbinghaus size-contrast illusion (also known as the Titchener circles, with two centrals circle surrounded by smaller or larger circles, causing the perceived size of the central circle to appear different when the two circles are the same size; Aglioti, DeSouza & Goodale, 1995). Here, the illusion effect was stronger on perceptual judgements made on the size of the central circles than on the measure of maximum grip aperture during central circle grasping (where graspable wooden 3D flat cylinders where placed in the arrays of illusory circles), again suggesting that vision for perception was different from vision for action.

The term *streams* is used to suggest that the ventral and dorsal systems are composed of a collection of networks. Therefore, the two visual systems should not be seen as two unique ways of processing vision (Gallese, 2007), but rather as a multiplicity of dissimilar types of function (e.g., pragmatic versus semantic perception; Jeannerod, 1997) that interact and contribute to each other (Goodale, 2014). In line with this, a further segregation has been proposed that consists of three visual streams; dorso-dorsal, ventro-dorsal and ventral streams (Gallese, 2007). In this suggestion, the dorso-dorsal stream unconsciously monitors the online control of action, while the ventro-dorsal stream participates in the conscious perception of space for action, the representation of action capabilities and the understanding of actions performed by other agents sharing our world. The ventral stream remains as a stream for general perception, not related to action. In the next section, I discuss how the dorsal stream is thought to be implicated in action perception processes.

1.2.1.2. Action observation

Research on brain and cognitive mechanisms involved in action observation and action understanding is so vast that entire theses (e.g., Letesson, 2015; Vannuscorps, 2013) and hundreds of articles are dedicated to the comprehension of their functional mechanisms. Observing the actions performed by others allows us to make sense of behavior, to infer intentions and goals, and to learn new possibilities of action through imitation. These

complex functions appear to engage motor processes emerging from the cortical motor system (Fadiga et al., 2000), and benefit from a particular kind of neuron within the Mirror Neuron System (MNS; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2008). Originally, these neurons were uncovered in primate physiological research within area F5 of the premotor cortex. Neurons in these areas responded both during the execution and observation of object directed hand actions (i.e., if the monkey grabs a piece of food, or observes the experimenter or another monkey performing the same action; Di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi & Gallese, 1996).

Neuroimaging and behavioral studies have extended these effects, bringing evidence for the existence of the MNS in humans (e.g., Buccino et al., 2001). Observing actions performed by different effectors (e.g., head-mouth, like biting an apple; hand-arms, like reaching and grasping a sphere; foot-legs, like kicking a ball) activated the premotor cortex somatotopically (e.g., in a similar configuration to that of the classical motor homunculus; Penfield & Rasmussen, 1952). Interestingly, observed actions directed to an object, or made to no object in the scene (e.g., transitive *vs.* intransitive movements respectively) revealed additional parietal activations for object compared to no object observed actions (again somatotopically organized; rostral part of inferior parital lobe for mouth actions; intraparietal sulcus for hand actions; posterior part of superior parietal lobe for leg actions). These findings extended the primate research by showing the existence of the MNS for different effectors, and suggesting that the mirror neuron system was not limited to the ventral premotor cortex, but should rather be seen as a broader system of diverse neuronal circuits.

Behavioral evidence for the MNS comes for action priming and action prediction studies. Based on the hypothesis that share neural processed between observation and execution should lead to priming, this research typically shows that observing someone performing an action influences the subsequent actions performed by the observer (Brass, Bekkering & Prinz, 2001; Edwards et al., 2003; Salama, Turner & Edwards, 2011). For instance,

if the observer sees a person making unusual reaching movements by exaggerating elevation in space, subsequent reaching actions performed by (observer) participants show an increased upward deviation in their subsequent executed movement kinematics (Hardwick & Edwards, 2011). Action priming has also been demonstrated with grasping force, where participants had to consistently produce 50% of their maximal grip force on a dynamometer after observing a grip force of 0%, 50%, 100%. The results showed that observation of 100% force caused participants to make stronger than 50% grip force responses (Salama et al., 2011). Experiments investigating action prediction show that the observation of action can lead to participants correctly predicting the outcome of the observed action before the goal is complete. For example, Letesson, Grade & Edwards (2015) recently showed a pattern of eye-movements during action observation that facilitated participants making early selections of the action goal, and facilitating or priming (from observation), their subsequent action execution.

Therefore, from this discussion, it might be conceived that the process of action prediction might be related to judging (or predicting) the action capabilities of others, and in doing so, having to determine the limits of their reaching range. Like in prediction, the observer's own sensory-motor processes and MNS might be used to predict the possible sensory motor capabilities of observed actions, made either by the self, or by others (Lamm, Fischer & Decety, 2007; see also Chapter 4 of the present thesis). In the next section, I discuss how action imagery or action simulation might emerge from the cortical motor system, and might provide an underlying cognitive mechanism for embodied space perception.

1.2.1.3. Motor imagery and action simulation

Covert (internal or mental) embodied action simulation has been described as an indispensable dorsal stream process underlying a wide variety of cognitive functions, from action representation, affordance, and action understanding, to spatial perceptual cognition (Gallese, 2007; Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015; Gallese, 2016; Gallese &

Golman, 1998; Glenberg, Witt & Metcaslfe, 2014; Jeannerod, 2001; Proffitt, 2006, 2013; Wilson & Knoblish, 2005; Witt, 2011). A unifying proposal for motor imagery and action simulation was put forward by Jeannerod (2001), where he proposed that the neural simulation of action could be used for a wide variety of cognitive functions that would benefit from understanding the outcome of an action. He defined the terms '*action imagery' or 'simulation'* as the possibility to mentally, covertly and actively simulate or represent an action without any overt behavior (i.e., without action execution). This covert simulation could be considered as analogous to the planning stages of action, where the consequences of actions and their goals are represented, but no action is executed (Jeannerod, 2001).

Evidence on mental imagery comes from experimental paradigms using mental chronometry that demonstrate the close links between action execution and simulation (Decety & Jeannerod, 1996; Decety, Jeannerod & Prablanc, 1989). For example, in a motor imagery experiment, Decety et al. (1989) asked participants to physically walk toward targets placed at distances of 5, 10 and 15 meters in an active condition, or to simply imagine themselves walking to the target in a mental imagery condition. Results showed equivalence between actual and mental walking time measured in both conditions for the participants. This demonstrated equivalence between the imagined and executed actions. Moreover, in a subsequent experiment, they asked the same participants to carry 25kg load with the use of a backpack, and to perform the two tasks again. Results showed that the weight did not influence walking time in the active condition, but increased mental walking time by about 30% (Decety et al., 1989). Therefore, the mental simulation took into account the supplemental effort in doing the walking action, while physical locomotion was adapted to maintain a normal walking speed, unaffected by the effort. Similar research using fMRI tested whether action imagery and execution behaviors would rely on overlapping brain areas (Hanakawa, Dimyan and Hallett, 2008). Here, participants physically executed, or mentally simulated finger tapping movements to number stimuli that instructed finger-tapping sequences of movements. Results showed partially overlapping activity in parietal and motor areas for finger tapping movement imagery and execution. The

authors suggested that motor imagery could be seen as a "*dynamic activation of a 'potential' movement"*, either triggered by an imperative stimulus, or recruited by higher level cognitive processes or volitional simulation, emulation, reactivation or rehearsal (Hanakawa et al., 2008).

As proposed by Gallese (2003; 2007; 2016), online simulation of the body combined with action capability, as well as internal representations of action sequences, may participate to a multitude of other cognitive functions, including space perception (Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015; Fadiga, et al., 2000; Proffitt, 2006, 2013 Witt & Proffitt, 2008). By means of embodied or grounded cognition, perception, cognition and knowledge of space may be rooted in integrated sensorimotor systems, allowing for perceptual judgements based on action simulation (Barsalou, 2008; Coello & Iachini, 2015; Philbeck & Witt, 2015). Therefore, the cortical motor system would not only be dedicated to action implementation, but would also contribute to perceptual processing through embodied sensorimotor simulations (Fadiga et al., 2000; Gallese, 2016). In the next section, I discuss how embodied simulation could be used for the perception of space.

1.2.2. Embodiment of space perception.

1.2.2.1. <u>Perceiving the boundary of peripersonal space.</u>

As discussed in the previous section, action simulation mechanisms originating from the cortical motor system may be used to shape space perception, where covert representations of action generate online calibrations, scaling or constraints that are used for the (immediate) perception of the environment (Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015; Fadiga, 2000; Gallese, 2003, 2007; Rizzolatti et al., 1997). For example, if participants are asked to visually determine (without performing an overt movement), whether an object located in front of them is reachable (thus determining the boundary of peripersonal space; see Section 1.1.2), the perceptual process involved in the decision process is believed to recruit action simulation mechanisms (Coello & Delevoye-

Turrell, 2007). In this sense, mentally simulating online the capabilities of the body actions allows perceivers to simulate whether or not they would be able to reach the object, and therefore, allows them to answer the perceptual question. This simulation would contribute to near-reaching-peripersonal space perception, but not far-out of reach-extrapersonal space. It should be noted that throughout the present thesis, the terms body capability or action capability will be used rather than body and action capacities (with both terms used in the literature). Even though the terms are near-synonyms, capacity is more related to volumes (e.g., the capacity of the water tank), while capability refers more specifically to the concept of 'being able of doing something' (ability, aptitude, potential). In the literature, it is likely that peripersonal space capacity represents the volume of space occupied by peripersonal space. However, in the current thesis, our main focus is on the role of action and the body in space perception, and so capability seems the more appropriate term.

Many studies have investigated peripersonal space perception using the task of reachability judgement (for reviews, see: Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015). Variation of this task requires participants to decide the moment when an approaching target enters peripersonal reaching space (Rochat & Wraga, 1997). The investigation of behavior in these tasks shows that perceived reachability can be influenced by many action execution factors. For instance, the presence of postural or action constrains that change action capability can have a direct impact on reachability judgements (e.g., being seated versus standing up; standing on one or two legs; being seated at lower vs. higher tables, placing barriers preventing reach; augmenting effort with wrist weights; Carello, Grosofsky, Reichel, Solomon, & Turvey, 1989; Fischer, 2000; Gabbard, Cordova, & Lee, 2007; Rochat & Wraga, 1997). Rather like the relation between imagery and action execution discussed in the previous section, manipulation of action capability can moderate how targets are visually judged as reachable (Bourgeois & Coello, 2012), demonstrating that reachability perception uses action simulation processes.

A few years ago, a neuro-cognitive model of space categorization and action selection was put forward by Coello and Delevoye-Turrell (2007; see Figure 1.6). The model argued that experiential body representations (i.e., body orientation and midline representation at a given moment) would contribute to peripersonal space perception using a body-centered (ego-centric) reference frame that uses trunk-centered coordinates in peripersonal space. At the same time, functional body representation coding for action capability would participate to the delimitation of peripersonal space boundary (i.e., determining the maximal extent of peripersonal reaching space). Both processes operating together would allow for internal, pre-reflective or up-stream sensory and motor simulations that contribute to the perception of space (Coello & Delevoye-Turrell, 2007). The important focus of the model was to emphasize the contribution of body and action capability representations in space perception (see also Section 1.2.1.3). They suggested that internal motor representations implied in movement planning, and allowing for the preparation and prediction of goal directed actions, could be used to simulate actions, as well as defining space perception and reachability estimates (Bourgeois & Coello, 2012; Coello & Delevoye-Turrell, 2007; Coello et al., 2008). Described in the model, a prior intention towards a goal triggers the generation of an action plan (inverse model). A copy of this model is then used to predict the outcome of the planned action in terms of sensory variations caused by action execution (forward model). This adjustment relies on prior interactions between sensory processing and experienced or functional body representations that evaluate the cost/benefit or the planned action, as well as the feasibility for achieving the intended goal. The forward model can be used to adjust and refine the inverse model action plan, correcting for predicted problems in execution. Within this adjustment, the goal is the determinant, defined by location in space, object or another person, where or with what or who interaction will take place. The goal object can also elicit affordance processes, where action patterns activate in correspondence to the properties of perceived objects (e.g., orientation, size, shape etc.; Gibson, 1979), but also semantic properties such as the object's potential dangerousness.

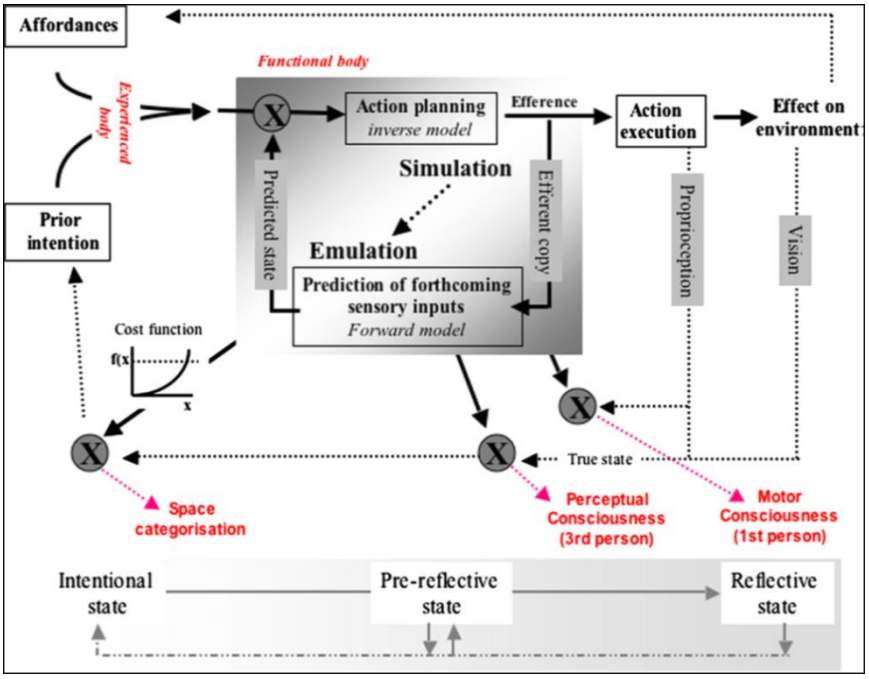

Figure 1.6: *The neurocognitive model proposed by Coello & Delevoye-Turrell (2007) proposes that the categorization of reachable space benefits from action simulation processes. A prior intention will trigger the elaboration of an action plan, used for both action execution and action prediction. Predictive processes would code the sensory consequences of the action using body and external representations of space. Altogether, these simulation mechanisms would allow for a conscious access to action capability involved in space perception.*

In support of Coello and Delevoye-Turrell (2007) model, recent studies have demonstrated that the perception of reachable space is partly derived from motor representations, with support from methods using action adaptation (Bourgeois & Coello, 2012), Transcranial Magnetic Stimulation (TMS; Coello et al., 2008) and fMRI (Bartolo et al., 2014). Bourgeois and Coello (2012) showed that with the repetition of distorted visual feedback during pointing movements, it was possible to reduce or extend perceived reachable space. For example, the visual feedback of pointing movements was shifted further away from actual position, trial after trial, so that the participant believed the target to be further away, despite reduced amplitude of action. This manipulation caused the visual perception of peripersonal space boundary to also shift further away, suggesting a remapped

correspondence between action and the believed spatial capability of the action. These findings demonstrate that the visual perception of reaching space must be derived from the participant's current action experiences (Bourgeois & Coello, 2012). Interestingly, when the shift of the visual feedback was random (sometimes further away, sometimes nearer from participant's body), a subtle reduction of perceived peripersonal space extent was observed, as if participants adopted a more conservative strategy that compensated for noise and uncertainty in their action-space correspondence (Bourgeois & Coello, 2012).

Further support to Coello and Delevoye-Turrell (2007) model came from studies using cognitive neuroscience methods. Firstly, Coello et al., (2008) showed that applying TMS over the left hemisphere hand motor cortex moderated response latencies in a reachability judgement task, in particular for targets placed near the boundary of peripersonal space. This suggested a role of the motor cortex in the perception of space, particularly at the edge of peripersonal space. These effects were replicated in neuroimaging data, where participants performing reachability judgements on virtual stimuli at different egocentric distances showed activation of a fronto-parietal-cerebellum network, relative to other control perceptual tasks (Bartolo et al., 2014). Interestingly, this pattern of activity was similar to that observed during action execution and motor imagery tasks (involving activity of the MNS; Hanakawa et al., 2008). Furthermore, Bartolo et al. (2014) showed a correlation between the fronto-parietal-cerebellum activation and the proximity by which the target approached the extent of peripersonal space, providing further support for the role of action processes in the perception of space. In the next section, I will extend this introduction of body representation and action simulation for the perception of distance.

1.2.2.2. Distance estimation and action simulation

Over the last few decades, a great number of studies have brought forward the idea that distance space perception benefits from internal body and action capability representations (Linkenauger, Bulthoff & Mohler, 2015; Proffitt, 2006; 2013; Proffitt & Linkenauger 2013; Philbeck & Witt, 2015;

Witt, 2011). For example, Proffitt (2006) argued that perception is an embodied process using body representations in actual and situated states to derive perception. This proposal argued that visual information used for perceiving the external environment is based on angular projected cues on the retina, and that as the body moves through space, the orientation parameters of these visual angles change (Gibson, 1979; Proffitt, 2013). Knowing where the body is in space, along with knowing the body's action capabilities, would allow for an interpretation of the moving visual information, making a 3D representation of the space (Gogel, 1963, 1964; Merleau-ponty, 1945; Proffitt, 2013). This interpretation of the mechanism underlying distance perception is not quite the same as the interpretation of reachability perception, though the proposal for both mechanisms states that body and action calibrate perceptual processes, demonstrating a similarity between the two types of space perception task.

As reviewed earlier in this introduction, there are many visual and ocular cues that can be used by the perceiver to estimate distance (Cutting & Vishton, 1995; Foley, 1978, 1980; Loomis et al., 2012). Research on the impact of action on distance perception has been carried out by a number of authors (e.g., Morgado et al., 2013; Osiurak, Morgado & Palluel-Germain, 2012; Proffitt, Stefanucci, Banton & Epstein, 2003; Witt & Proffitt, 2008). For example, similar to the experiment of Decety et al. (1989), Proffitt et al., (2003) asked participants to estimate a total of 12 egocentric distances ranging from 1 to 14 meters, either while wearing a backpack with weights totaling one fifth of their own body weight, or while not wearing any backpack. Results showed than verbal distance estimates were higher in the group of participants wearing backpacks than in the group without the backpack, suggesting that body load increased their action effort, and this had an impact on their perception of distance. Similarly, Witt, Proffitt and Epstein (2004) asked participants to throw balls toward targets at a distance of 4, 6, 8 and 10m, and then to estimate the egocentric distance of targets. Results across several experiments showed that any increase in effort associated with throwing the ball (e.g., manipulated weight of the ball), induced an increase in distance estimates. Therefore, it seems that the physical effort associated with performing action directed toward a target

(walking or throwing), influenced the estimation of that target's distance. One explanation of this finding might be from a generalized system for magnitude processing (Walsh, 2003; see Section 1.3.1.), where magnitudes of weight and distance would share overlapping representations or cognitive processes that mutually influence estimation.

In the previous examples, the emphasis was on effort in action. However, some studies have focused on the role of action simulation mechanisms in distance perception; the action-specific account of perception (Philbeck & Witt, 2015; Witt, 2011). This model proposes that on top of crucial visual-spatial / depth cues (i.e., absolute disparity; angular declination; see Cutting & Vishton, 1995; Section 1.2.1.), some non-visual factors may contribute to the final perception of distance, among which action capabilities, effort and expertise. The role of action factors in distance perception, as proposed by the action-specific model of perception has raised fierce debate (Firestone, 2013). It is argued that output-level factors (demand biases, experimenter, or memory effects) that take place during response production are not sufficiently taken into account in the action-specific account of perception. Further, it is argued that action simulation may not be necessary for distance perception, and that "top-down" effects of action factors, such as effort, would influence perception is unlikely (Durgin et al., 2009; 2012; Firestone & Scholl, 2014). Finally, the model does not take into account the medium used to report verbal estimates of distances or sizes. Indeed, the cognitive mechanisms involved in the estimation of spatial magnitudes seem very intricate with those underlying the representation and manipulation of numbers and numerical magnitudes. Estimating a distance requires the translation from a non-symbolic distance to a symbolic label (i.e. the number of centimeters; Crollen, Grade, Pesenti & Dormal, 2013). The various cognitive mechanisms involved in numerical magnitude processing will be addressed in the next section.

1.3. Space as a collection of magnitudes

1.3.1. Magnitude coding of space

The relation between cognitive processes dedicated to space processing and magnitude is perhaps not surprising, as environmental space is sometimes described as a collection of points, lines, contrasts, shapes, areas, surfaces, textures that can be coded as a function of their intensity or magnitude. The physical properties represented in different dimensions of the physical world are referred in the literature as *prothetic*[1] (i.e., quantifiable dimensions or perceptual continua that can be experienced as *how much, more than, less than, the amount of*, etc.; Stevens, 1957; Walsh, 2003; or sensory magnitudes, e.g., light intensity, sound loudness, pressure on the skin, pain intensity etc.; Poulton., 1979). The cognitive processing of distances, durations, sizes, quantities and other magnitudes are of great importance for action execution and external world perception (Dormal & Pesenti, 2012; Jeannerod, 1997; Walsh, 2003). In this thesis, we will use the terms *magnitude* to generally refer to all perceptual continua regarding their intensity, and *magnitude coding or processing* to refer to their treatment, apprehension, use and manipulation (e.g., quantifying judgements, verbal estimation of magnitudes; production of magnitudes, etc.).

A Theory Of Magnitude (ATOM; Bueti & Walsh, 2009; Walsh, 2003) has proposed the existence of a general magnitude processing system engaged in representing and processing distances, sizes, numerosities (expressed by collections of individual elements or discrete quantities), durations and other magnitudes which could all imply a common shared metric system coding magnitude independently of the dimension (Walsh, 2003; see Figure 1.7). The ATOM model was partly based on literature investigating time, space and number magnitudes, showing that their cognitive processing relied on overlapping neural processes in the parietal cortex.

[1] Stevens (1957) also describes a second type of perceptual continua : *methatetic*, which refers to continua linked to position (*what kind, where, which direction*)

This is illustrated by studies investigating conjointly, the processing of different magnitudes, as well as their mutual associations and interactions (see also Section 1.3.2.), and suggesting partially overlapping, but also independent cognitive mechanisms that underlie the processing of magnitudes (Bueti & Walsh, 2009; Dormal & Pesenti, 2012; Walsh, 2003). One important aspect of the model states that sensorimotor transformations taking into account information about time, space and quantity in interactions with the environment are crucial for magnitude coding (see also Section 1.3.3.). This suggests that in order to perceive space, magnitude processing would occur in PC and prefrontal areas dedicated to perception and action sensorimotor transformations (Bueti & Walsh, 2009; Dormal & Pesenti, 2012; Freund, 2001; Gotlieb, 2007; Walsh, 2003; see also Section 1.2.1.) This does not suggest that the PC activity involves perceptual-motor processes, but rather that some of the perceptual-motor processes in these brain areas include processing of magnitudes.

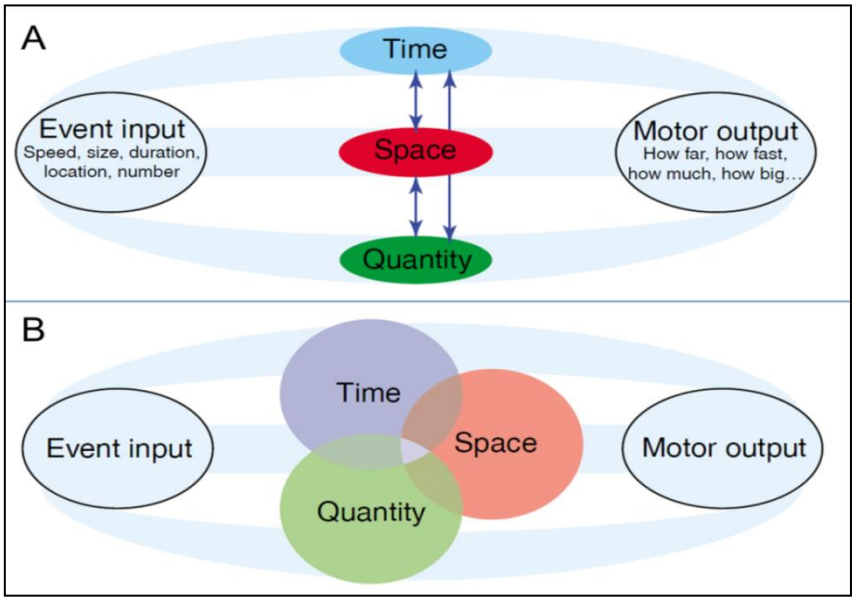

Figure 1.7: *A Theory of Magnitude (ATOM) models proposals (from Walsh, 2003; see also Bueti & Walsh, 2009). Version A shows separate processing of the three magnitudes which comparison is done each using their own individual metric and B shows, in line with the ATOM proposal, intricate processing of the three magnitude sharing a common metric.*

Evidence for the ATOM model can be drawn from behavioral and psychophysical studies investigating magnitude estimation and categorization, and in the comparison of sensory magnitudes (Crollen, Grade, Pesenti & Dormal, 2013; Dormal & Pesenti, 2012; Poulton 1967; 1979; Stevens, 1957). Half way through last century, the focus of the literature was in psychophysical studies that established laws based on recurrent biases observed during quantifiable judgements (e.g., loudness, brightness, visual distance, taste, visual length, visual area, duration, lightness, shades of gray, finger span, numerousness, heaviness, visual velocity, visual flash rate…etc.; for reviews see Poulton, 1967; 1979; Stevens, 1957). Many of these laws assumed that *visual space* (i.e., the space perceived, experienced and represented) was a distorted transformation of *physical space* (i.e., the reality; Gilinsky, 1951). For example, the Weber-Fechner law predicted that if physical-sensation intensity of a stimulus increased, the response estimates and variability would also increase following a scalar variability principle based the relation between sensation intensity and perceived intensity (e.g., Crollen, Castranovo & Seron, 2011). The Weber-Fechner law also explained the distance effect observed in comparison and categorization tasks with various magnitudes (e.g., length, size, duration, tonality, luminosity and even with animal ferocity; for a review see Dormal & Pesenti, 2012). This distance effect was observed when comparing two magnitudes, or when categorizing a magnitude. It refers to the fact that the greater the difference between the two compared intensities, the easier (faster) their discrimination. Studies have also revealed that conflicting or incongruent situations between two different magnitudes expressed in one stimulus (e.g., array or line made of dots with quantity of dots and the space/area occupied by those dots being two different magnitude) can lead to interference in the processing of the other (Crollen, Castranovo & Seron, 2011; Dormal & Pesenti, 2007, 2012b; Dormal, Seron & Pesenti, 2006; Piazza et al., 2004; Gebuis & Reynvoet, 2012). Indeed, manipulating spatial properties of dot arrays (e.g., size of the dots, inter-dot distance, total surface occupied) influences the estimation or comparison of these numerosities. Interestingly, spatial processing can also

interact with the processing of symbolic numbers (e.g., comparisons, random generation). I will discuss this factor in the next section.

1.3.2. Number space associations

Studying the cognitive processes involved in the mental representation and manipulation of numbers (i.e., numerical cognition) is primordial since we live in a numerical world where numbers are used to communicate about, and describe the magnitudes of the environment (Pesenti, 2012). Indeed, to wake up the morning, we need to correctly set our alarm clock to a numerical point in time, and then we need to check the expiration date of the milk, otherwise our breakfast could turn disastrous. While driving, our speed must be monitored to avoid breaking the law, as well as how many kilometers we can travel before needing to refill at the gas station. We also check how much money is left on our bank account, to be sure to be able to eat during the remaining days of the month. These particular numerical symbols, and the magnitudes they represent, have been used for millennia, in many different cultures, and under numerous possible formats (see Ifrah, 1981).

It has been proposed that the internal representation, processing and manipulation of numbers map onto an analog non-symbolic magnitude representation. The Triple code model of Dehaene (1992; see Figure 1.8) proposes the existence of three distinct but related categories of mental representation (two symbolic and one non-symbolic). First, the visual Arabic number form (symbolic) refers to a visual representation like Arabic symbols (e.g., "5"), accessed in parity judgement or multi-digit operations (e.g. the combination of several digits to represent numbers above 9 using a specific lexicon and a defined syntax, where 1056 is different from 6501). This visual number form is obviously not exclusively Arabic, as other cultures use very diverse symbols having their own lexicon and syntax (e.g., Japanese: 五; Hindi: ५; Roman: V). Second, the auditory verbal word frame (symbolic) refers to the specific words used to describe numbers (e.g., "*five"*). This representational format was developed for linguistic processing of verbal numerals allowing for auditory and visual (reading)

comprehension, spoken (articulatory) and written (orthographic) production of verbal numerals. According to the triple code model, the two symbolic representational formats do not convey semantic information about numerical magnitude. The meaning of numbers is rather handled by the third representational format, the analog magnitude representation (non-symbolic) that supports the semantic representation of numbers underlying the comparison of two different numerical magnitudes (e.g., knowing that 87 is larger than 69), or the approximation of a number of elements within a collection (e.g., estimating how many biscuits are left in a transparent cookie jar). It was proposed that numerical magnitude would be represented on a mental continuum where depending on the activated zone within the continuum, the represented magnitude would be small or large. This continuum is commonly referred to as the *mental number line*. Finally, the model assumes bidirectional transcoding pathways between the different representations, allowing for the conversion from one form to another, and providing non-symbolic significance in terms of magnitude to a priori meaningless symbols.

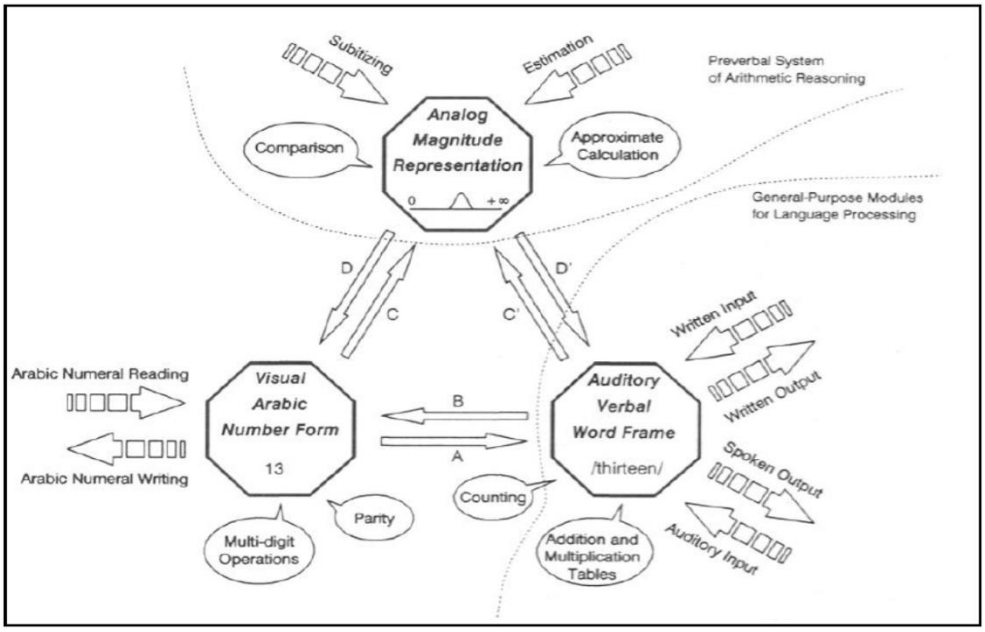

Figure 1.8: *The triple code model of number processing architecture (Dehaene, 1992).*

The mental number line corresponds to the idea that numerical magnitude can be represented and mapped onto a spatial continuum that is logarithmically compressed and oriented from left to right (i.e., starting on the left side of space with small numbers, and with numbers becoming increasingly larger with more displacement towards the right side of space). The logarithmic compression was proposed to take into account the Weber-Fechner law (see Section, 1.3.1.), that explains distance and size correspondence effects (Gallistell & Gelmann, 2000; Moyer and Landauer, 1967). For example, the subjective distance between "65" and "68" will seem less than between "3" and "6" although the numerical distance is identical, suggesting a progressive compression of the mental continuum. Small numbers occupy wide portions of the mental number line, while large numbers will occupy narrower portions as their numerical magnitude increases (Gallistell & Gelmann, 2000; Moyer and Landauer, 1967).

Over the last few decades, a myriad of spatial congruency effects have been reported in experimental tasks involving number processing. One of the most known behavioral interactions between the processing of numbers and space is the Spatial-Numerical Association of Response Code effect (*SNARC effect*; Dehaene, Bossini & Giraux, 1993). During parity, magnitude or color judgements about a displayed number, left-sided compared to right-sided response keys are pressed faster in response to small numbers, while the opposite effect occurs in response to large numbers (Hubbard et al., 2005; Wood, Willmes, Nuerk & Fischer, 2008). These associations are not only seen with hand or finger responses made on computer keyboards, but have also been reported with saccadic responses (Schwarz & Keus, 2004), pointing movements (Fischer et al., 2003a) and head movement (Loetsher & Brugger, 2008). Similar effects have also demonstrated that processing numerical magnitude can cause an implicit reorientation of visuo-spatial attention, whereby numbers presented centrally induce an attentional bias to the left side of space if they are small and to the right side of space if they are large. This attentional shifting was originally observed during Posner-like attentional tasks (Fischer, Castel, Dodd & Pratt, 2003b; Galfano, Rusconi & Umiltà, 2006), where a number was used as a central endogenous cue. These effects were thought to result

from attention in visual space shifting leftward with the processing of small numbers, and rightward with the processing of large numbers, explained by analogous attentional mechanisms that would be involved both in physical and mental number space (Ranzini et al., 2015, 2016). In support of this argument, similar effects were found, but in an opposite direction, whereby observing leftward or rightward gaze movements (known to automatically trigger an attentional shift toward the gaze direction; Friesen, Moore, & Kingstone, 2005; see also Letesson et al., 2015) influenced random number generation. For example, observation of leftward gaze led participants to randomly produce more small numbers compared to the observation of rightward gaze (Grade, Lefèvre & Pesenti, 2013).

This tight coupling between numbers and space can also be found with the investigation of numerical cognition in unilateral spatial neglect patients, who show impairments in orienting their attention towards stimuli or representations in contra-lesional space (Heilman, 1979; Zorzi, Priftis, Meneghello, Marenzi & Umiltà, 2006; Zorzi, Priftis & Umiltà, 2002). When asked to perform a standard comparison task in which they had to judge a number as smaller or larger than a fixed reference (e.g., *5*), patients with left unilateral neglect showed slower responses for numbers smaller than the referent (i.e., 4 and 3; just on the left on the numerical continuum). This bias was shown to move with the referent when comparisons were made with "7" as the referent, now with responses for smaller numbers (6 and 5) being slowed down (Vuilleumier, Ortigue & Brugger, 2004). These findings suggest that neglect does not alter the representation of numbers *per se*, but rather induces a failure to orient attention toward the left side of the mental number line relative to the central point of the representational space (Bisiach & Luzzati, 1978; Vuillemier et al., 2004).

Despite a clear majority of these number space associations being reported on a horizontal or left-right continuum, these associations have also been observed on other dimensions of space, such as in the vertical or sagittal spatial axes (for a review, see Winter, Matlock, Shaki & Fischer, 2015), but also with physical size or proximity (Henik & Tzelgov, 1982; Santens & Gevers, 2008). Indeed, alternative SNARC effects have been observed with

down-up organized responses keys settings, where down responses were faster in response to small than large numbers (Gevers, Lammertyn, Notebaert, Verguts & Fias, 2006; Ito & Hatta, 2004). Moreover, SNARC like effects reported with saccadic responses also showed that eye movement initiation speed was moderated by number magnitude, with small numbers causing faster initiation of downward saccades, and large numbers causing faster initiation of upward saccades (Schwarz & Keus, 2004). Similarly, the observation of downward gaze induced an increase of random small number production compared to observation of upward or neutral (static) gaze observation (Grade et al., 2013).

Other literature supports these number space effects. Using a numerical stroop task, Henik and Tzelgov (1982) showed that when participants judged the magnitude or the physical size (i.e., font/police size) of numbers presented on a screen, the physical size of the number influenced the processing speed of magnitude as a function of congruence. Hence, numerical magnitude influenced the speed of judgement responses based on font size. Therefore, not only spatial position, but also size of the stimulus interacts with numbers processing. Beyond this numerical stroop task, number space associations in relation to size have also been investigated in relation to object dimension and grasping aperture. In the next section, I will discuss the relation between action and number processing.

1.3.3. Grasping and reaching numbers

In embodiment theories, it is proposed that numbers and other magnitudes might be mentally represented, at least partially, through sensorimotor mechanisms, where numbers and actions share common cognitive processes dedicated to magnitude processing (Lindemann, Abolafia, Girardi, & Bekkering, 2007). In ATOM (Bueti & Walsh, 2009; Walsh, 2003), a generalized system integrating different components of an input (e.g., size and location of an object) was proposed to implement an appropriate motor output (e.g., grip aperture amplitude or reaching trajectory). Accordingly numbers may acquire part of their semantic meaning by being mapped on these magnitude representations arising from sensorimotor transformations.

In support of this embodied view of number meaning, interactions between finger grasping actions and number processing have been reported, with numerical magnitude processing influencing the kinematics of grasping movements (Andres, Ostry, Nicol, & Paus, 2008; Lindemann et al., 2007; Moretto & di Pellegrino, 2008), or vice versa, grasping action observation influencing number processing (Badets, Bouquet, Ric, & Pesenti, 2012; Badets & Pesenti, 2011). For example, studies showed that precision grip actions to small objects were facilitated by small number processing, while power grip actions to larger objects were facilitated by large number processing (Lindemann et al., 2007; Moretto & di Pellegrino, 2008). Other studies have shown that semantic information about magnitude can also influence planning and kinematics of reach to grasp actions (e.g., Gentilucci & Gangitano, 1998; Glover & Dixon, 2002; Glover, Rosenbaum, Graham, & Dixon, 2004). When participants were required to pick up objects (e.g., rectangular solids) with magnitude words written on them, the amplitude of the grip during the early stage of the grasp was influenced, with grip aperture being smaller for objects printed with the word "short" compared to the same sized objects printed with the word "long" (Gentilucci & Gangitano, 1998; Glover & Dixon, 2002).

A fronto-parietal network including the intraparietal sulcus (IPS) has been suggested to process numerical magnitude and physical size (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Pesenti, Thioux, Seron & De Volder 2000; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Santens, Roggeman, Fias, & Verguts, 2010) as well as to be involved in the implementation of grasping hand movement (Burnold et al., 1999; Castiello, 2005; Culham & Valyear, 2006; Ehrsson, Fagergren, & Forssberg, 2001). However, grasping might not be the only action related to magnitude processing. In Jeannerod's (1997) model of human prehension, visuomotor channels coded size for grasp preparation, and distance for reaching actions. This might suggest that size magnitude may be associated to size-number processing, whereas distance magnitude may be associated to space-number processing, although this relation has so far, not been investigated.

1.4. Outline of the thesis

In this introduction of the thesis, I provided a review of the literature in three main sections, focusing on a discussion of the potential contribution of motor and magnitude processing in the perception of space. I argued that space perception is optimized and adjusted by the integration of multiple sources of information and cognitive sensory-motor processes. I suggested that manipulation of action capability and numbers processing both affect spatial cognition. Moreover, I reviewed various findings suggesting similarity and proximity in the pattern of brain areas involved in the representation of space(s), goal directed actions, numbers and sensory-motor contingencies (Andersen et al., 1997; Dehaene et al., 2003; Dormal & Pesenti, 2012; Gotlieb, 2007; Freund, 2001; Goodale & Milner, 1992; Pesenti et al., 2000; Simon et al., 2002; Ungerleider & Mishkin, 1982). In general, all of the different cognitive processes reviewed, activated or used the dorsal-stream network. It remains debated whether there is a functional reason for this proximity, or whether it a mere coincidence. Common or overlapping magnitude coding mechanisms seem to be involved in a wide range of cognitive processes (Walsh, 2003). From behavioral priming effects (e.g., the SNARC), it is suggested that number space representations appear to share overlapping cognitive processes. Support for this comes from studies showing that the physical size of a number influences the processing of its numerical magnitude, and that magnitude processing influences hand responses lateralized in space. In this thesis, I aim to build on this literature in order to investigate the relations between number, magnitude, action and space.

In the empirical part of the thesis, Chapter 2 will investigate the interactions between spatial and numerical processing, with a particular focus on the near-far dimension of space in comparison to horizontal left-to-right space. Egocentric distance will be used as the fundamental component of external space perception, with investigations centered on the bi-directional relations between number representation and space. We will also explore their associations and interactions regarding near and far spaces along the sagittal axis.

From Chapter 3, I will investigate the role of the body and action capability in spatial cognition, and whether action contributes, constrains or calibrates the perception of external space. I will test whether space perception benefits from the ability to mentally and covertly represent action capabilities in embodied action simulation processes (Gallese, 2016). These simulation processes are considered to play a role in determining the boundary of the spatial area lying within reaching capability, and provides a means to investigate space perception using reachability judgements (i.e., visually determining if a target object can be reached or not without any walking behavior; Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015). In parallel, an action-specific account of perception inspired by the ecological approach of perception (Gibson, 1979) suggests that individuals perceive elements of the environment (e.g., distances, sizes, geographical slant) as a function of their ability to interact with them (Philbeck & Witt, 2015; Proffitt, 2006, 2013; Witt & Proffitt, 2008). In this sense, reaching action simulation could participate to distance estimation by providing a calibration metric that scales the surrounding external space in reference to body- and action-based coordinates.

Empirical Chapters 3, 4 and 5 will investigate reachability judgement and distance estimation with the same group of participants. Chapter 3 will test if motoric dual tasks (e.g., executing repetitive squeezing movements on a foam ball) interfere with dynamic action simulation processes, leading to a disturbance in spatial processing (Witt & Proffitt, 2008). If the assumptions presented in the previous paragraph are correct, then interfering with action simulation processes should impact both reachability judgement and distance estimation similarly. The rationale here is that the cortical motor system will be engaged in both execution and simulation of actions, causing a competition of available motor and cognitive resources. Based on studies showing overlapping mechanisms and brain regions for action execution, action planning, simulation and motor imagery, a concurrent motor dual task should make internal/covert action simulation less efficient.

Chapter 4 will test the relation between altercentric (other-centered) space perception and action simulation. Here we aimed to observe the effect that

the presence of another person in a scene has on distance estimation (Fini et al., 2015), as well as how reachability judgement is performed when centered on another person (Fischer, 2003; Lamm et al., 2007). Two different body postures of an actor were used to evaluate the impact of different static body information on altercentric reachability and distance estimation tasks. Furthermore, the impact of observing the actor performing movements was investigated in both tasks. This was done to evaluate whether acquiring dynamic action representations of the actor influenced the perception of altercentric space.

For the purpose of Chapter 5, a virtual environment was created where it was possible to virtually augment the action capabilities of a user with the use of virtual reality technology (Linkenauger et al., 2015). More specifically, different virtual distortions were made possible in order to test if the augmentation of hand reaching capabilities (dynamic body capabilities) and the augmentation of hand size (static body information and body proportion) would differentially influence space perception. It was expected that an increase in reaching action capabilities would impact the perception of the virtual environment's space, measured by reachability and distance estimation.

Finally, Chapter 6 will discuss the main findings of the empirical chapters of the thesis in relation to three main thesis objectives, and in relation to the general literature review presented here in Chapter 1. The first objective will be to investigate how distance and number processing involve magnitude coding, and how distance and number dimensions interact with each other when processed independently versus together. The aim is to provide new understanding about the potential overlapping cognitive processes underlying position and number processing in horizontal and sagittal space (Chapter 2). The second objective will focus on how body capability representation and action simulation contribute to space perception by providing a reference point (origin), a calibration metric (scaling) and a delimitation of subspaces (peri- vs extra-personal space). If space perception relies on stimulation, moderating motor processes or action capability through interference (Chapter 3), observation (Chapter 4) and virtual re-

calibration (Chapter 5) should moderate both reachability and distance perception. The final objective will be to investigate the underlying mechanisms and cognitive functioning of action simulation. It remains unclear whether the motor simulation of reaching movements is based on long-term fixed body capabilities representation or whether body capabilities representation is continuously recomputed and adapted online. Empirical Chapters 3, 4 and 5 will investigate the flexibility and adaptability of action simulation system by moderating body proportions capabilities. Chapter 6 will end with a description of the methodological limitations of the research and concluding discussion of future research perspectives that could test and extend the findings of the thesis.

CHAPTER 2:

GOING BEYOND THE SCREEN: BIDIRECTIONAL NUMBER SPACE ASSOCIATIONS ON SAGITTAL AND HORIZONTAL AXES

Abstract

Various findings reported in the scientific literature suggest that numbers may be mentally represented on a visuo-spatial continuum, with small numbers associated with left, and large numbers with right sides of horizontal mental space projected onto external space. However, number space associations have also been observed with vertical and sagittal lower-upper and near-far axes, where the lower and near parts of space are associated with small numbers, and the upper and far parts of space with large numbers, suggesting that the number space associations are not restricted to the horizontal axis. In the present study, we investigated whether bidirectional space-to-number and number-to-space associations would manifest similarly or differently on the horizontal and sagittal dimensions of space. Forty-eight participants were individually tested. They sat in front of a table that was used as a projector display surface, on which numerical stimuli (numbers 1 to 9, except for 5) were displayed at different spatial locations (i.e., on the left, right, near, far from a central fixation position). Participants were assigned to one of three experiments, and asked to: (1) make magnitude judgements on the numbers by making a standard comparison to 5; (2) report the perceived location of the stimulus, and; (3) perform both location and magnitude judgements alternately within the same trial block. Experiment 1 showed significant number space interactions for both horizontal and sagittal axes, whereas Experiment 2 only showed a number space interaction for the sagittal axis, with responses being quicker to small numbers in near space and to large numbers in far space. Experiment 3 also showed significant number space interactions, again for both axes as in Experiment 1. Altogether, these number space associations show that both distance and numbers might benefit from, and share overlapping cognitive processes dedicated to magnitude representation. These findings are discussed with the aim to constrain current models of number representations.

* *This chapter is an adapted version of*: Grade, S., Edwards, M.G., & Pesenti, M. (In preparation), Going beyond the screen: bidirectional numbers space associations on sagittal and horizontal axes.

2.1. Introduction

Behavioral studies investigating the interactions between space and numerical magnitude processing have repeatedly shown that the two factors moderate each other, suggesting that they are processed by shared (parietal) brain networks (Hubbard, Piazza, Pinel & Dehaene, 2005). The explanation typically given for the overlapping processes is based on the idea that the representation, processing and manipulation of numbers would benefit from visuospatial and attentional cognitive processes (Fischer, Castel, Dodd & Pratt, 2003; Ranzini, Dehaene, Piazza & Hubbard, 2009; Ranzini et al., 2015; Ranzini, Lisi & Zorzi, 2016; Schuller, Hoffmann, Goffaux & Schiltz, 2014). These processes would allow for a representation and manipulation of numerical magnitude along a spatial mental number line, or even within a mental number space ordered by magnitude (Dehaene, Bossini & Giraux, 1993; Grade, Lefèvre & Pesenti, 2013; Restle, 1970; Seron et al., 1992; Winter, Matlock, Shaki & Fischer, 2015). It has also been proposed that number and space processing could be supported by common magnitude coding cognitive processes. Indeed, a theory of magnitude (ATOM; Bueti & Walsh, 2009; Walsh, 2003) postulates that when perceiving distances, sizes, durations, quantities or other prothetic dimensions (Stevens, 1957), a generalized magnitude coding system underlies all of these cognitive representations. The recruitment of this common cognitive mechanism during the processing of spatial and numerical dimensions would lead to interferences or associations between the two related dimensions if processed concurrently.

A frequently evoked argument to support number space associations is the so called Spatial Numerical Association of Response Code effect, more commonly referred to as the SNARC effect. The effect is frequently observed with parity judgement or magnitude categorization tasks. These tasks require participants to judge the parity (*is it odd or even?*) or the magnitude (i.e., *is it smaller or larger than a referent number?*, usually 5) of a single number presented individually on a computer screen by using lateralized key presses on a keyboard (e.g., if odd/even or small/large press

the left/right response key). Participants typically respond faster with left-sided than right-sided key press responses to small numbers, and faster with right-sided than left-sided key press responses to large numbers (Dehaene et al., 1993). Number space interactions have been reported extensively in the literature, for various experimental set-ups and input modalities (Nuerk, Wood & Wilmes, 2005), for different effectors used for different lateralized responses (i.e., manual or saccadic responses; Dehaene et al., 1993; Schwarz & Keus, 2004), or for different response types (e.g., for manual vs. verbal spoken responses; Gevers et al., 2010; Kramer, Stoianov, Umilta Zorzi, 2011; Stoianov Kramer, Umilta & Zorzi, 2008). Interestingly, the influence between numbers and space is bi-directional. Number processing moderates lateralized responses or visuo-spatial attention orientation (e.g., Dehaene et al., 1993; Fischer et al., 2003; Galfano, Rusconi & Umiltà, 2006), and space processing moderates number comparison (Kramer et al., 2011). For example, Kramer et al. (2011) showed that parity judgement and number comparison were influenced by the presentation of lateralized visual cues, with delayed verbal responses to small (*vs.* large) numbers during the processing of left (*vs.* right) lateralized cues. Similarly, inducing attentional shifts through gaze observation influences random numbers production, with observing left compared to right gaze causing participants to more likely produce a small than a large number (Grade et al., 2013; see also Loetsher, Schwarz, Schubiger & Brugger, 2008; for similar findings with head turns). Similar bidirectional influences have also been reported in mental arithmetic, with problem solving inducing or being affected by spatial shifts of attention. In these experiments, performing addition caused rightward shifts of attention (Masson & Pesenti, 2014), while lateralized flickering of right distractors, attracting attention to the right, caused participants to solve more slowly addition problems (Masson & Pesenti, 2015). Together, these studies suggest that the representation and manipulation of numerical magnitude is linked to visuospatial attentional processes, where one cognitive process influences the other, suggesting shared cognitive mechanisms.

Chapter 2: Sagittal and horizontal number space associations.

Most of the number–space associations that have been reported in the literature suggest spatial coding along the horizontal axis (i.e., left-right). However, similar effects have also been observed with the vertical axis (i.e., bottom-top; Gevers, et al., 2006; Grade et al., 2013; Ito & Hatta, 2004; Loetscher, Bockisch, Nicholls & Brugger, 2010; Schwarz & Keus, 2004). For example, during parity judgements where participants responded by performing eye movements, upward saccadic responses were faster to large compared to small numbers, while downward saccades were faster to small compared to large numbers (Schwarz & Keus, 2004). Similarly, in random number generation tasks, where participants spontaneously give a random number, participants produced more small or large numbers when they were looking down or up respectively (Loetsher et al., 2010; Winter & Matlock, 2013), or when they observed someone else gazing downward or upward (Grade et al., 2013). Spatio-numerical associations therefore appear not limited to the horizontal axis, challenging the idea of a unique left-to-right oriented mental number line, and raising the possibility of the existence of either a mental number map, three-dimensional number space, multiple mental number lines coexisting, or even a single line reoriented according to task requirements (Gevers & Lammertyn, 2005; Grade et al., 2013; Winter et al., 2015).

Even if the literature offers more support for horizontal and vertical number space associations, few studies have investigated number space associations on the sagittal axis (i.e., near *vs.* far), or with distance-based mappings (close *vs.* distant; Chen, Zhou & Yeh, 2015; Gianelli et al., 2012; Santens & Gevers, 2008). One possible reason for this could be due to most experimental set-ups using computer screens. Interestingly, in Santens and Gevers (2008), response keys were arranged in such a way that one response key was close to the starting position of a responding finger, while another response key was further away from the starting positon (both in left to right and right to left orientation). Participants had to perform parity judgements by pressing the close or distant response keys, and results showed that small/large numbers were associated with close/distant response keys, regardless of orientation. In another study, participants also performed

parity judgements, but the two response keys were located near and far (27 or 44 centimeters) from the participants, along their mid-sagittal axis (Chen et al., 2015). Results showed that small numbers were responded to faster when paired with near compared to far response keys, while it was the reverse for large numbers. The authors interpreted the results as evidence of a mapping between number magnitude and near-far distance occurring within a generalized magnitude representation system (Chen et al., 2015; Bueti & Walsh, 2009).

Although the relation with numerical magnitude has been rarely investigated in the near-far sagittal dimension of space, this axis has been extensively studied in the cognitive neurosciences for perception and action behaviors (see: Coello & Delevoye-Turrell, 2007; Cutting & Vishton, 1995; Previc, 1998; Proffitt, 2013; Rizzolatti, Fadiga, Fogassi & Gallese, 1997). This is particularly the case for the processing of the area of space near to the body (i.e., within reaching range; termed *peripersonal* or *near space*, with further space termed *extrapersonal* or *far space*). There is consistent evidence showing that these spaces are processed by different cognitive processes, for example, demonstrated in neuropsychological studies of hemineglect (Halligan & Marshall, 1991; Vuilleumier et al., 1998), neuroimaging studies (Bartolo et al., 2014; Weis et al., 2000), and behavioral studies (Grade, Pesenti & Edwards, 2015; Longo & Lourenco, 2006, 2007). For example, physical line bisection typically deviates leftward when the lines are presented near to the participants, while this bias reverses to rightward when the lines are presented far from participants (Longo & Lourenco, 2007). Interestingly, the moment of transition from leftward to rightward bias can be predicted by participants' reaching capabilities. Similarly, when participants performed number interval bisections (i.e., estimating the number being midway between two numbers) in near and far space, the same transition from leftward bias (underestimation) to rightward bias (overestimation) was observed for near and far space respectively (Longo & Lourenco, 2010).

Findings support the idea that the processing of distance would uses magnitude processing mechanism. ATOM proposed not only common mechanisms for time, space and quantities, but also a system coding magnitude for sensorimotor transformations (Bueti and Walsh, 2009; Freund, 2001; Walsh, 2003). Indeed, when interacting with an object, one must process its distance and size in order to reach and grasp it (Jeannerod, 1997), or walk towards it to reach and grasp the object. To do so, visual information must be processed and converted to implement accurate movements, possibly by magnitude coding (e.g., matching the magnitude of visual distance of the object, or the magnitude of executed reaching or walking action). Support for these underlying magnitude coding processes has already been reported in studies investigating the links between grasping actions, object size and number processing (Andres, Davare, Pesenti, Olivier, & Seron, 2004; Badets, Andres, Di Luca, & Pesenti, 2007; Badets & Pesenti, 2010, 2011; Grade, Badets, & Pesenti, 2016; Lindemann, Abolafia, Girardi, & Bekkering, 2007; Moretto & di Pellegrino, 2008), but few studies have investigated the links between reaching or walking actions, distances and number processing (Gianelli et al., 2012; Chen et al., 2015).

As reviewed above, support for number space associations has now been reported several times on horizontal and vertical axes, but very little is known about their existence on the sagittal axis. The spatial representation of near-far distances might contribute to the representation of numbers, and numerical magnitude might also contribute to near-far spatial categorization. Recent studies challenge the idea that numbers are only represented on a left-to-right oriented number line since number space interactions appear with other orientations in space. A global investigation of the common mechanisms shared between space and number representation should thus be taken into account for all dimensions of space. In the present study, we capitalized on the findings reported above to test the presence of bidirectional number space interactions on the left-right horizontal and near-far sagittal axes. The experimental procedure took place on a horizontal plane (a table), as computer screens being on a frontal/coronal plane might enhance horizontal and vertical dimensions, while greatly reducing the

sagittal dimension. Verbal responses were used to avoid interference of manual laterality with the use of response keys. Three experiments were conducted, assessing both the horizontal and sagittal dimensions of space, as well as the different directions of number space interactions. This was done to investigate if bidirectional (i.e., space-to-number or number-to-space) associations would manifest similarly or differently on two dimensions of space. Experiment 1 tested how different spatial locations of a target number would influence the categorization of numerical magnitude (i.e., smaller *vs.* larger compared to 5). Quicker responses were expected for small compared to large numbers when presented on a left or near location, while the opposite was expected for locations on the right or far. Experiment 2 tested how the numerical magnitude of a target number would influence the categorization of spatial location (i.e., left *vs.* right or near *vs.* far). Faster left and near responses were expected when the target number was small, while faster right and far responses were expected for large target numbers. Experiment 3 consisted of a combination of Experiments 1 and 2, where participants processed the numerical magnitude and the spatial location of target numbers alternatively. This was done to make both the spatial location and magnitude of the stimulus relevant during a single task. Stronger interactions between space and numbers were expected as participants would need to recruit both spatial and numerical representations in the same experimental block, therefore increasing the likelihood of cognitive overlapping resulting in stronger facilitation and interfering effects.

2.2. Methods

2.2.1. Participants

Forty-eight undergraduate French-speaking students from the Université catholique de Louvain (28 females; 8 left-handed) took part in the study for course credits. They were aged between 18 and 28 years (M = 20.7; SD = 1.8 years), had normal or corrected-to-normal vision, and were unaware of the goal of the study prior to the experimentation. They were sequentially

assigned to one of the three experiments (i.e., the first 16 participants took part in Experiment 1 and so on), with 16 participants in each. The experiments were non-invasive and approved by the Ethics Committee of the Institut de recherche en Sciences Psychologiques of the Université catholique de Louvain, in accordance with the ethical standards established by the Declaration of Helsinki (1964).

2.2.2. Apparatus, stimuli and procedures

The apparatus consisted of a projector positioned approximately 250 cm above a white table (215 cm long, 122 cm wide and 70 cm high), which was used to project an image onto the table surface. Black curtains surrounded the table in order to reduce distractions, and to isolate participants inside the experimental environment. Participants sat on a chair situated in the middle of table width, and a microphone was placed above their head in order to record response latencies with a voice-key. Chair height was adjusted so that each participant's eye level was 115 centimeters (M = 114.5, SD = 1.8) from the floor, and chair position was fixed for every participant to maintain consistency of viewing angle across participants. Customized E-prime software (Schneider, Eshmann & Zuccolotto, 2002) was used to display the stimuli on the table using the projector, and to control the experimental procedures. Stimuli were white Arabic numerals (from 1 to 9, except 5) displayed on a black background, and could appear at various locations on the table. For each experiment, trials started with a white square displayed on the table horizontal center, 70 cm from participants, for random durations of 600 and 1200 ms to prevent response anticipation. The participants were asked to fixate the square at the beginning of each trial. Then, a single number or letter was displayed 35 centimeters from the fixation square position, either on the left or on the right (horizontal condition) or further away or closer from participants (sagittal condition; see Figure 2.1.). Only two positions were used at a time within a single block; horizontal and sagittal positions were never mixed. The target number remained on the table until the participant made a response, or for a time-out duration of 1800 ms if no answer was given. Finally, the table remained blank for 800

ms, after which the next trial started. Since all responses implied speaking aloud different words, there was a possibility that the speed at which the word was articulated might differ for each type of response (i.e., near, far, left, right, small and large). To control for this difference, we also created a reading task where the participant had to read aloud as fast as possible the response words of the experiment displayed on the table; each word was presented 6 times. This control task was performed at the very end of the experiment, just before giving a debriefing to the participants before they left the laboratory. For each participant, the response latencies of the control task were subtracted from the responses latencies of the experimental task (see Section 2.3.3.).

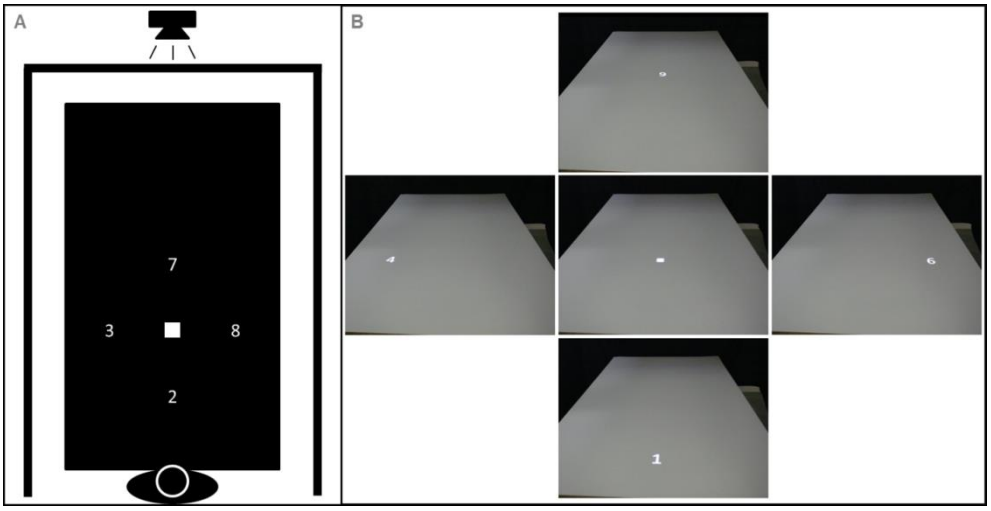

Figure 2.1.: (A) *Schematic representation of the experimental apparatus. A projector placed above the table displayed the stimulus at various positions (i.e., left, right, near, far; with only one number appearing at a time). Dark curtains surrounded the table in order to isolate the experimental environment from the rest of the room.* ***(B)*** *Some photographs taken from the participant viewpoint showing an example of different experimental stimuli.*

2.2.2.1. Experiment 1: Magnitude categorization

In Experiment 1, the impact of target number location (i.e., left-right; near-far) on numerical magnitude processing (i.e., smaller-larger than 5) was

assessed. Each target number (from 1 to 9, except 5) was presented 8 times at each of the 4 locations, resulting in a total of 256 trials. These trials were divided into four blocks of 64 trials, with two blocks containing horizontal axis locations, and two blocks containing sagittal axis locations. The two axes were therefore tested separately, with half of the participants starting with the horizontal blocks, and the other half with the sagittal blocks (i.e., block order was counterbalanced). Participants were asked to categorize numbers as smaller or larger than the referent number 5. They were required to answer as fast as possible, while avoiding making errors, and to make their responses by speaking aloud. In order to maintain a similarity between the procedures of Experiments 1 and 2, and to ensure a processing of the target (particularly required in Experiment 2, see below), participants had to follow a go/no go parity rule by only answering to even numbers in the first block, and only to odd numbers in the second block with the odd-even rule order counterbalanced across participants. To familiarize participants with the task, they performed a practice block of 8 trials at the beginning of each spatial axis condition.

2.2.2.2. Experiment 2: Spatial categorization.

In Experiment 2, the impact of numerical magnitude on spatial processing was assessed. This experiment was identical to Experiment 1, with the exception that participants had to categorize the spatial location of the target number by saying aloud "left" *vs.* "right" or "near" *vs.* "far" (in French). Here, the go/no go parity rule ensured that the target numbers were actually processed, since spatial categorization did not require that the target was identified.

2.2.2.3. Experiment 3: Dual task; spatial and magnitude categorization.

Experiment 3 consisted of a combination of Experiments 1 and 2, with the go/no go parity rule being replaced by a task switching parity rule. The parity of the target number indicated participants which task they had to

perform. If the number was even, half of the participants had to categorize spatial location, and if the number was odd, they had to categorize magnitude (the reverse parity rule was given to the other half of participants). Given the increased difficulty of Experiment 3, the practice trials were twice as numerous (16), and there was no time limit for participant responses. Participants were instructed to answer as fast as possible, while avoiding making errors.

2.2.3. Data analyses

Prior to the data analyses, response latencies (RL) associated with errors (i.e., incorrect answer or a breach in the parity rules) and microphone failures were excluded (2.8% and 2.03% of total data respectively). Then, for each participant, each experiment and the horizontal versus sagittal conditions, trials on which response latency were above or below 2.5 standard deviations from the mean were considered as outliers and removed from the analyses (2.45% of the total data). The mean response latencies of the control reading task performed at the end of the experiment, and were subtracted from the categorization tasks response latencies, separately for each participant and response type in order to obtain corrected response latencies that were then used for the analyses.

To assess the bidirectional interactions between target location and numerical magnitude, two series of analyses were performed for each of the three experiments. First, for Experiments 1 and 2, 2x2 repeated measures analyses of variance (ANOVA) were conducted on the corrected response latencies, with target location (one ANOVA for left *vs.* right, and another ANOVA for near *vs.* far), and target magnitude (i.e., smaller than 5: 1, 2, 3, 4 *vs.* larger than 5: 6, 7, 8, 9) as within-subject variables. For Experiment 3, two 2x2x2 ANOVA for repeated measures were conducted on the corrected response latencies with task (magnitude *vs.* location), target location (left *vs.* right; near *vs.* far) and target magnitude (i.e., smaller *vs.* than 5) as within-subject variables. Separate ANOVAs were conducted for horizontal and sagittal conditions to avoid arbitrary pairing between the location condition

(e.g., left-near and right-far or left-far and right-near). The reported *p*-values were always two-tailed; Bonferroni correction (BC) was applied when multiple post-hoc comparisons were used.

An alternative method has been used in the literature to assess the SNARC effect, or other types of number space associations by computing the difference between left and right response latencies for each target number (Fias, Brysbaert, Geypens & d'Idewalle, 1996). Computed differences (right minus left) are then analyzed using regression analyses for repeated measures, where target magnitude (1, 2, 3, 4, 6, 7, 8, 9) is set as a predictor, and slope coefficients are extracted separately for each participant (Lorch & Myers, 1990). If smaller than 5 numbers are associated with left/near space, and larger than 5 numbers with right/far space, the computed difference decreases as number magnitude increases. Therefore, negative slopes indicate the presence of expected number space associations. Slope coefficient means are compared to 0 using one-sample *t*-tests in order to assess the significance of the number space associations.

2.3. Results

2.3.1. Experiment 1: Magnitude categorization.

In the horizontal condition, the ANOVA showed no significant main effects of target location ($F(1,15) = 1.3$, $p > .05$, $\eta_p^2 = .08$) or target magnitude ($F(1,15) = 1.7$, $p > .05$, $\eta_p^2 = .1$). There was however a significant interaction between target location and magnitude ($F(1, 15) = 5.8$, $p < .05$, $\eta_p^2 = .28$; see Figure 2.2A). To decompose, pairwise comparisons between left and right target locations were conducted separately for smaller and larger numbers using paired *t*-tests. For smaller numbers, corrected responses were faster for left-sided ($M = 252$, $SD = 102$) compared to right-sided locations ($M = 277$, $SD = 108$; $t(15) = -3.2$, $p_{BC} < .05$). However, for large numbers, there was no significant difference between left and right locations ($t(15) = 0.6$, $p_{BC} > .05$). Moreover, pairwise comparisons between smaller and larger numbers were also performed separately for left- and

right-sided locations. This difference was only significant for the left position with faster responses for smaller numbers ($t(15) = 4.3$, $p_{BC} < .01$; right position: $t(15) = 1.1$, $p_{BC} > .05$). The regression analysis showed that the mean slope coefficient of magnitude predictor on response latency differences (right minus left locations) was significantly lower than 0 ($M = -7.26$, $SD = 10.2$; $t(15) = -2.8$, $p < .05$; Mean slope equation : $y = 44.1 * -7.2X$). This significant negative slope indicates that an increase in target numerical magnitude leads to a decrease in response latency differences (right – left locations; see Figure 2.2B).

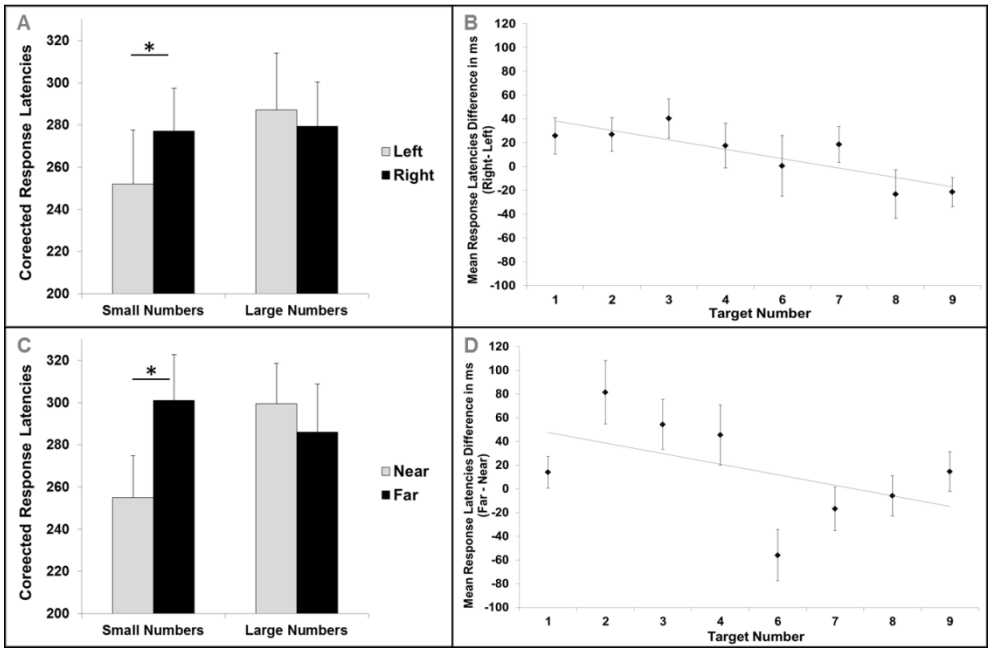

Figure 2.2: *Main results of Experiment 1; magnitude categorization task:* ***(A)*** *Mean corrected response latencies as a function of target magnitude and location in the horizontal condition, and;* ***(B)*** *the regression line mean Response Latencies (RL) differences between right minus left locations as a function of numerical magnitude;* ***(C)*** *Mean corrected response latencies as a function of target magnitude and location in the sagittal condition, and;* ***(D)*** *the regression line plotted on mean RL differences between far minus near locations as a function of numerical magnitude, Error bars represent 1 Standard Error of the Mean (SEM).*

In the sagittal condition, the ANOVA showed no significant main effect of target magnitude ($F(1,15) = 1.4$, $p > .05$, $\eta_p^2 = .08$), but a significant main effect of target location was observed ($F(1,15) = 7.2$, $p < .05$, $\eta_p^2 = .32$) with responses being faster in the near ($M = 277$, $SD = 83.5$) compared to the far ($M = 293$, $SD = 84$) locations. There was also a significant interaction between target location and magnitude ($F(1,15) = 21.4$, $p < .001$, $\eta_p^2 = .58$; see Figure 2.2C). Post-hoc pairwise comparisons showed that for smaller numbers, corrected responses were faster for near-located targets ($M = 254$, $SD = 80$) compared to far-located targets ($M = 301$, $SD = 76$; $t(15) = -6.02$, $p_{BC} < .001$). For larger numbers, there was no significant difference between near and far locations ($t(15) = 1.36$, $p_{BC} > .05$). Moreover, paired t-tests performed on the difference between response latencies showed that responses to small compared to large numbers were faster in the near location ($t(15) = 4.8$, $p_{BC} < .05$), but not in the far location ($t(15) = 0.5$, $p_{BC} > .05$). Then, regression analyses for repeated measures showed that the mean slope coefficient of the magnitude predictor on response latency differences (far minus near locations) was significantly different from 0 ($M = -8.4$, $SD = 9.7$; $t(15) = -3.4$, $p < .01$; mean slope equation: $y = 58.3 * -8.4X$; see Figure 2.2D). This indicates that the larger the target number, the faster responses were for far compared to near target locations. Finally, mean slope coefficients of the horizontal and sagittal axe conditions were compared using paired sample *t*-test. This analysis did not reveal a difference between the two mean slope coefficients ($t(15) = 1.13$, $p > .05$), suggesting that the strength of number space associations were equivalent for the two axes during a magnitude categorization task.

2.3.2. Experiment 2: Spatial categorization

In the horizontal condition, the ANOVA showed no significant main effects of target magnitude ($F(1,15) = 0.1$, $p > .05$, $\eta_p^2 = .001$), but only a marginal main effect of target location ($F(1,15) = 4.2$, $p = .056$, $\eta_p^2 = .22$), with responses to the right location ($M = 213$, $SD = 105$) being slightly faster than to the left location ($M = 245$, $SD = 134$). There was no significant interaction between target location and magnitude ($F(1, 15) = 0.66$, $p > .05$,

η_p^2 = .04; see Figure 2.3.A.). The regression analysis showed that the mean slope coefficient of the magnitude predictor on response latency differences (right locations minus left locations) was not significantly different than 0 (M = -1.5, SD = 7.4; $t(15)$ = -0.8, p > .05; mean slope equation : y = -24.4 * -1.5X; see Figue 2.3.B.).

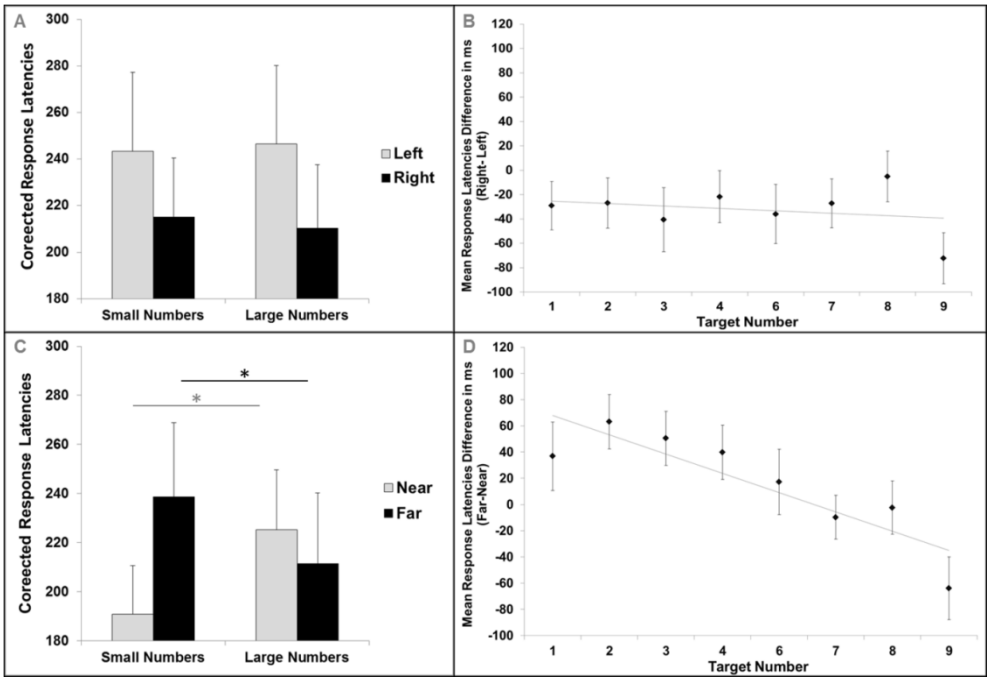

Figure 2.3: *Main results of Experiment 2; spatial categorization task.* ***(A)*** *Mean corrected response latencies as a function of target magnitude and location in the horizontal condition, and* ***(B)*** *the regression line of mean RL differences between right minus left locations as a function of numerical magnitude.* ***(C)*** *Mean corrected response latencies as a function of target magnitude and location in the sagittal condition and* ***(D)*** *the regression line mean RL differences between far minus near locations as a function of numerical magnitude; Error bars represent 1 Standard Error of the Mean (SEM).*

In the sagittal condition, the ANOVA showed no significant main effect of target magnitude ($F(1,15)$ = 0.3, p > .05, η_p^2 = .02) or of target location ($F(1,15)$ = 1.2, p > .05, η_p^2 = .07). A significant interaction between target magnitude and spatial location was observed ($F(1,15)$ = 17.5, p < .001, η_p^2 = .53). Post-hoc pairwise comparisons showed that for smaller numbers,

corrected responses were marginally faster for near-located targets (M = 191, SD = 79) compared to far-located targets (M = 238.6, SD = 121; $t(15) = 2.7$, $p_{BC} = .064$). For larger numbers, there was no significant difference between near and far locations ($t(15) = 0.8$, $p_{BC} > .05$). Moreover, pairwise comparisons also tested the difference between smaller and larger numbers separately for near and far locations. For the near location, smaller numbers (M = 191, SD = 79) led to significantly faster corrected responses than larger numbers (M = 225, SD = 97.5; $t(15) = -3.5$, $p_{BC} < .01$), while for the far location, smaller numbers (M = 238, SD = 121) led to significantly slower corrected responses compared to larger numbers (M = 211, SD = 115; $t(15) = 2.8$, $p_{BC} = .052$; see Figure 2.3.C.). Additionally, the regression analysis showed that the mean slope coefficient of the magnitude predictor on response latencies differences (far locations minus near locations) was significantly lower than 0 (M = -12.3, SD = 11.7; $t(15) = -4.2$, $p < .001$; mean slope equation : $y = 60.2 * -12.3X$; see Figure 2.3.D.). This indicated that the larger the target number, the faster responses were for far compared to near target locations. Finally, mean slope coefficients of the horizontal and sagittal axes conditions were compared using t-test for paired sample. This analysis revealed a significant difference between the two mean slope coefficients ($t(15) = 2.4$, $p > .05$), suggesting that the number space associations were stronger for the sagittal than the horizontal axes during a spatial categorization task.

2.3.3. Experiment 3: Dual task.

For the horizontal condition, the ANOVA revealed no significant main effects of target magnitude ($F(1, 15) = 0.6$, $p > .05$, $\eta_p^2 = .04$), target location ($F(1, 15) = 0.5$, $p > .05$, $\eta_p^2 = .03$), or task ($F(1, 15) = 0.2$, $p > .05$, $\eta_p^2 = .01$). There was a significant interaction between task and target magnitude ($F(1,15) = 8.8$, $p < .01$, $\eta_p^2 = .37$). Pairwise comparisons between smaller and larger numbers performed separately for the magnitude and spatial categorization tasks showed significantly faster corrected responses for smaller compared to larger numbers, but only in the magnitude categorization task ($t(15) = 2.7$, $p < .05$), and not in the spatial

categorization task ($t(15) = 1.5$, $p > .05$). The interaction between target magnitude and location fell short of significance ($F(1, 15) = 4.4$, $p = .052$, $\eta_p^2 = .23$; see Figure 2.4.A.). The remaining interactions were not significant (all $p > .5$). The regression analysis showed that the mean slope coefficient of the magnitude predictor on response latency differences (right locations minus left locations) was significantly different than 0 ($M = -7.5$, $SD = 12.9$; $t(15) = -2.3$, $p < .05$; mean slope equation : $y = 49.8 * -7.5X$; see Figure 2.4.B.).

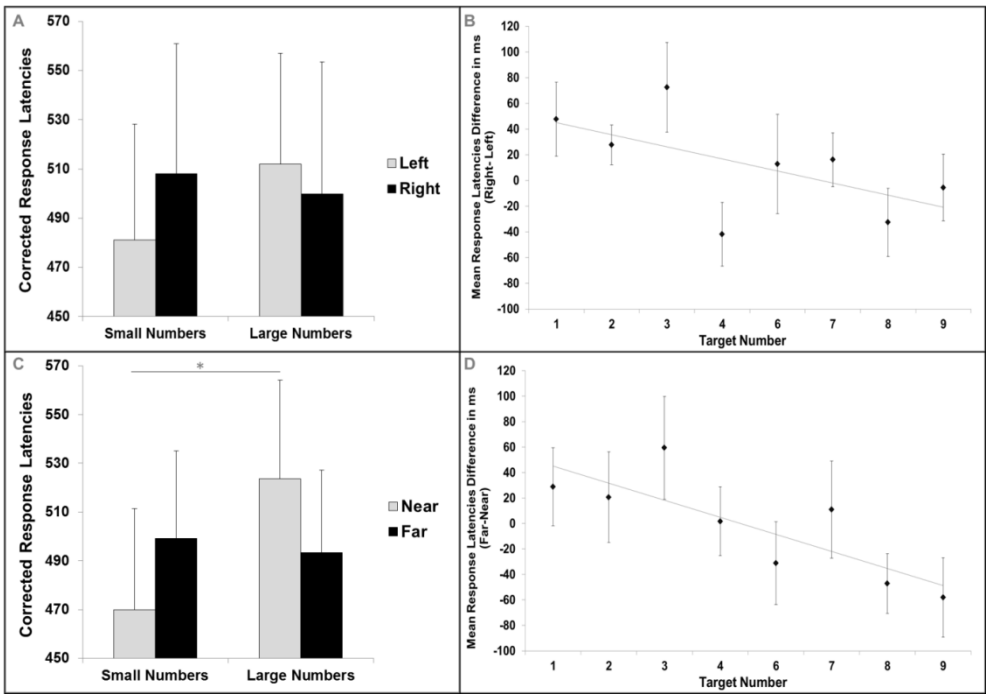

Figure 2.4: *Main results of Experiment 3; dual-task, spatial and magnitude categorization alternately.* ***(A)*** *Mean corrected response latencies as a function of target magnitude and location in the horizontal condition.* ***(B)*** *The regression line mean RL differences between right minus left locations as a function of numerical magnitude.* ***(C)*** *Mean corrected response latencies as a function of target magnitude and location in the sagittal condition.* ***(D)*** *The regression line mean RL differences between far minus near locations as a function of numerical magnitude. Error bars represent 1 Standard Error of the Mean (SEM).*

For the sagittal condition, the ANOVA showed a significant main effect of task ($F(1,15) = 9.2$, $p < .01$, $\eta_p^2 = .38$), with spatial categorization being significantly faster ($M = 472$, $SD = 146$) than the magnitude categorization ($M = 520$, $SD = 150$). There was no significant main effect of target location ($F(1,15) = 0.001$, $p > .05$, $\eta_p^2 = .00$) or target magnitude ($F(1,15) = 4.3$, $p = .056$, $\eta_p^2 = .22$). The ANOVA also showed a significant interaction between target location and task ($F(1,15) = 15.7$, $p < .01$, $\eta_p^2 = .51$). Pairwise comparisons showed that for targets appearing far, responses were faster in the spatial compared to the magnitude categorization task ($t(15) = -3.9$, $p_{BC} < .01$), while this difference was not significant for targets appearing at the near location ($t(15) = 0.99$, $p_{BC} > .05$). More importantly, there was a significant interaction between target magnitude and location ($F(1,15) = 9.6$, $p > .01$, $\eta_p^2 = .39$), with smaller numbers responded to faster than larger numbers, but only when displayed near to the participants ($t(15) = -3.4$, $p_{BC} < .01$). When displayed on the far location, the difference between smaller and larger numbers was not significant ($t(15) = 0.4$, $p_{BC} > .05$). Other pairwise comparisons showed no significant differences between near and far locations for small or large numbers (small: $t(15) = 1.2$, $p_{BC} > .05$; large: $t(15) = -2$, $p_{BC} > .05$; see Figure 2.4.C.). The regression analysis showed that the mean slope coefficient of the magnitude predictor on response latencies differences (far locations minus near locations) was significantly different from 0 ($M = -11.3$, $SD = 15$; $t(15) = -2.9$, $p < .05$; mean slope equation : $y = 54.9 * -11.3X$ see Figure. 2.4.D.). Finally, the comparison of horizontal and sagittal mean slope coefficients showed no significant difference ($t(15) = 0.7$, $p > .05$).

2.4. Discussion

The aim of the present study was to investigate bi-directional interactions between numbers and space in the near-far and left-right dimensions. These interactions were assessed along the horizontal axis to replicate previous effects, but also the sagittal axis allowing for mutual comparisons of numerical magnitude and spatial location, in both directions across the different experimental tasks. In the magnitude categorization task, the

spatial location of a numerical target influenced the processing of magnitude. Indeed, when the target was positioned near to the participants, or on the left, participants were faster to respond to smaller numbers compared to larger numbers. The strength of the interaction was comparable on the horizontal and sagittal axes during magnitude categorization. Target location moderated the speed of numerical magnitude processing and response production. In the spatial categorization task, an interaction between numerical magnitude and location was only observed with the near-far sagittal axis, and not with the left-right horizontal axis. Participants were faster to categorize as near smaller than larger numbers, while it was the opposite for far responses, demonstrating an influence of numerical magnitude on the categorization of near and far spaces (number-to-space direction) (however absent for left-right categorization). In experiment 3, results showed again clear number space associations for the sagittal axis, while the effect was less salient for the horizontal axis.

Throughout all three experiments, clear near-small/far-large associations were observed in both number-to-space and space-to-number directions. For the horizontal axis, results were less consistent across the three experiments, this being somewhat unexpected as bidirectional number space associations have already been reported in the literature (space-to-number: Grade et al., 2013; Loetsher et al., 2008; Kramer et al., 2010; number to space: Dehaene et al., 1993; Fischer et al., 2003; Galfano et al., 2006). It is possible that in the present experimental set-up, the relevance of the left-right dimension was diminished in favor of the near-far dimension, since the experiment took place on a horizontal plane and not on a computer screen (on which reading often happens). The effects of near-small/far-large associations in both number-to-space and space-to-number directions were clear and consistent in the near-far dimension.

The present experiments show that space–number associations go beyond the recurrently observed left–right axis, as associations were observed on both the horizontal and sagittal axes. A common explanation for the left–small and right–large associations refers to the mental number line

(Dehaene et al., 1993; Dehaene et al., 2003). However, observing space–number associations on the sagittal axis, as found here in the current study (see also Chen et al., 2015; Santens & Gevers, 2008; Gianelli et al., 2012) or on a vertical axis (Gevers et al., 2006; Grade et al., 2013; Ito & Hatta, 2004; Schwarz & Keus, 2004), is difficult to reconcile with the mental number line account. Rather, these findings imply either a unique number line somehow self-reoriented to respond to task demands, multiple coexisting number lines oriented in various directions, or the existence of a three-dimensional mental number space on which numerical representations are mapped (Gevers & Lammertyn, 2005; Grade et al., 2013; Holmes & Lourenco, 2011; Winter et al., 2015). Alternatively, it could also be that space-number associations result from a common coding of magnitude across both spatial and numerical dimensions (Bueti & Walsh, 2009; Gevers et al., 2010; Walsh, 2003). This latter proposal fits with the fact that, in the present study, associations were observed in both number-to-space and space-to-number directions, suggesting that magnitude coding had a mediating influence on number space associations on the near-far sagittal axis.

Bidirectional effects were not observed on the horizontal axis the interaction in the number-to-space direction being not significant. This suggests different underlying processes between number space associations on different dimensions of space. These differences between the two dimensions are in line with previous studies proposing different origins or underlying mechanisms for number space associations observed on the horizontal, vertical and sagittal spatial axes (Fischer, 2012; Grade et al., 2013; Winter et al., 2015). For example, it has been proposed that left-right spaces refer to two different directions, while near-far spaces refer to two different magnitudes of distance (Chen et al., 2015). With this in mind, horizontal number space mappings might be more linked to visuo-spatial attentional mechanisms, while sagittal number space mappings might be underlain by overlapping magnitude coding processes. Additionally, it was also suggested that number knowledge could be represented in a hierarchy of grounded, embodied and situated cognitive processes as an attempt to

explain the variety of observed associations between numbers and space (Fischer, 2012; Fischer & Brugger, 2011). For example, horizontal number–space associations are thought to emerge due to cultural left to right reading and writing habits, an interpretation supported by inverted SNARC effects observed in cultures reading from right to left (Shaki and Fischer, 2008; Shaki, Fischer & Petrusic, 2009; Shaki, Fischer & Göbel, 2012). However, this interpretation is difficult to reconcile for sagittal or vertical associations, as reading on a sheet of paper usually starts at the top of the page (or far from the body), but top and far parts of space seem associated with large numbers. Therefore, the association between small numbers and the near part of space might be better explained by associations driven by a generalized magnitude system, rather than by associations driven by cultural habits. It might be driven by grounded cognition mechanisms shaped by how human beings process their environment, with the ground as a natural zero point for vertical heights (Clark, 1973), while the observer's body could act as a natural zero point for sagittal distance. These associations on vertical and sagittal axes should therefore be observed in any culture, and therefore in opposition to the horizontal axis which might be more dependent on cultural reading–writing habits.

Vertical and sagittal compared to horizontal and sagittal number space associations could possibly share underlying mechanisms (Winter et al., 2015). Indeed, some reviews have pointed out the relations between vertical dimension of space and distance. Near space is mostly processed in the lower part of the visual field, leading to a functional association between the near and bottom parts of space (Previc, 1998). Moreover, the height of a location in the visual field, or vertical elevation is a significant visual cue contributing to distance and depth perception (Cutting & Vishton, 1995). Usually, individuals look down when processing near space, while they look up when they fixate a location further away. Therefore, the lower visual field space often overlaps with near space, while upper visual field space overlaps with far space. Responses labels used by participants for sagittal space were "near" and "far" rather than "up", "above", "down" or "below", suggesting that the participants represented the targets in terms of distance

rather than vertical retinal projection. Moreover, the retinal visual angles for the two horizontal positions were larger than the two sagittal positions due to in depth compression, even though the absolute location of targets was fixed at 35cm from fixation. This might have led to easier position discrimination in the horizontal conditions. For the present study, this potential problem does not impact our findings as horizontal and sagittal conditions were tested in separate experimental blocks. Future studies might overcome these limitations, in particular if wanting to directly contrast or mix the two spatial axes within the same experiment.

In Experiment 3, results showed that spatial categorization was faster than magnitude categorization, suggesting that space processing was faster than number processing. This may be the reason why the horizontal condition of Experiment 2 did not show number-space associations, as perhaps space processing was possibly too quick to be interfered by the slower magnitude processing. The fact that number-space associations were observed in the sagittal condition of Experiment 2 could be by the fact (as discussed above) that categorization responses in sagittal space were slower than categorization responses in horizontal spatial, leaving enough time for number magnitude to be processed and cause interference effects.

Several studies have reported significant interactions between the processing of numbers and grasping actions (Andres et al., 2004; Badets, et al., 2007; Badets & Pesenti, 2010, 2011; Grade et al., 2016; Lindemann et al., 2007; Moretto & di Pellegrino, 2008). It was shown that the processing of small numbers speeds up finger grip closing, and slows down grip opening (Andres et al., 2004). Similarly, observing finger grip closing can increase small number production in a random number generation task (Badets, Bouquet, Ric & Pesenti, 2012; Grade et al., 2016). These effects were believed to arise because numerical magnitude might be partly grounded in the sensorimotor transformations involved in the implementation of goal-directed actions, suggesting a motor contribution to the representation of number semantics (Andres, Olivier & Badets, 2008; Badets & Pesenti, 2010; Barsalou, 2008). Moreover, in ATOM, it was stated

that magnitude representations arise through interactions with the environment, where event inputs (e.g., size and distance of an object) are put in relation with motor outputs (e.g., grasp aperture and reaching amplitude), possibly with the help of a generalized magnitude coding system linking perception and action (Bueti & Walsh, 2009; Walsh, 2003). It is therefore possible that the near-small/far-large number–space associations observed in the present study reflects the common magnitude coding processes involved in distance perception and reaching movement implementation. It can also be predicted that the bidirectional effects observed between number processing and grasping actions would also be observed with reaching actions. This assumption is actually foreshadowed by studies suggesting that internal simulations of reaching actions contribute to distance perception (Coello & Delevoye-Turrell, 2007; Grade, Pesenti & Edwards, 2015; Morgado, Gentaz, Guinet, Osiurak, & Palluel-Germain, 2013; Witt & Proffitt, 2008). Future research might provide further evidence for links between numbers, space, magnitude and reaching actions when processing the sagittal dimension.

In conclusion, the present study brings firm evidence for the existence of numbers-space associations along the sagittal axis, supporting the idea of common processes for the representation of numbers and space. The congruence or incongruence between the magnitude of the distance (e.g., near, small distance) and the numerical magnitude of the target numbers probably caused facilitation or interference. The present study suggests that the representation of numbers can be mapped onto different spatial axes, and that the perception of distance is supported by cognitive processes dedicated to magnitude coding.

CHAPTER 3:

EVIDENCE FOR THE EMBODIMENT OF SPACE PERCEPTION; CONCURRENT HAND BUT NOT ARM ACTION MODERATES REACHABILITY AND EGOCENTRIC DISTANCE PERCEPTION

Abstract

The perception of reachability (i.e., whether an object is within reach) relies on body representations and action simulation. Similarly, egocentric distance estimation (i.e., the perception of the distance an object is from the self) is thought to be partly derived from embodied action simulation. Although motor simulation is important for both, it is unclear whether the cognitive processes underlying these behaviors rely on the same motor processes. To investigate this, we measured the impact of a motor interference dual-task paradigm on reachability judgement, egocentric distance estimation, and allocentric length estimation (i.e., how distant two stimuli are from each other independent from the self) was used as a control task. Participants were required to make concurrent actions with either hand actions of foam ball grip squeezing or arm actions of weight lifting, or no concurrent actions. Results showed that concurrent squeeze actions significantly slowed response speed in the reachability judgement and egocentric distance estimation tasks, but that there was no impact of the concurrent actions on allocentric length estimation. Together, these results suggest that reachability and distance perception, both egocentric perspective tasks, and in contrast to the allocentric perspective task, involve action simulation cognitive processes. The results are discussed in terms of the implication of action simulation when evaluating the position of a target relative to the observer's body, supporting an embodied view of spatial cognition.

* *This chapter is an adapted version of:* Grade S., Pesenti M., & Edwards M.G. (2015). Evidence for the embodiment of space perception: concurrent hand but not arm action moderates reachability and egocentric distance perception. *Frontiers in psychology, 6.*

3.1. Introduction

Space perception arises from multimodal integration (Andersen, Snyder, Bradley, & Xing, 1997). Some studies show that neurons are active for both tactile and visual stimulation within a delimited space surrounding and anchored to specific body parts (see Graziano, Yap & Gross, 1994; Gross & Graziano, 1995; Fadiga, Fogassi, Gallese, & Rizzolatti, 2000), while other studies indicate that space perception can be derived from sensorimotor processes, for example, in the discrimination of peripersonal space (i.e., portion of space within arm reach allowing manual interaction with objects) and extrapersonal space (i.e., space beyond reaching capability; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997; Gallese, Craighero, Fadiga, Fogassi, & Parma, 1999; Rizzolatti, Fogassi, & Gallese, 2002; Coello & Delevoye-Turrell, 2007; Gallese, 2007). These findings suggest that space may be represented by multiple sub-spatial maps partly delimited by body and action capabilities (Gross & Graziano, 1995; Rizzolatti et al., 1997). Therefore, it appears that the motor system not only plans and controls actions, but that the same neural processes appear to be involved in internal simulation of actions (Fadiga et al., 2000; Jeannerod, 2001), and that these simulations may be used to derive an embodied perception of space (Witt & Proffitt, 2008).

Space perception being delimited into different subspaces regarding action capacities has also been emphasized in neuropsychological (see Previc, 1998 for a review) and neuroimaging research (Weiss et al., 2000; Committeri et al., 2007; Quinlan & Culham, 2007; Brozzoli, Gentile, & Ehrsson, 2012). Peripersonal space (for visuomotor interaction in reaching range) differs from three extrapersonal spaces (focal extrapersonal, action extrapersonal and ambient extrapersonal; for visual scanning and orientation in space); proposed to rely on different cortical networks (Previc, 1998). For example, bisecting lines in near space has been shown to activate dorsal visuomotor areas, whereas performing the same task on a more distant screen was shown to use ventral perceptual areas (Weiss et al., 2000). In addition to different subspaces, other neuroimaging studies have highlighted

neural differences between the frames of reference taken by a participant (Committeri et al., 2004; Zaehle et al., 2007; Galati, Pelle, Berthoz, & Committeri, 2010). The egocentric perspective (i.e., the location of an object from one's own body; also termed body-referencing) involves a bilateral but mainly right-sided fronto-parietal network related to goal-directed action planning (Vallar et al., 1999; Galati et al., 2000). The allocentric perspective (i.e., the location of an object relative to the location of another object or person) involves activation of similar areas of the dorsal stream to the egocentric perspective, though to a lesser extent, but also many additional areas in the ventral stream (for a review see Galati et al., 2010). These observations suggest that egocentric perspective might recruit motor representations to a greater extent than the allocentric perspective. Consistent with these arguments, it has also been shown that the perception of reachable versus unreachable objects activates fronto-parietal networks (i.e., the precuneus and the parieto-occipital junction, the anterior parts of the cingulate gyrus and superior and medial frontal gyri, bilaterally) and the cerebellum, suggesting a contribution of dynamic motor representations facilitating the perceptive discrimination of peri- and extrapersonal spaces (Gallivan, Cavina-Pratesi, & Culham, 2009; Bartolo et al., 2014).

Visually determining whether an object is at a reachable distance is thought to rely on pre-reflective representations of body capacities for action (for a review, see Coello & Delevoye-Turrell, 2007). In reachability judgements tasks, it has been shown that perceived reaching limit can be influenced by the manipulation of action capability, with postural or environmental constrains (Carello, Grosofsky, Reichel, Solomon, & Turvey, 1989; Fischer, 2000; Gabbard, Cordova, & Lee, 2007; Rochat & Wraga, 1997), height or position of the table where stimuli are presented (Carello et al., 1989), or participants wearing weights on the wrist (Rochat & Wraga, 1997). For example, hiding participants' hands and providing them a biased visual feedback about the end-point location of their pointing movement has been used to modify a person's perceived action capacity, and the manipulation has shown a moderation to perceived reachable space (Bourgeois & Coello, 2012). In a second example, a study used a motor constraint paradigm (i.e.,

by blocking the arms of participants) and showed response speed and accuracy interference for spatial localization decisions of stimuli within peripersonal space (Iachini, Ruggiero; Ruotolo & Vinciguerra, 2014). Further, physical (non manipulated) differences in action capability such as handedness and visual laterality of target placement can also moderate reachability judgements (Fischer, 2005a; Gabbard, Ammar, & Rodrigues, 2005a, 2005b). Finally, motor disruption, for example through the use of Transcranial Magnetic Stimulation (TMS) applied over the hand motor cortex of the left hemisphere, was shown to moderate response latencies in reachability judgements, particularly for stimuli positioned near the boundary of peripersonal space (Coello et al., 2008). Therefore, together, these effects demonstrate that moderations that normally influence action, also influence judgements of reachability, suggesting that reachability may be based on action representations that are constrained by the context in which the action could be performed (Fischer, 2000).

In parallel, studies focusing on the cognitive processes underlying distance perception have observed similar behavioral effects of action manipulation on distance estimation tasks (Proffitt, 2006; Witt, 2011). For instance, participants wearing a heavy backpack showed an increase in egocentric distance estimation compared to not wearing any backpack (Proffitt, Stefanucci, Banton, & Epstein, 2003). Also, throwing a heavy compared to light ball to a target caused a subsequent greater estimation of the distance between the person and the same target (Witt, Proffitt, & Epstein, 2004). These two studies demonstrated that the manipulation of the effort associated with the action influenced space perception (Proffitt, 2006). In a further study, Witt and Proffitt (2008) added a concurrent ball squeezing task to the ball throwing task. It appeared that squeezing a rubber ball during distance estimation eliminated the influence of the heavy ball throwing, presumably through preventing ball throwing simulation (Witt & Proffitt, 2008). Distance estimation has also been investigated following the use of tools, understood to extend peripersonal space (Berti & Frassinetti, 2000; Farné & Ladavas, 2000; Longo & Lourenco, 2006). For instance, after using a tool, participants perceived targets as closer than when no tool

was used (Witt, Proffitt & Epstein, 2005; Witt & Proffitt, 2008; Osiurak, Morgado & Palluel-Germain, 2012). Interestingly, when participants squeezed a rubber ball while making distance estimation judgements, the impact of tool use on distance estimation was reduced compared to making judgements without ball squeezing (Witt & Proffitt, 2008). As distance perception was moderated by tool use, and because the dual-task of ball squeezing reduced this moderation, it seems that motor simulation must provide a calibration metric for distance perception.

Altogether, these findings suggest that space perception benefits and is scaled to the representations of the body and its capacities. However, whether internal simulated actions do contribute to the perception of spatial distance is still an open question (Proffitt, 2013). The goal of the present study was to examine the contribution of action representations in both reachability and distance perception behaviors by investigating whether a concurrent motor task that may disrupt internal action representations would influence the perception of space. To assess this, participants completed three different spatial perceptual tasks (i.e., reachability, egocentric distance and allocentric length estimation) while performing concurrent hand (i.e., foam ball squeezing; Witt & Proffitt, 2008) or arm (i.e., weight lifting) actions in a within-participant design. With this manipulation, we tested whether similar interference of the concurrent actions would be observed in the reachability judgement task and the egocentric distance estimation task. We propose that these two tasks should show similar patterns of response time interference as, in previous studies, the manipulation of reach capacities influenced distance estimation (Witt & Proffitt, 2008; Osiurak et al., 2012; Morgado, Gentaz, Guinet, Osiurak & Palluel-Germain 2013). In contrast, no dual-task moderation is expected in the allocentric length estimation task. Indeed, we argue that allocentric length estimation does not involve spatial localization relative to the body (or body referencing) and that action simulation processes are thus not recruited in this task. For the reachability judgement task, we predict a typical increase of response latency and error rate for targets placed near the boundary of peripersonal space (Gabbard et al., 2007; Bartolo et al., 2014). Moreover, an interaction

between target location and dual-task for response latencies is expected in the reachability judgement task, with a stronger action dual-task effect for stimuli placed near the boundary of peripersonal space (Coello et al., 2008).

3.2. Method

3.2.1. Participants

There were eighteen participants (aged between 18-25 years, *M* = 20.3 *SD* = 2.2, 9 woman, 3 left-handed), all with normal or corrected-to-normal visual acuity and all naïve to the purpose of the experiment. The experiment was non-invasive and was approved by the ethics committee of the Institut de recherche en Sciences Psychologiques of the Université catholique de Louvain, in accordance with the ethical standards established by the Declaration of Helsinki.

3.2.2. Apparatus, stimuli and procedures

The apparatus consisted of a projector placed above a white table that was 215 cm long, 122 cm wide and 70 cm high. Black curtains surrounded the table in order to isolate the experimental environment from the rest of the room and reduce distractions. Participants sat on a chair situated in the middle of the small edge of the table and a microphone was placed above their head in order to record response latencies. The stimuli were composed of white rectangles (5 cm width and 2,5 cm length) displayed on a black background at various locations on the table (see Figure 3.1). A customized E-prime program (Schneider, Eshmann & Zuccolotto, 2002) was used to display the stimuli on the table and to control the experimental procedures.

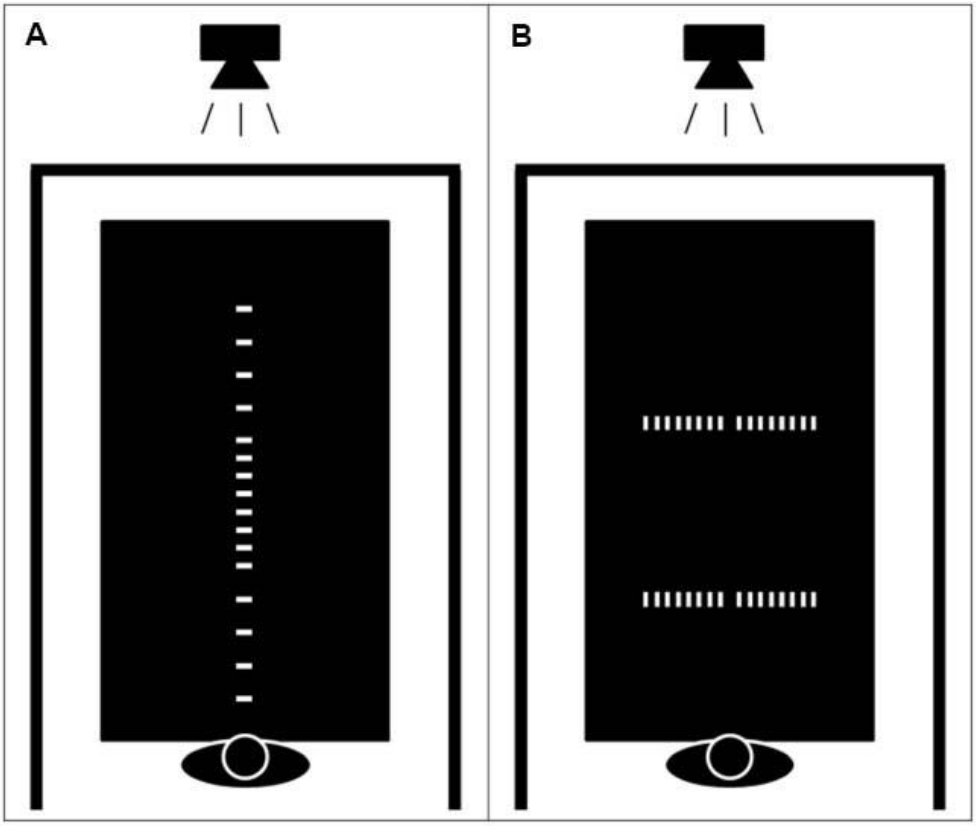

Figure 3.1: *A projector placed above the table displayed the stimulus at various positions. Dark curtains surrounded the table in order to isolate the experimental environment from the rest of the room. Participants were seated on a fixed chair with their trunk touching the edge of the table. Possible locations of the stimuli in the reachability judgement and the egocentric distance estimation tasks (A). Possible locations of the stimuli in the allocentric length estimation task (B).*

All participants were required to perform three different tasks: reachability judgement, egocentric distance estimation, and allocentric length estimation. The reachability judgement and egocentric distance estimation tasks were made to the same stimuli. Rectangular shapes were projected on the tabletop at 16 different distances along the participant's sagittal body-midline axis (35; 55; 65; 75; 80; 85; 87.5; 90; 92.5; 95; 100; 105; 115; 125; 145; and 165 cm), such that approximately half of the stimuli was placed within reach and the other half out of reach, with more closely spaced stimuli placed at the boundary of reach space). In the reachability judgement task, participants

were asked to judge whether they could touch the stimuli displayed on the table without actually performing any reaching actions. They responded aloud "yes" if they thought that they could touch the rectangle, or "no" if they thought that the stimulus was out of reach. It was explicitly mentioned that they could imagine themselves leaning forward, but that their bottom could not leave the chair in their action simulation. Moreover, they were asked to keep their back against the chair backrest during the entire experiment. In the egocentric distance estimation task, participants were asked to estimate the distance in centimeters separating them from the rectangular stimulus. In the allocentric length estimation task, they estimated the distance separating two rectangles presented on the tabletop. The two rectangles were presented either at 70 cm or 130 cm from the participant (i.e., within and out of reach space), and there were 8 possible lengths between the rectangles (8; 16; 24; 32; 40; 48; 56; and 64 cm). The two rectangles were always equidistant from the center of the table compared to the participant's sagittal body mid-line. Within each task, the participants performed three different conditions of dual-task (run in separate trial blocks and counterbalanced within the tasks). Participants were either instructed to simply place their hands on the edge of the table (baseline condition), to perform arm actions (i.e., from fully laterally outstretch arm span to the flexion of elbows with the hands above the shoulders) with one-kilogram weights (arm action condition), or to perform foam ball squeezing hand actions placing their arms alongside their body (hand action condition). They were also trained with a metronome in order to perform the different actions at a specific rate (i.e., 40 per minutes).

Task order was counterbalanced across the participants. Each task consisted of 3 blocks of trials, each with a different dual-task condition (order of dual-tasks was also counterbalanced). Each block consisted of 16 different stimuli repeated 4 times, resulting in 64 randomized trials per block. Each trial started with a beep sound lasting 700 ms, then a stimulus displayed until participants responded, and finally, a blank screen for 1000 ms. In all tasks, the participant had to respond as fast as possible while keeping errors to a minimum. Each task started with a small practice session to make sure

that participants fully understood the instructions and experimental set up, and that they performed the different dual-task actions at a specific frequency paced by a metronome. At the end of the experiment, the experimenter measured the height of participant's eyes, the length of their arms (from neck base to the edge of the middle finger) and their actual reaching limit (the participants furthest reach while being seated on the chair).

3.2.3. Data analyses

For the reachability judgement and egocentric distance estimation tasks, the 16 distances were averaged into 4 different distance categories (i.e., very close with distances 35; 55; 65; 75; close with distances 80; 85; 87.5; 90; far with distances 92.5; 95; 100; 105; and very far with distances 115; 125; 145; 165). Repeated measures analyses of variance (ANOVAs) were conducted with distance categories and dual-task conditions (i.e., no actions; arm actions or hand actions) as within-subject factors. For the allocentric length estimation task, two length categories were formed from the 8 different stimuli (short: 8; 16; 24; 32; long: 40; 48; 56; 64). Repeated measures ANOVAs were conducted with length categories, the position from the participant (70 cm vs. 130 cm) and the dual-task conditions as within subject factors. The dependent variables were response latency and accuracy. For the reachability judgement, accuracy was computed on the basis of the participant's real reach capability measured at the end of experiment. For each stimuli distance, a trial was considered as an error when participants under-estimated (i.e., responded that they could not reach a target when they could) or over-estimated (i.e., responded that they could reach a target when they could not) their reachability. To assess accuracy for egocentric distance and allocentric length estimations independently of the magnitude of the target to be estimated, an error rate was computed by subtracting the actual distance from the participant's response and dividing this difference by the actual distance (i.e., [(participant's response – actual distance) / actual distance]; where a positive value indicates overestimation, a negative value indicates underestimation, and a value of 0 means perfect accuracy for a similar index, see Crollen, Grade, Pesenti & Dormal, 2013).

Bonferroni correction ($_{BC}$) was applied where multiple *post-hoc* comparisons were used. Data from unreliable trials (no response or microphone failures), and outlier responses (on which response latency was above or below 2.5 standard deviations from the overall mean) were excluded from the analyses. This led to the removal of 2.6%, 1.0% and 4.2% of unreliable trials, and 2.8%, 2.3% and 1.3% of outlier response latencies from the total trials of the reachability judgement, egocentric distance estimation and allocentric length estimation tasks respectively.

3.3. Results

3.3.1. Reachability judgement task.

The analysis of response latency revealed a significant main effect of the dual-task conditions ($F(2,34) = 3.5$, $p < .05$), with the hand action condition ($M = 610$, $SD = 76$) being significantly slower compared to the no action condition ($M = 579$, $SD = 93$; $p_{BC} < .05$, $\eta_p^2 = .17$). A significant main effect of the distance categories was observed ($F(3,51) = 10.1$, $p < .001$, $\eta_p^2 = .37$), with the very near ($M = 558$, $SD = 90$) and very far ($M = 583$, $SD = 71$) categories not being significantly different from each other ($p_{BC} > .05$), but significantly faster from the near ($M = 606$, $SD = 98$) and far ($M = 624$, $SD = 82$) categories (all $p_{BC} < .05$). The difference between the near and far categories wasn't significant ($p_{BC} > .05$). The interaction between the two variables was significant ($F(6,102) = 3.6$, $p > .01$, $\eta_p^2 = .17$). Separate ANOVAs were run for each distance category with the dual-task condition as factor. A significant effect of the dual-task was only observed in the near distance category ($F(2,34) = 7.3$, $p < .01$, $\eta_p^2 = .30$), and pairwise comparisons showed that the hand action condition was significantly different from the arm action and the no action conditions ($p_{BC} < .05$) (see Figure 3.2A).

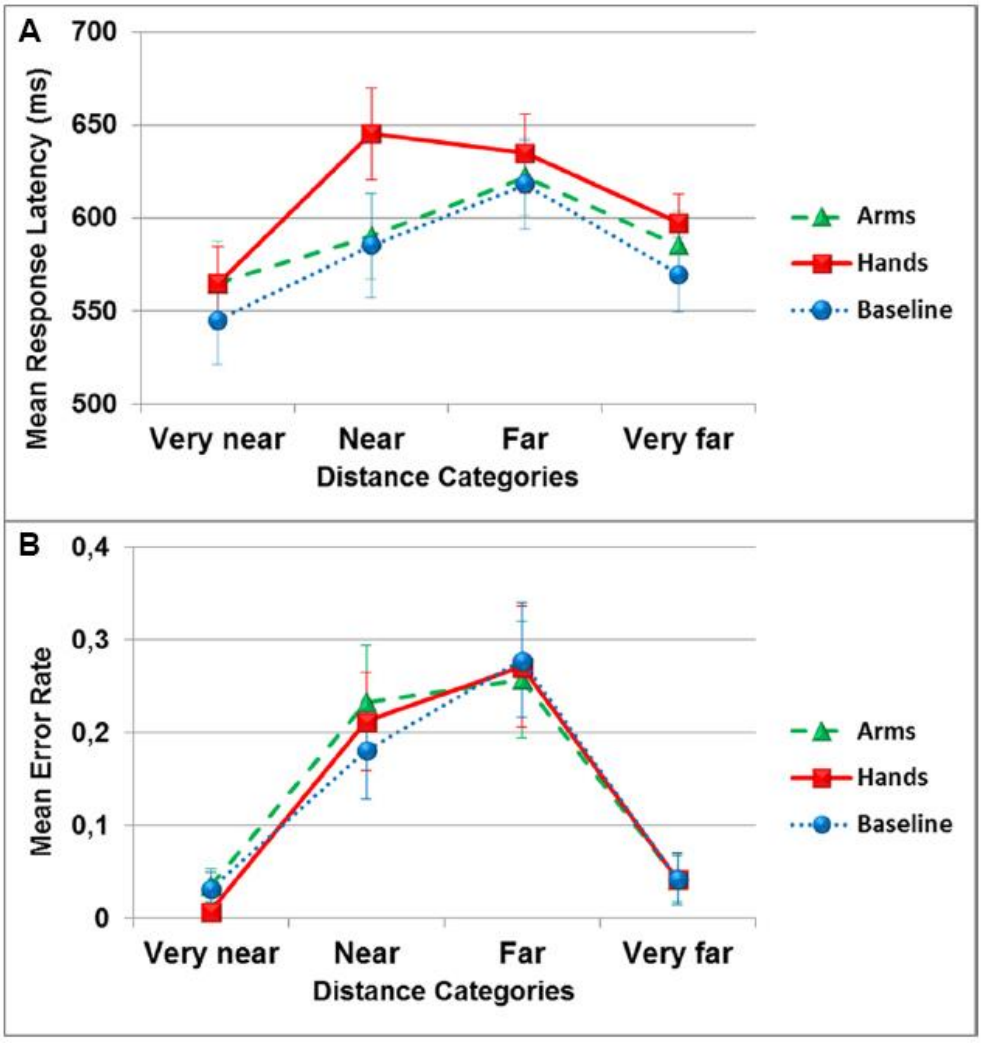

Figure 3.2: *Mean response latency in milliseconds (A) and mean error rate (B) in the reachability judgement task as a function of distance categories and dual-task conditions (circles: no action, triangles: arm actions, squares: hand actions). Error bars represent 1 Standard Error of the Mean (SEM).*

The analysis of accuracy (i.e., absolute error, irrespective of over or underestimation of reach) showed a significant main effect of distance categories ($F(3,51) = 8.5$, $p < .001$, $\eta_p^2 = .33$), with the very close ($M = 0.024$, $SD = 0.042$) and the very far ($M = 0.042$, $SD = 0.11$) distances significantly different from the close ($M = 0.21$, $SD = 0.19$) and far ($M =$

0.26, *SD* = 0.24) distances (all $p_{BC} < .05$). Participants made more errors for distances situated on the boundary between reachable and unreachable space than for the very close or very far distances. There was no main effect of the dual-task conditions ($F(2,34) = 0.12$, $p > .05$, $\eta_p^2 = .007$), and no interaction between distance categories and dual-task conditions ($F(6,102) = 1$, $p > .05$, $\eta_p^2 = .03$) (see Figure 3.2B).

3.3.2. Egocentric distance estimation task.

The ANOVA on response latencies revealed a significant main effect of the dual-task condition ($F(2,34) = 9.5$, $p < .01$, $\eta_p^2 = .36$), with the hand action condition (*M* = 1176, *SD* = 221) significantly different from the no action condition (*M* = 1082, *SD* = 195; $p_{BC} < .01$). A significant main effect of the distances was also observed ($F(3,51) = 6.3$, $p < .01$, $\eta_p^2 = .27$), with the very near category (*M* = 1159, *SD* = 196) significantly different from the near category (*M* = 1091, *SD* = 197; $p_{BC} < .05$). The two variables did not interact ($F(6,102) = 0.87$, $p > .05$, $\eta_p^2 = .05$; see Figure 3.3A).

The analysis of accuracy revealed no effect of the dual-task conditions ($F(2,34) = 2.12$, $p = .15$, $\eta_p^2 = .11$), of the distance category ($F(3,51) = 2.9$, $p = .069$, $\eta_p^2 = .15$), and no interaction ($F(6,102) = 0.36$, $p > .05$, $\eta_p^2 = .02$; see Figure 3.3B).

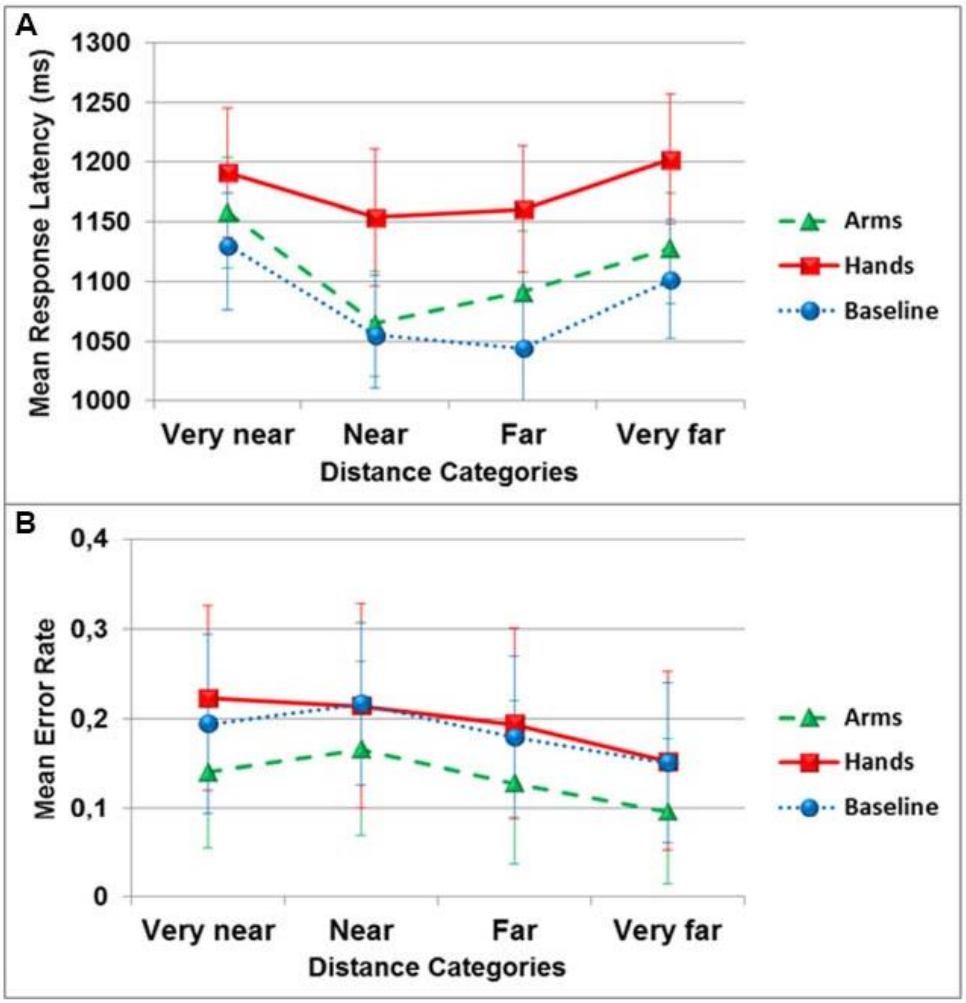

Figure 3.3: *Mean response latency in milliseconds (**a**) and mean error rate (**b**) in the egocentric distance estimation task as a function of distance categories and dual-task conditions (circles: no action, triangles: arm actions, squares: hand actions). Error bars represent 1 Standard Error of the Mean (SEM).*

3.3.3. Allocentric length estimation task.

The ANOVA of the response latencies did not reveal a significant main effect of the dual-task conditions ($F(2,34) = 0.8$, $p > .05$, $\eta_p^2 = .04$). There was however a significant main effect of the position ($F(1,17) = 10.8$, $p < .01$, $\eta_p^2 = .39$) indicating that lengths positioned near ($M = 1084$, $SD = 186$)

the participants were responded to faster than lengths presented further away (M = 1114, SD = 195). There was also a significant main effect of length category ($F(1,17) = 9.9$, $p < .01$, $\eta_p^2 = .37$), with participants responding faster to shorter (M = 1071, SD = 172) than longer (M = 1127, SD = 216) lengths. There were no significant interactions (see Figure 3.4A).

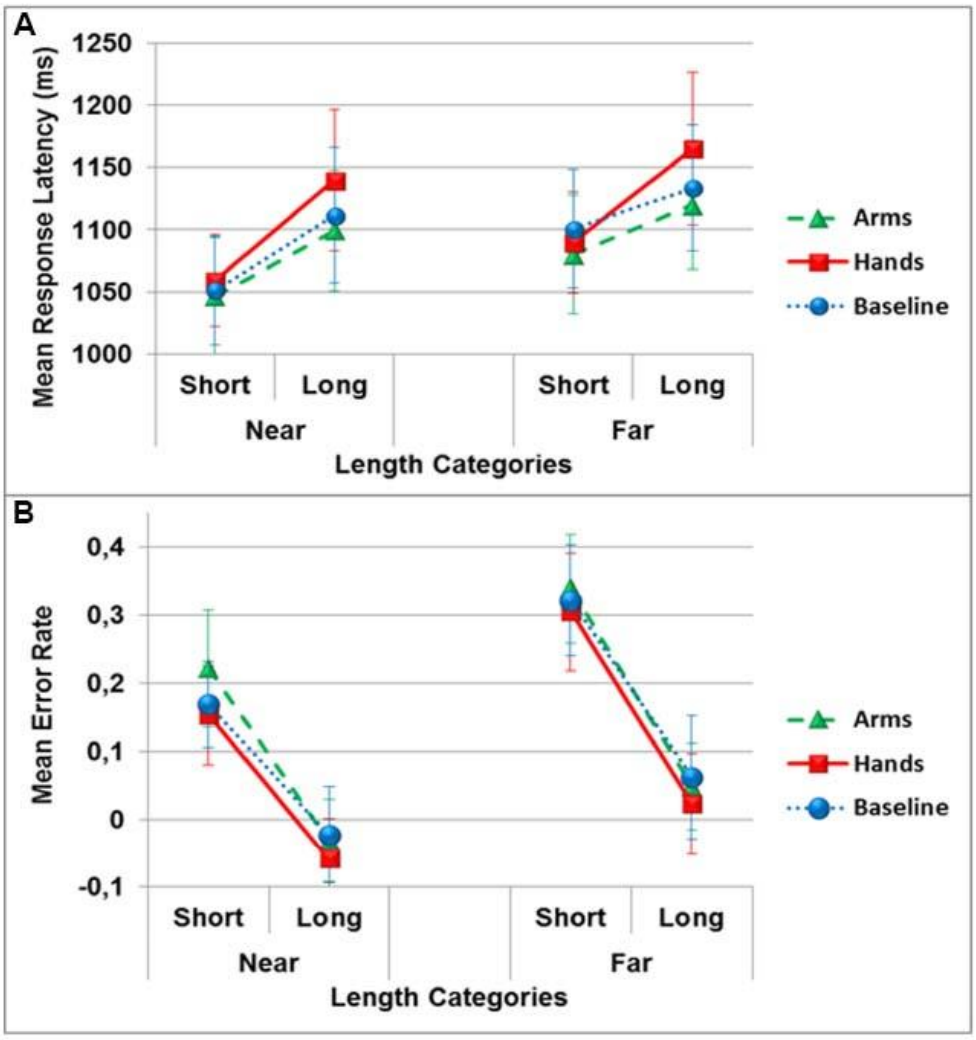

Figure 3.4: *Mean reaction time in milliseconds (**a**) and mean error rate (**b**) in the allocentric length estimation task as a function of distance categories and dual-task conditions (circles: no action, triangles: arm actions, squares: hand actions). Error bars represent 1 Standard Error of the Mean (SEM).*

The analysis of accuracy showed no significant main effect of dual-task conditions ($F(2,34) = 0.76$, $p > .05$, $\eta_p^2 = .04$), but a significant main effect of the position ($F(1,17) = 38,9$, $p < .001$, $\eta_p^2 = .69$), with the lengths appearing near ($M = 0.072$, $SD = 0.25$) showing a smaller overestimation bias than lengths appearing far ($M = 0.18$, $SD = 0.30$) from participants. There was also an effect of length categories ($F(1,17) = 30.3$, $p < .001$, $\eta_p^2 = .64$), with short lengths (i.e., 8; 16; 24; 32 cm; $M = 0.252$, $SD = 0.31$) showing a larger overestimation bias than long lengths (i.e., 40; 48; 56; 64 cm; $M = 0.004$, $SD = 0.28$). The only significant interaction observed was the one between positions and length categories ($F(1,17) = 4.9$, $p < .05$, $\eta_p^2 = .22$). Accuracy differences between short and long lengths was significantly smaller in the near compared to far position ($t(17) = 2.2$, $p < .05$; see Figure 3.4B).

3.4. Discussion

The perception of space is thought to benefit from the ability to mentally represent action (Rizzolatti et al., 1997; Gallese, 2007; Witt & Proffitt, 2008), and to use action capability as an index for understanding how objects are positioned relative to ourselves (Coello & Delevoye-Turrell, 2007; Witt & Proffitt, 2008; Proffitt, 2013). As many findings show similarities between action execution and action simulation (Decety, Jeannerod & Prablanc, 1989; Parsons, 1994; Hanakawa, Dimyan & Hallett, 2008), an interference of action execution on action simulation and beyond it, on space processing, is expected. However, it is currently unclear if reachability judgement (whether an object is in reach) and egocentric distance estimation (the distance between the viewer and the object) rely on the same body capability representations and action simulation processes. The aim of the present study was to evaluate whether performing a motor dual-task interfering with motor simulation processes would moderate space perception (extending dual-task effects to distance estimation; Witt & Proffitt, 2008). Furthermore, within the same participants, we wanted to determine for the first time whether two commonly used measures of space

perception (reachability judgement and egocentric distance estimation) were based on a common action simulation mechanism.

For the reachability judgement task, significantly slower and less accurate responses were observed for targets presented close to the boundary between reachable and unreachable spaces, in comparison to the distances further from the boundary (very near and very far). This finding is in accordance with other studies investigating reachability judgement (e.g., Fischer, 2005b; Gabbard et al., 2005; Gabbard et al., 2007; Bartolo et al., 2014). Furthermore, the dual-task conditions only affected response latencies, where performing foam ball squeezing actions significantly increased response latencies compared to the arm action and the control condition. This was particularly the case for judgements to targets placed in peripersonal space and near the boundary between peri- and extrapersonal spaces. This observation extends the finding that TMS application to the hand associated motor cortex slowed down participants perceptual judgements of whether a target was reachable or not, with a greater disruption when the targets appeared at the boundary of peripersonal space (Coello et al., 2008). Therefore, using the current method, we support the argument that when performing visually based judgements of whether a target is reachable, internal motor representations appeared to be recruited rather than being an epiphenomenal consequence of the reachability judgement (Coello & Delevoye-Turrell, 2007; Bartolo et al., 2014).

For egocentric distance estimation, participants tended to respond faster to targets positioned near compared to very near, but there was no influence of target position on accuracy. Although the influence of distance on the speed of response had a different profile than the one observed in the reachability judgement task, the ball-squeezing dual-task again slowed participant's responses relative to the no-action condition, but showed no interaction between target distance and the dual-task condition. This result supports the idea that motor simulation processes are involved in perceiving egocentric distances of objects (Witt et al., 2004; Proffitt, 2006; Witt & Proffitt, 2008; Proffitt, 2013), and that the simulation of reach capability may serve as a calibration metric for distance perception scaling spatial locations in the

environment relative to body and its capacities (Witt et al., 2005; Linkenauger, Witt, Stefanucci, Bakdash, & Proffitt, 2009; Osiurak et al., 2012; Morgado et al., 2013).

In opposition to reachability judgement and egocentric distance estimation, allocentric length estimation was not influenced by the concurrent actions. This suggests that allocentric length estimation does not rely on motor simulation processes or body representation. An effect of stimulus magnitude was observed with participant's overestimating short compared to long lengths. This effect can be attributed to a contraction bias described in the literature, where participants have their magnitude estimations pulled toward the stimuli range center, leading to the underestimation of large and the overestimation of small stimuli (Poulton, 1979). Additionally, an effect of position was observed, where participants made faster and more accurate responses to targets positioned near compared to far from them. More specifically, participants reported far positioned lengths as being longer than near positioned length despite the fact that the stimuli were identical in length. This effect may be due to a compensation of size constancy in depth where objects presented further from participants appear smaller (Gregory, 1963). This effect could also be due to a Ponzo illusion (Ponzo, 1912), where identical lines are perceived as different when placed within a triangle or a trapezoid shape (Fisher, 1968). In our experimental set up, even if the table was rectangular, it appeared as a trapeze for participants (i.e., near edge is visually larger than the far edge of the table) perhaps causing Ponzo illusion-like effect on the stimuli in this task.

Interestingly, only the ball squeezing dual-task interfered with reachability judgement and egocentric distance estimation. Although one might have expected that the concurrent arm movement would have had a similar disruptive effect, this was not the case. An interpretation of this interaction effect could be the manner that reaching actions might be internally simulated or represented. The ball squeezing actions specifically required acting on an object rather than just moving the object continuously as in the arm action dual-task. We propose that the object or goal directed actions may be more interfering, involving both reach and grasp integrated

representations (Paulignan, Frak, Toni, & Jeannerod, 1997; Jeannerod, 1997). Perhaps similarly, the effect could be explained by the Theory of Event Coding (TEC) framework for interactions between perception and action (Hommel, Muesseler, Aschersleben, & Prinz, 2001; Hommel, 2009). According to TEC, perceived events and action intentions/goals (or to be produced events) are coded within a common representational medium of distal events. Perception thus includes action planning or simulation that takes into account the goals an individual has regarding a distal event (i.e., the intended change to be performed). In the present study, the ball-squeezing dual-task required participants to act upon an object with the intention of modifying the object structure, generating an object-directed distal event. As the target stimuli in the reachability and distance estimation tasks were also processed as distal events, the two different events would have had to be represented simultaneously, and this competition in representation might have caused interference in event coding processes leading to longer response latencies. Moreover, for goal directed grasping in peripersonal space, the representation of the object position had to be coded in hand-centered coordinates rather than regarding arm position (Brozzoli et al., 2012). Experiments have shown that multisensory coding of peripersonal space (measured with cross-modal visual-tactile interactions) was particularly influenced by object oriented grasping actions (Brozzoli et al., 2009; Brozzoli, Cardinali, Pavani & Farné, 2010). Their results showed that cross-modal congruency effects were stronger during action execution compared to a static condition (Brozzoli et al., 2009) and that this congruency effect was stronger during the execution of grasping action compared to pointing (reaching) action (Brozzoli et al., 2010). If the perception of peripersonal space was equally considered to be based on hand-centred simulation processes, then only the squeezing dual-task would influence space perception, and not the arm action dual-task condition.

From the common finding of the dual-task effects on both reachability judgement and egocentric distance estimation, we argue that egocentric space processing requires motor simulation processes where the viewer evaluates the position of a target in relation to their body and simulate an

action within their capacity. This finding is consistent with several fMRI studies showing that, in egocentric perceptual tasks (e.g., judging which of two objects are closest to the viewer), there was a greater activation of a fronto-parietal network including the posterior parietal cortex and premotor areas (Committeri et al., 2004; Galati et al., 2010). These brain areas are used for action planning processes and, furthermore, are shown to be active when participants imagine executing actions (Hanakawa et al., 2008; Macuga & Frey, 2012). This is in contrast to allocentric perceptual tasks (e.g., judging which of two objects are closest to a third one) that show activations scattered across both the ventral and dorsal areas (Committeri et al., 2004; Galati et al., 2010), suggesting that allocentric length estimation may require different cognitive processes not related to action simulation.

In the present study, the effect of the dual-task was limited to response latency effects. Our analyses showed that the dual-task conditions had no influence on actual reachability judgements or distance estimates. This finding is consistent with previous dual-task experiments (Witt & Proffitt, 2008), where it was reported that squeezing soft balls at the same time as estimating the distance of targets showed no moderation of the reported distances when no tool was present. This suggests that represented body metrics are not modified by the concomitant execution of actions, as no extension or reduction of perceived peripersonal space was observed. Another interesting finding was that the response latency of the ball squeezing dual-task differed for reachability judgement and egocentric distance estimation. For reachability judgement, responses were slowed specifically for targets in the peripersonal space whereas the dual-task slowed responses to all target positions for egocentric distance estimation. These two findings suggest that while common motor resources are recruited for the two tasks, the manner in which those motor resources are used might be different. For reachability judgements, responses are particularly slowed for peripersonal targets close to the boundary between peripersonal and extrapersonal space. This could be explained through inefficiency or difficulty in the use of action simulation when at the limit of the participant's capability. For egocentric distance estimation however, the

perceptual response latencies were similar for all targets, irrespective of whether they were within or outside of reach.

In conclusion, our study supports the idea that internal representations of action contribute to the perception of external space (Coello & Delevoye-Turrell, 2007; Witt & Proffitt, 2008; Bartolo et al., 2014). Visually determining what is reachable engages the simulation of a motor act that can be interfered with a hand motor dual-task. Moreover, we find that similar internal simulations of reach might also serve as a metric for egocentric distance perception. Therefore, reachability and egocentric distance perception appear to be linked (Osiurak et al., 2012; Morgado et al., 2013), requiring overlapping reaching simulation cognitive processes. However, despite the finding that similar motor resources appeared to be recruited for both behaviors, it could be that these resources are used differently for each behavior. This motor contribution to egocentric space perception may require body referencing, and we argue that in allocentric space, no such motor contribution is recruited. These findings suggest that in order to perceive the environmental layout surrounding a person, the viewer not only represents perceived space from sensorial inputs, but they also simulate the potential body and action interactions within space, supporting an embodied view of space perception (Coello & Delevoye-Turrell, 2007; Proffitt, 2013).

CHAPTER 4:

EXTRACTING AND CALIBRATING SPATIAL INFORMATION FROM OTHER'S BODY DIMENSION AND THEIR ACTIONS

Abstract

Space perception is a multimodal construct, with recent findings suggesting that action and body representations contribute to spatial cognition. Space is thought to be subdivided into different subspaces, calibrated to body size and proportion. In this sense, spatial cognition benefits from action simulation processes when visually perceiving (for the self), if an object is within reachable space. Moreover, somatosensory representations of an observer, and action simulation mechanisms are also recruited when evaluating the reaching range of other people, which may for example represent the posture of the observed actor. In the present study, we investigated how different actor postures and reaching actions would moderate third-person reachability judgement and distance estimation tasks. Participants had to judge the reachability of an actor presented from a third person view, and estimate verbally the distances separating the actor from objects. Two different postures (low vs high) were depicted on the stimuli to see whether static body information would be sufficient to influence participants' responses in the two tasks. Moreover, participants observed the actor performing reaching action before and after two separate estimation sessions to see how action observation would moderate their responses. Results showed a significant influence of actor posture in both tasks, but in opposite directions. Furthermore, after observing actor's reaching actions, participant's responses in both tasks were more accurate as if a calibration of the environment occurred through action observation. Finally, one participant's responses were analyzed separately using a single case study as the participant presented with a malformation of the upper limbs and was excluded from the analyses of the main study. Our aim was to investigate if this particular participant would have different response profiles compared to the other participants. The results showed some differences, but also some similarities, and they are discussed regarding how action simulation processes seems to be malleable, going beyond the observer's own body proportions when perceiving space centered on others (i.e., altercentric space).

* *This chapter is an adapted version of:* Grade S., D'Ursel S., Letesson C., Pesenti M., & Edwards M.G. (In preparation). Extracting and calibrating spatial information from other's body dimension and their actions.

4.1. Introduction

Studies have shown that space perception could rely on embodied motor cognitive processes (Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015; Fadiga, Fogassi, Gallese & Rizzolatti, 2000; Gallese, 2005; 2007; 2015; Gallese, Craighero, Fadiga & Fogassi, 1999). In order to perceive space, it is believed that action simulation of reaching movements are performed internally (without overt movement), and this serves as a scaling metric for understanding and perceiving the space and distance from which objects are placed relative to the self (Linkenauger et al., 2015; Linkenauger, Witt, Stefanucci, Bakdash & Proffitt, 2009; Witt & Proffitt; 2008). The main body of evidence reported in the literature has focused on an egocentric perspective (i.e., the reference frame centered on the perceiver), and egocentric action simulation for space perception (e.g., Bourgeois & Coello, 2008; Fischer, 2000; Grade, Pesenti & Edwards, 2015). Few studies have investigated whether similar contributions of motor cognitive processes are used for altercentric distance perception (i.e., the distance between one point and another person; Fini, Brass & Committeri, 2015). In this sense, not only the representation of our own body and its capabilities would be recruited for scaling the environmental space, but also the body and capabilities of the observed other would need to be coded (Fini et al., 2015; Fini, Costantini & Committeri, 2014). This process could benefit from the extraction of motoric information, either derived from the perceptual observation of the other's body (e.g., arm length, posture), or from the observation of other's reaching capabilities during observed action (Fischer, 2003; 2005; Lamm, Fischer & Decety, 2007). Evidence for understanding the metric by which altercentric distance is scaled is currently lacking, and it is unclear whether perceiving another's body or reaching capabilities in action allows for an accurate estimation of distance separating the other person from an object, or whether recruiting similar motor cognitive processes as that used for egocentric distance perception would allow for altercentric distance perception. As an attempt to clarify these issues, the present study aimed to investigate how altercentric distance estimation and other's reachability judgement would be affected by the

observation of a static other person, versus this other person performing actions to objects.

Although there has been little research to understand the cognitive processes underlying altercentric distance perception, an important amount of research has been dedicated to understanding how one is capable of making sense of other's actions (see Letesson, 2016). When observing conspecifics, humans are able to perceive the actual observed action, and extract meaningful information to infer the aims and intentions of the actor (Blakemore & Decety, 2001; Wilson & Knoblish, 2005). It was proposed that the cognitive mechanisms implied in these processes involve internal action simulation (Jeannerod, 2001), where observers use their own motor system to simulate, predict and understand other's action behaviors (Gallese & Goldman, 1998; Gallese, 2015).

The mechanism by which observers can predict and understand observed actions is believed to be based on shared neural processes between action observation and execution. Neurophysiological studies in monkeys have brought support for such resonance between the observed action and the observer's own motor system with the investigation of the mirror neuron system (for a review, see Rizzolatti and Craighero, 2004). In the first findings, it was demonstrated that specific neurons located in the macaque ventral premotor area F5 discharged both when the primate executed action to grasp a piece of food, and when observing of another primate or a human performing the same actions (Di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi & Gallese, 1996). In the human brain, similar findings were shown with overlapping brain activations when participants executed, observed or imagined actions (Buccino et al., 2001; Ehrson, Geyer & Naito, 2003; Hanakawa et al., 2008; Macuga & Frey, 2012). Further, evidence from cognitive psychology research demonstrated action priming, where the observation of someone else performing an action could influence the observer's subsequent execution of a similar action (Edwards, Humphreys & Castiello, 2003; Griffiths & Tipper, 2009), providing behavioral support for an overlap between the observed and executed actions.

Chapter 4: Action observation and altercentric space perception

Being able to map observed other's actions onto the observer's own motor system appears necessary in order to predict and understand the meaning of other's actions (Blakemore & Decety, 2001; Wilson & Knoblish, 2005). However, caution may need to be taken when using this view when considering whether we can perceive the space perception of the actor (from their perspective), as simulation of other's action capabilities may be strictly limited to the observer's motor repertoire. It may be problematic to perceive, simulate and understand actions that are performed by agents who are of different sizes, for example, when observing the actions of two persons with short versus long arms. It is perhaps unclear how the observer's own motor repertoire could simulate the actions of the two physically different observed agents, and perceive a difference in their reach capabilities relative to each other.

The issue of whether observers can perceive the actor's space using their own motor repertoire becomes increasingly problematic if observers perceive actions that they have never performed before. In a recent paper by Vannuscorps, Andres and Pillon (2013), they demonstrated that a person born without upper limbs was able to perceive and understand observed actions (equally as well as control participants), even though they were incapable of performing the actions. This implies that in order to perceive and understand observed actions, this particular observer did not need a motor repertoire that matched that of the observed action but had sufficient information with the visual analysis of body shape and motion. In the present research, we will also test such a participant. From the findings of Vannuscorps et al (2013), we expect that a generic action simulation mechanism exists for observation of other's actions that is able to simulate general characteristics of action, with some flexibility allowing for variations in the body dimension of the observed agents. The cognitive process of perceiving distance, normally using the observer's own motor repertoire (e.g., Grade et al 2016) combined with a simulation mechanism, might also use a flexible representation that maps the dimensions of the other's body onto the action simulation mechanism, thereby allowing the observer to perceive the actor's altercentric distance.

A second point to consider is whether distance estimation and reachability (where the participant visually determines if an object is reachable or not), relies on the same simulation mechanism (Lamm, Fischer & Decety, 2007). Reachability tasks are usually performed in a first person perspective (requiring an egocentric reachability judgement), and is considered to imply action simulation that covertly represents the range and capabilities of the body in action (Coello & Delevoye-Turrell, 2007). Evidence for this has been provided by studies inducing motor interference, for example with the use of Transcranial Magnetic Stimulation (TMS) or dual-task paradigms, both of which have been shown to slow down participants reachability judgements to particular targets situated on the boundary of peripersonal reachable space (Coello et al., 2008; Grade et al., 2015). This replicates other findings demonstrating that egocentric reachability judgement responses are slower and less accurate for targets situated around the limit of reachable (or peripersonal) space, compared to very near or very far targets (Bartolo et al., 2014; Fischer, 2000; Gabbard, Ammar & Lee, 2006; Gabbard, Ammar & Rodrigues, 2004).

Interestingly, altercentric (other-centered) reachability judgements also show slower and less accurate responses for targets situated around the observed other's maximum reaching range, compared to close and far objects (Fischer, 2005; Lamm et al., 2007). Recurrent overestimation of reaching capabilities have been reported in both egocentric and altercentric perspectives (Carello et al., 1989; Fischer, 2000; 2003; 2005; Gabbard et al., 2004; 2006; Lamm, 2007), suggesting similar action simulation processes when perceiving the reaching range of the self and others (or at least, simulation processes obeying the same rules and respecting the same body constrains; Fischer, 2003). However, returning to the discussion in an earlier previous paragraph, simulating another person's action using first-person action simulation might be only appropriate if the observers can adjust their motor repertoire to represent the body dimensions of the observed agent. Interestingly, the distance between the agent and the object in altercentric space will be the same irrespective of body size, whereas altercentric reachability judgements will be dependent upon the observer's size or

posture (Fischer, 2003, 2005). Returning to the question in the previous paragraph, this may suggest similar cognitive processes for altercentric and egocentric reachability judgements, which would also be involved in (or transferred to) distance estimation. Still, brain areas activated during these altercentric reachability judgement tasks may not entirely rely on motor imagery from a first-person perspective, but rather from a third-person perspective, perhaps like that of third-person action observation (Lamm et al., 2007). It therefore seems possible that different forms of action simulation may coexist, even if they might rely on similar motor resources and body representations (Fischer, 2003).

In the research on spatial cognition, distance perception is believed to benefit from action simulation, where representing the body and its capabilities serves as a scaling metric for processing distance (Linkenauger et al., 2015; Proffitt, 2013; Witt & Proffitt, 2008). When manipulating the effort or reaching capabilities associated with a target directed action, the egocentric distance estimation of that target is modulated (Morgado, Gentaz, Guinet, Osiurak & Palluel-Germain, 2013; Osiurak, Morgado & Palluel-Germain, 2012; Witt & Proffitt, 2008; Witt, Proffitt & Epstein, 2004). Actions requiring less effort, or actions made with a tool (e.g., rakes or rods), extend reaching capability, and leads to a reduction of distance estimation (e.g., Osiurak et al., 2012; Witt, Proffitt & Epstein, 2005). Interestingly, studies have shown that having another person who sits next to the participant and performs pointing actions with a stick (65 cm), also induced perceived space compression, with lower distance estimates made by participants after tool use observation (Bloesch, Davoli, Roth, Brockmole, & Abrams, 2012; see also Constantini, Ambrosini, Sinigaglia & Gallese, 2011). This suggests that the observed action, as well as the extended arm length was encoded by the observing participant.

It is possible that in the previous example, it was not necessary to observe the action (activating mirror neuron system processes). It could be that the mere observation of the actor with the stick was enough to drive the moderation effect. Support for this comes from a study where virtual umbrella targets were categorized as at near or far egocentric locations on a

computer generated 3D scene. The results showed that the presence of a 3D virtual human avatar in the scene increased the number of locations judged as near (Fini et al., 2014). Moreover, in a complementary study (Fini et al., 2015), when those near-far categorizations were altercentered (other- or 3rd person avatar-centered), more targets were judged as near if the avatar was free to move compared to a situation where the avatar is tied up, or where he was replaced by an another virtual object (umbrella). It seems that other's bodies, and their potential to make actions influenced how the external space was perceived, possibly serving as a body dimension scaling cue.

From this brief introduction, we can summarize that a participant's motor system is recruited for the perception of the space surrounding our body (Coello & Iachini, 2015; Gallese, 2015; Grade et al., 2015), and that it seems reasonable to assume that a similar contribution of the motor system (perhaps including the mirror neurons system) is used when perceiving the space surrounding others (Coello & Iachini, 2015; Fini et al., 2015; Lamm et al., 2007). However, at the moment, there is no clear evidence for explaining how the space of others is represented, or whether egocentric and altercentric space perception rely on common motor cognitive processes. For egocentric perspective, reachability and distance estimation have already been demonstrated to be linked; where action simulation of reaching actions would serve as a common ground for both behaviors (Grade et al., 2015; Morgado et al., 2013; Osiurak et al., 2012). We propose that it might also be the case for altercentric perspective (Fini et al., 2015; Fischer, 2003; 2005), also relying on common cognitive processes of action simulation for altercentric reachability and distance estimation.

In the present experiment, participants viewed scenes depicting an actor seated at a table, and judged whether a single target object placed on the table was reachable by the actor, and then how far in centimeters the object was from the actor. We expected that manipulating the reaching capabilities of an actor with different (static) postural contexts, and manipulating the knowledge or awareness of reaching capabilities following (dynamic) action observation would influence both altercentric reachability and distance perception. Assuming a common cognitive process between the two

behaviors, we predicted that a higher actor's posture should lead to more positive reachability responses, and smaller distance estimates, as perceived reachability and distance seem inversely related (i.e., more/less reachable, less/more distant; Morgado et al., 2013; Osiurak et al., 2012). A second prediction was that the observation of the actor performing reaching actions toward the targets should influence both tasks by calibrating spatial perception (Bourgeois & Coello, 2012; Linkenauger et al., 2015), providing a stronger metric to define reachability and distance estimation responses. Therefore, if decisions are more accurate following action observation, it suggests that action observation processes are necessary for altercentric space cognition, whereas if there is no difference before and after observation, it suggests that observation of body posture alone is sufficient to determine the actor's altercentric space.

In a supplementary part to the research, we had the unexpected spontaneous participation of an individual who was born with unusually short upper limbs (i.e., a student who participated to the experiment for course credits). Their data was analyzed independently, and in comparison to the other participants. This case study allowed us to investigate how a person without hands and elbows would represent the reaching capabilities of others, and altercentric distance perception in comparison to other participants. If they were equally able to perceive the reachability and distance of the actor, it would suggest that reachability and distance perception does not require the observer having a motor repertoire.

4.2. Method

4.2.1. Participants

Sixteen healthy psychology students took part in the experiment for course credits (aged between 19-29 years, M = 21.4, SD = 2.9; 2 males; 1 left-handed). All participants had normal or corrected-to-normal visual acuity, gave their written consent to take part in the experimentation, and were all naïve to the purpose of the study. The experiment was non-invasive, and was approved by the ethics committee of the Institut de recherche en

Sciences Psychologiques of the Université catholique de Louvain, in accordance with the ethical standards established by the Declaration of Helsinki.

There was a seventeenth participant who took part in the experiment (aged 29), but she was excluded from the main data analyses on the basis of having upper limp malformation and shorter reaching action capabilities. The arms of the participant were very short (below the elbow length), and only two fingers were present on each hand.

4.2.2. Apparatus and stimuli

The experiment took place in a laboratory room equipped with a computer, monitor (47.5 cm length & 27 cm height) and a regular keyboard, placed on a standard table. A chair was adjusted in front of the table and monitor, so that participants had their eyes positioned at approximately 60 cm from the computer screen. Participants were instructed that they were required to keep their head still, and their back against the chair back during the experiment. A customized E-prime program (Schneider, Eshmann, & Zuccolotto, 2002) was used to control the experimental procedure.

The stimuli in the experiment consisted of pictures of a male adult who sat on the right side of a white table (215 cm length & 122 cm depth), and on which an object (a wooden cylinder; 5cm diameter & 5cm height) was presented. The scene was photographed from a side profile view, and a black sheet covered the background (see Figure 4.1). A total of 36 different pictures were taken that showed a single wooden cylinder that could be at one of eighteen different distances (25, 35, 45, 55, 65, 75, 80, 85, 90, 95, 100, 105, 110, 115, 125, 135, 145 and 155 cm) from the male adult actor. There were two sets of these pictures (2 x 18), corresponding to each of the male actor's postures. The actor could be sat at one of two different seat heights (40 vs. 55cm) providing extended reach capability in the higher seat posture. Additionally, 36 video clips were also created where the actor performed reaching and grasping movements towards the cylinder, grasping the object, leaving it at the target location, and then returning to the original

start position (with their arms along the body and hand not visible; see Figure 4.2). In the high posture reach videos, the actor could reach up to 110 cm, while in the low posture videos, he could reach up to 85 cm. In the video clips where the cylinder was out of reach of the actor, he still made a reaching movement towards the object up to the point of maximal reaching capability, and then came back to the initial body position.

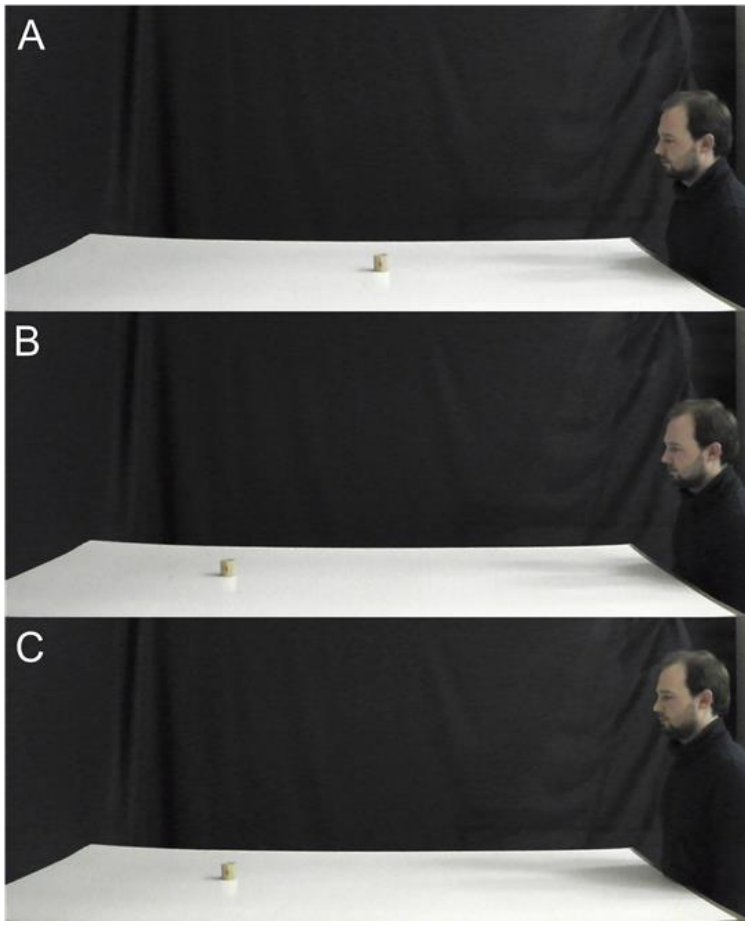

Figure 4.1 : *Examples of the stimuli used in the experiment, with* ***(A)*** *target object located at 95cm from the actor who was in the low posture;* ***(B)*** *target object located at 145cm from the actor who was in the low posture;* ***(C)*** *target object located at 145cm from the actor who was in the high posture.*

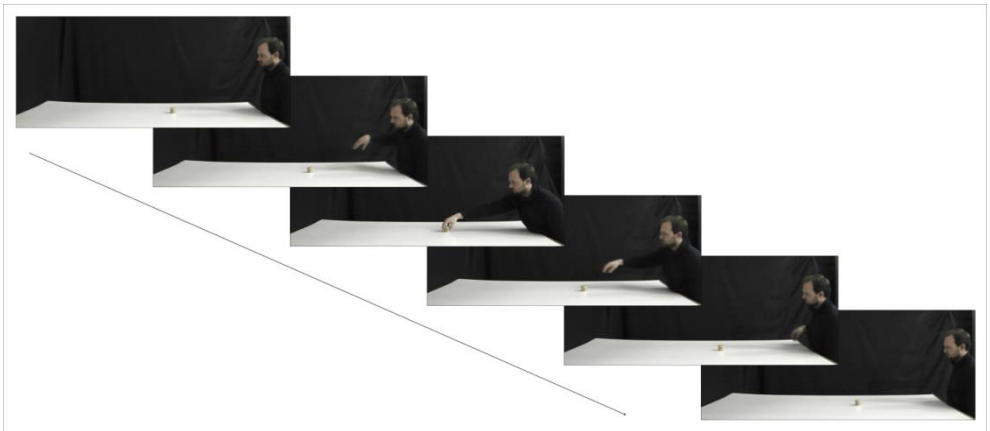

Figure 4.2: *Sequential screenshots of one of the video clips displaying the actor making a reaching action.*

4.2.3. Procedure

Participants first started with a first estimation session where they were required to estimate the reachability of the actor. This was followed by the distance estimation, where the distance between the actor and the target object was estimated. In a second phase, the participants observed the action videos in a passive viewing task. Then, in a third phase, they performed a second estimation session. The duration of the entire experiment was approximately 45 minutes. The two estimation sessions consisted of one block of 144 randomly ordered trials, with the 36 picture stimuli repeated 4 times each, and assessed by the participant for both reachability judgments and distance estimation (performed on those static pictures). Each trial started with a black screen remaining for 1000 ms, directly followed by one of the possible stimuli. The appearance of the stimuli was the imperative signal informing the participants to provide a reachability judgement response (could the actor touch the cylinder? yes or no) with responses recorded using the up or down keys of the keyboard (to collect response latencies; key assignment was counterbalanced across participants). Immediately after the response, a blank screen was displayed for 30 ms, informing both the participants and experimenter that the reachability response had been recorded. This was followed by the same stimulus being displayed a second time, and now where the participants had to estimate the

distance separating the actor from the cylinder (in centimeters), by saying out loud a number that was encoded by the experimenter. After each trial, the participant was free to launch the next trial by pressing the keyboard's spacebar. Note that in the instructions, an emphasis was put on the fact that participants should not estimate the absolute distance as presented on the screen (as the screen was only 45 cm long), but rather that they had to estimate the distances in respect to the original environment.

To familiarize participants with the estimation tasks, they were provided with a practice session of 8 trials at the beginning of the experiment (not included in the analyses). The action observation session took place immediately after the first estimation session, and participants were requested to pay attention and watch the 18 video clips of reaching actions, one for each possible distance, presented in a random order. The observation of posture height in the videos was separated so that half the participants watched the videos depicting the actor with a larger reaching capability (caused by a high posture), and the other half of participants observed the videos of the actor with a smaller reaching capability (caused by a low posture). Finally, once the action observation (video clips) session was complete, participants performed the estimation session a second time.

4.2.4. Data analysis

To evaluate the impact of reaching action observation, as well as the impact of the two different actor's body postures on participants altercentric reachability and distance estimations, several analyses were conducted. First, for reachability judgements, both response latencies and percentages of yes (reachable) responses were analyzed. For response latencies, data from outlier responses (on which response latency was above or below 2.5 *SD* from the overall mean; 2.7 %) were excluded from the analyses. Then both the response latencies and percentages of yes (reachable) responses were then submitted to a mixed measures analysis of variance (ANOVA), with repeated factors of the estimation session (pre- *vs.* post-action observation session), altercentric distance (gathered into 4 categories : very near, 25, 35, 45, 55, 65 cm; near, 75, 80, 85, 90 cm; far 95, 100, 105, 110

cm; very far, 115, 125, 135, 145, 155 cm), and actor body posture (low *vs.* high in the estimation stimuli), and a between groups factor for the action observation reaching capability (small *vs.* large; for the low and high posture used in the observation videos).

To evaluate performances in the altercentric distance estimation task, an error rate was calculated by taking the difference between estimated and actual distance, and dividing this difference by the actual distance (i.e., [participant's response - actual distance]/actual distance; where negative values indicate underestimation, and positive values indicate overestimation, and a value of 0 reflects perfect accuracy; for a similar index, see Crollen et al., 2013 or Grade et al., 2015). This error rate was relatively independent from the target's distance magnitude, allowing for an equitable investigation of participant's accuracy whatever the magnitude of targets (e.g., an error of 10 cm does not have the same significance if the target's distance was estimated as 20 or 100 cm). These computed error rates were then submitted to the same 2X2X4X2 mixed measures ANOVA. Finally, for all analyses, the reported p-values were always two-tailed and Bonferroni corrected (BC) when multiple post-hoc comparisons were used.

4.3. Results

4.3.1. Altercentric reachability judgements

The ANOVA on reachability judgement response latencies first revealed a significant main effect of session ($F(1, 14) = 10.1$, $p < .01$, $\eta_p^2 = .42$), with responses in session 1 (the pre-action observation session; $M = 1239$, $SD = 402$) being slower than in session 2 (the post-action observation session; $M = 1003$, $SD = 281$). The ANOVA also showed a main effect of distance categories ($F(3, 42) = 8$, $p < .001$, $\eta_p^2 = .36$). Pairwise comparisons showed that the near category was significantly slower than the very near category (respectively: $M = 1226$, $SD = 431$; $M = 965$, $SD = 213$; $p_{BC} = .013$), and marginally for the very far category ($M = 1073$, $SD = 286$; $p_{BC} = .061$). A similar, but marginally significant effect showed slower responses in the far ($M = 1221$, $SD = 459$) compared to very near category ($p_{BC} = .066$), while

the remaining pairwise comparisons did not reach significance (all p_{BC}*'s* > .1). The remaining main effects for posture (stimuli) and reaching capability (observation) were not significant (respectively: $F(1, 14) = 0.3$, $p > .05$, $\eta_p^2 = .02$; $F(1, 14) = 0.1$, $p > .05$, $\eta_p^2 = .007$), and there were no significant interactions (all *p's* > .05).

The ANOVA for percentage of yes responses showed no reliable difference between session ($F(1, 14) = 1.04$, $p > .05$, $\eta_p^2 = .07$), but did show a significant main effect of distance categories ($F(3, 42) = 137.2$, $p < .001$, $\eta_p^2 = .9$), with all distance categories being significantly different from each other (very near > near > far >very far; all p_{BC}*'s* < .01). There was also significant main effect of body posture ($F(1, 14) = 8$, $p < .05$, $\eta_p^2 = .36$), with the high posture stimuli having significantly more "yes" responses than the low posture stimuli (respectively: $M = 53.8$, $SD = 10.2$; $M = 51.4$, $SD = 9.7$; See Figure 4.3A). There was no between group effect for reaching capability of the observed actions ($F(1, 14) = 0.19$, $p > .05$, $\eta_p^2 = .014$). The analyses showed several interactions. There were two significant two-way interactions, one between session and observed action reaching capabilities ($F(1,14) = 17.2$, $p < .001$, $\eta_p^2 = .55$), and one between session and distance categories ($F(3, 42) = 4.9$, $p < .01$, $\eta_p^2 = .26$). Finally there was also a three-way interaction between estimation session, observed action reaching capabilities and distance categories ($F(3, 42) = 14.2$, $p < .001$, $\eta_p^2 = .5$). All other interactions were not significant (all *p*s >.05).

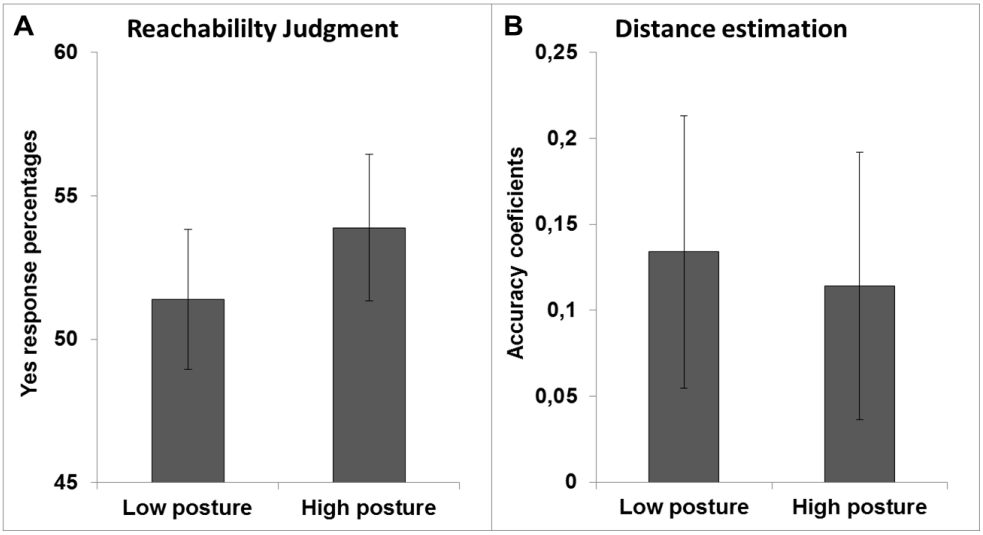

Figure 4.3*: Mean percentages of "yes" responses in the reachability judgement task* ***(A),*** *and mean accuracy coefficients of responses in the distance estimation task* ***(B);*** *both as a function of the two possible actor's body postures displayed on the stimulus. Error bars represent Standard Error of the Mean (SEM).*

In order to decompose the three-way interaction, two ANOVAs with distance categories as within-subject and reaching capabilities (observation) as between-subject variables were conducted separately for session 1 and 2. For session 1 (pre-action observation), there was a significant main effect of distance categories ($F(3, 42) = 42.3$, $p < .001$, $\eta_p^2 = .75$; very near > near > far > very far; all p_{BC}*'s* $< .05$), but no main effect of observed reaching capability ($F(1,14) = 3.8$, $p > .05$, $\eta_p^2 = .21$), and no two way interaction ($F(3, 42) = 1.3$, $p > .05$, $\eta_p^2 = .08$). For session 2 (post-action observation), there was also significant main effect of distance categories ($F(3, 42) = 249.5$, $p < .001$, $\eta_p^2 = .94$; very near > near > far > very far; all p_{BC}*'s* $< .001$), but there was also a significant main effect of reaching capability ($F(1,14) = 39.1$, $p < .001$, $\eta_p^2 = .73$; large reach video: $M = 68$, $SD = 11$; small reach video: $M = 43.1$, $SD = 11$), and a significant interaction between the two variables ($F(3, 42) = 27.2$, $p < .001$, $\eta_p^2 = .66$). To decompose the two way interaction (only observed in the post-action observation session), four independent *t*-tests were conducted to compare the two action video type groups separately for each distance category. This analysis showed

significantly more yes responses following the large compared to the small reach action observation in the near ($t(14) = 4.8$, $p_{BC} < .01$) and far ($t(14) = 6.4$, $p_{BC} < .001$) distance categories, but not in the very near ($t(14) = -0.8$, $p_{BC} > .05$ and very far ($t(14) = 1.8$, $p_{BC} > .05$) distance categories.

In a further post-hoc analysis, we computed the differences between sessions 1 and 2 (post and pre-action observation) responses separately for each participant, and each distance category. As described in the Method, positive values of this difference (i.e., post – pre; percentages of "yes/reachable" responses) indicate an increase in the actor's perceived reachability induced by action observation, while negative values indicate a decrease. These differences were analyzed using a 4x2 ANOVA, with distance categories and observed reaching capability as within- and between-subject variables. This showed a main effect of distance categories ($F(3, 42) = 4.9$, $p < .01$, $\eta_p^2 = .26$) and reaching capability ($F(1,14) = 17.2$, $p = .001$, $\eta_p^2 = .55$; large reach video: $M = 27.9$ $SD = 30,4$; small reach video: $M = -16.9$, $SD = 30.4$), and a significant interaction ($F(3, 42) = 14.2$, $p < .001$, $\eta_p^2 = .504$; see Figure 4.4). Four independent *t*-tests were conducted to compare the large and small reach capabilities (observation) for each distance category. The results showed significant differences, with more positive responses in the large compared to small reach action observation, but only in the near ($t(14) = 3.39$, $p_{BC} < .05$) and far ($t(14) = 4.72$, $p_{BC} < .001$) distance categories, and not in the very near ($t(14) = 2.15$, $p_{BC} > .05$ and very far ($t(14) = 1.78$, $p_{BC} > .05$) distance categories (see Figure 4.4).

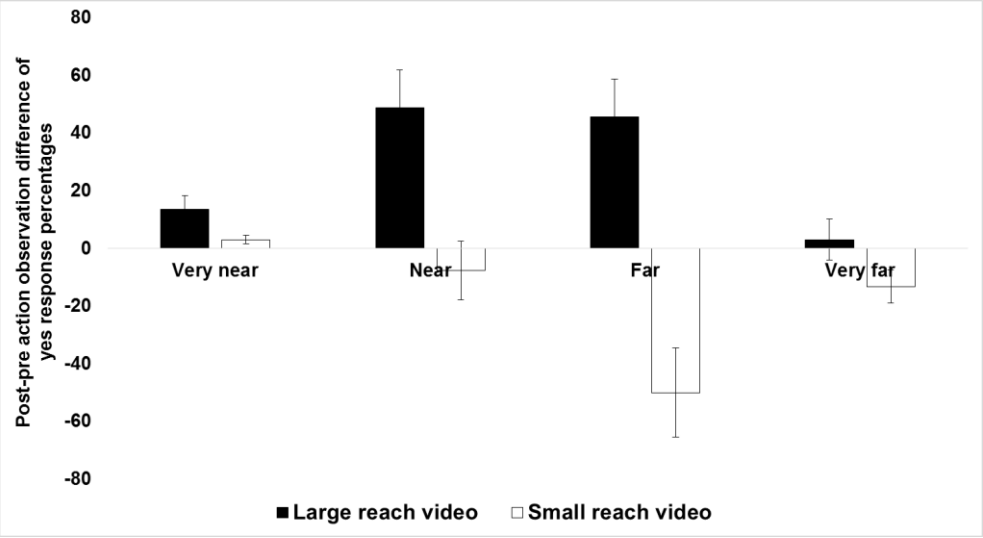

Figure 4.4: *Mean differences between the "yes" response percentages of the reachability judgement task occurring in sessions 1 and 2 (pre- and post- action observation) as a function of distance categories and reaching action video types/groups. Error bars represent Standard Error of the Mean (SEM).*

Finally, to assess the influence of posture and action observation on the perceived boundary of the actor's peripersonal space, reachability judgement responses were submitted to a logistic regression model. This model was used to fit the "yes/no" response occurrence to target distance using the following equation:

$$y = e^{(\alpha + \beta X)} / (1 + e^{(\alpha + \beta X)})$$

Here, y is the participant's "yes" response probability, X is the target distance and $(-\alpha / \beta)$ is the estimated value of x at which targets are no longer considered as reachable, delimiting the boundary of reachable space (for similar procedures see Bourgeois & Coello, 2014; Bourgeois, Farné & Coello, 2012; Coello et al., 2008). Separately for each participant and each condition (i.e., low vs. high postures; session 1 vs. 2), bisection points were calculated by taking the value of x when $y = 0.5$. Finally, the impact of experimental conditions on mean bisection point was assessed using a 2X2X2 (i.e., posture; session; observation group) repeated measure

ANOVA. The ANOVA revealed a main effect of posture, with high posture stimuli leading to greater bisection points (M = 96.6, SD = 12.9) compared to low posture stimuli (M = 93.6, SD = 12.9; $F(1, 14) = 18.1$, $p = .001$, $\eta_p^2 = .56$). The main effects of sessions ($F(1, 14) = 0.6$, $p > .05$, $\eta_p^2 = .04$) and group ($F(1, 15) = 0.004$, $p > .05$, $\eta_p^2 = .00$) did not reach significance. The interaction between group and sessions was significant ($F(1, 14) = 9.15$, $p < .01$, $\eta_p^2 = .39$). All other interactions were not significant (all $p > .05$). Independent t-tests were performed to compare the large and small reach action observation groups separately for session 1 and 2. There was no difference in session 1 (pre observation; $t(14) = 1.6$, $p > .05$), but in session 2 (post observation) participants who observed the large reach videos (M = 106.9, SD = 12.4) showed greater mean bisection point compared to participants who observed the small reach videos (M = 88.3, SD = 7.9; $t(14) = 3.56$, $p < .05$).

4.3.2. Altercentric distance estimations

The ANOVA investigating the effect of experimental conditions on distance estimation error rates showed no significant effect of session ($F(1, 14) = 0.523$, $p > .05$, $\eta_p^2 = .03$), but did show a significant main effect of distance categories ($F(3, 42) = 6.7$, $p < .01$, $\eta_p^2 = .32$), with the very far category mean error rate (M = 0.06, SD = 0.29) being significantly lower than in the near (M = 0.19, SD = 0.37) and far (M = 0.14, SD = 0.32; both $p_{BC} < .01$) categories, while the remaining pairwise comparisons were not significant (all $p_{BC} > .05$; very near: M = 0.11, SD = 0.31). The actor's body posture in the stimuli also showed a significant effect ($F(1, 14) = 24.4$, $p < .001$, $\eta_p^2 = .63$), with high body posture stimuli (M = 0.114, SD = 0.31) leading to lower estimations of distance than low body posture stimuli (M = 0.134, SD = 0.32; see Figure 4.3B). There was no between group difference for observation of reaching capability ($F(1, 14) = 0.525$, $p > .05$, $\eta_p^2 = .03$). Several interactions were observed.

First, the actor's body posture in the stimuli interacted with the reaching capabilities of the observed actions ($F(1, 14) = 5.64$, $p < .05$, $\eta_p^2 = .28$). To decompose this interaction, pairwise t-tests were conducted separately for

each reaching capability group to investigate body posture in the stimuli. Error rates were significantly lower for high body posture stimuli compared to low body posture stimuli, but only in the group that observed small reaching actions ($t(7) = 4.68$, $p_{BC} < .01$ and $t(7) = 2.38$, $p_{BC} > .05$). Second, there was an interaction between the stimuli's body posture and the session ($F(1, 14) = 4.6$, $p < .05$, $\eta_p^2 = .25$). Pairwise comparisons showed that in session 1 (pre-action observation), the high body posture led to lower error rates than low body posture ($t(14) = 4.06$, $p_{BC} < .01$), but that in session 2 (post-action observation), there was no difference ($t(14) = 2.02$, $p_{BC} > .05$). Third, there was a significant interaction between body posture and distance category ($F(3, 42) = 6.77$, $p < .01$, $\eta_p^2 = .32$). Separate paired *t*-tests for pairwise comparisons showed that stimuli containing a high body posture induced distances to appear shorter compared to when stimuli contained a low body posture, for the very near ($t(14) = 4.5$, $p_{BC} < .001$) and far ($t(14) = 3.7$, $p_{BC} < .01$), but not in the near ($t(14) = -0.11$, $p_{BC} > .05$) and very far ($t(14) = 2.3$, $p_{BC} = .144$, $p = .036$) distance categories. The final interaction was between distance categories and session ($F(3, 42) = 6.76$, $p < .01$, $\eta_p^2 = .32$). Pre-post differences were computed for each participant and each distance category, and submitted to an ANOVA with distance category as a within-participant variable. This showed a significant effect ($F(3, 45) = 6.9$, $p < .01$, $\eta_p^2 = .32$); pairwise comparisons showed greater differences between post- and pre-observation, where participants more likely estimated altercentric distances as shorter post- compared to pre-action observation session, particularly in the very far distance category compared to the very near ($p_{BC} < .01$), near ($p_{BC} = .067$; $p = .011$) and far ($p_{BC} < .05$) distance categories (i.e., the gap separating pre and post observation estimation sessions was greater in the very far compared to the other three categories; see Figure 4.5). Remaining pairwise comparisons did not show a difference (all *ps* > .05). No other significant interaction was observed (all *ps* > .05).

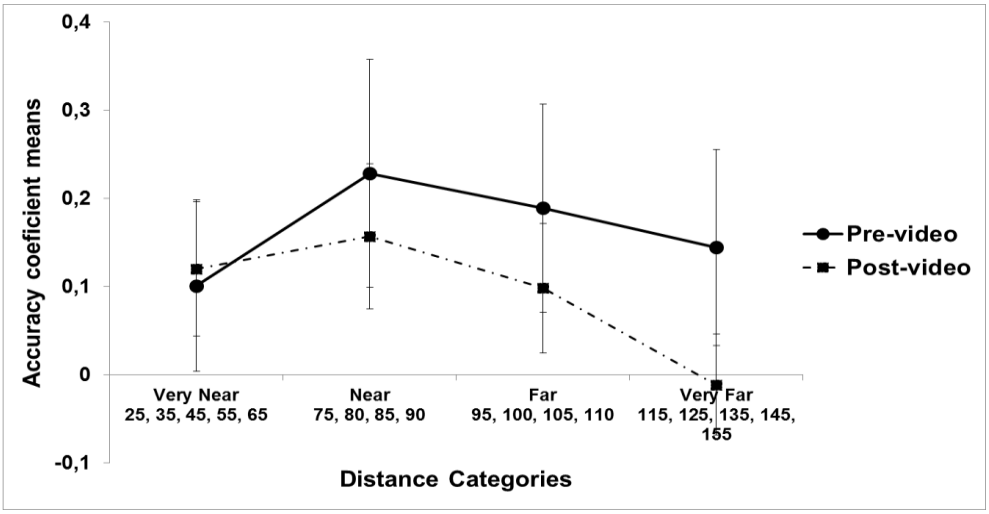

Figure 4.5: *Mean accuracy coefficients of the distance estimation task as a function of distance categories and estimation session (i.e., pre- vs post action observation). Error bars represent Standard Error of the Mean (SEM).*

4.3.3. Single-case analyses

Participant 17 followed through the same experiment as the controls, and was presented with the large reach video clips during the passive action observation. To investigate whether being born with shorter upper limbs could have an influence on how altercentric reachability and distance is estimated, several adapted *t*-tests for single case analyses were conducted (Crawford & Garthwaite, 2002; Crawford & Howell, 1998). These allowed for a comparison of participant 17 response profile with the participant mean and variance responses reported above. In order to perform these analyses, we separated reachability judgement responses for sessions 1 and 2. For yes response percentage in session 1, the percentage was significantly higher than the control's mean percentages (respectively: M = 99.1, SD = 8.5; M = 50.1, SD = 20.5; $t(15) = 2.37$, $p < .05$). At session 2, yes response percentage was no longer significantly different from the control's (respectively: M = 70.1, SD = 45.6; M = 55.19, SD = 13.6; $t(15) = 1.11$, $p > .05$; see Figure 4.6A), demonstrating that the observation calibrated their responses. Distance estimates, at session 1, showed that participant 17 mean accuracy coefficient was marginally lower in comparison to the control's

mean coefficient (respectively: M = -0.67, SD = 0.18; M = 0.16, SD = 0.4, $t(15)$ = -2.01, p = .062), and at session 2, distance estimates produced by participant 17 were not significantly different from the control's (respectively: M = -0.32, SD = 0.07; M = 0.08, SD = 0.27; $t(15)$ = -1.43, p > .05; see Figure 4.6B).

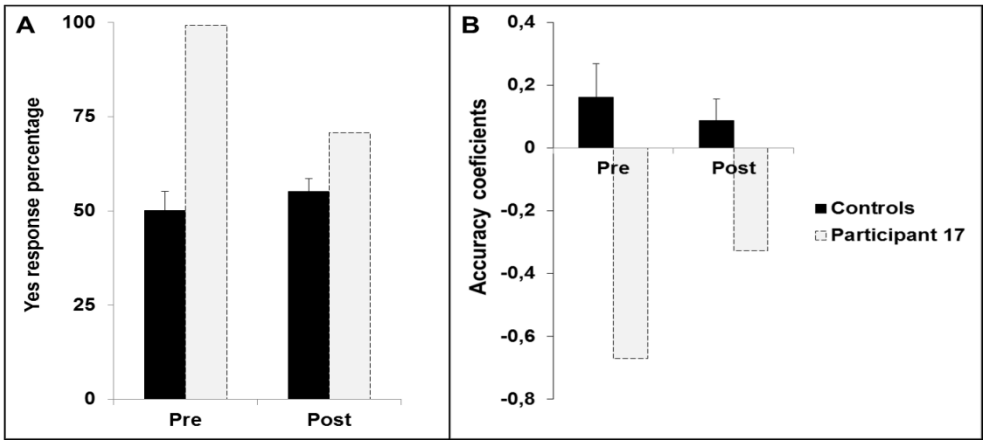

Figure 4.6: *Mean percentages of "yes" responses in the reachability judgement task* ***(A)*** *and mean accuracy coefficients of responses in the distance estimation task* ***(B)*** *both displayed for participant 17 (light grey) as well as the controls (in black) and as the function of estimation session time (i.e., pre- vs post action observation). Error bars represent Standard Error of the Mean (SEM).*

4.4. Discussion

Action simulation is considered to contribute to egocentric space perception. However, it remains unclear whether being able to simulate the actions of others could have an analogous contributing role for altercentric space perception. To assess this possible contribution, participants in the present study were asked to visually determine another person's reaching capabilities and estimate distances between another person and an object placed on a table. We evaluated the impact of different postures adopted by the actor, and the observation of the actor acting. For altercentric reachability judgements, the analyses showed that responses were slower for targets located close to the boundary of the actor's reaching space, compared to very near and very far targets, replicating previous findings

(Fischer, 2005; Lamm et al., 2007). Also, reachability responses were quicker after participants had observed the actor performing reaching, suggesting that the certainty of judging reachability was easier after observation. This result might seem obvious, since the actual true reaching range of the actor was unknown prior to observation, but made certain during action observation.

Analyses of positive response percentages showed several effects of the experimental conditions. First, an expected effect of the actor's body posture was observed, where participants responded more often that the object was reachable when the actor had a higher than lower posture on the stimuli. Therefore, participants appeared able to take into account the actor's trunk size in order to simulate and predict maximum reaching range. This result suggests that participants did not simulate the actor's reaching capabilities based on their own reaching capabilities, but rather that participants were able to simulate the actor's actions independently from their own body proportions and action capabilities. This might suggest the existence of different kind of action simulation processes for self and others (Fischer, 2003). Secondly, results showed an effect of action observation on participant's responses that were further modulated by the reach capability of the actor (i.e., large or small), and particularly in the near and far distance categories (i.e., around the boundary of reachable space). There was no difference between judged reach capability in the two groups of participants prior to action observation, but after observation, the group who watched the videos depicting large reaching capabilities increased their amount of reachable responses, while it was the opposite for the group watching the videos depicting small reaching capabilities. These observations suggest that participants adjusted their responses according to the actions they observed, therefore updating the profile of their internal action simulations, possibly calibrated by action observation similarly to the manner by which action execution calibrates first person reachability judgements (Bourgeois & Coello, 2012).

Results in altercentric distance estimation also revealed several effects. As expected, an effect of the actor's posture in the stimuli was also found in the

distance estimation task, where high postures led to distances being estimated as smaller compared to the low postures. This suggests that participants took into account the implicit reaching capabilities of the actor, and used this as a metric to scale the altercentric distances similarly to what is observed for egocentric distances (Linkenauger et al., 2015; Proffitt, 2013; Witt & Proffitt, 2008). This is perhaps an interesting effect as the distance between the object and the other person is identical in the low and high posture position. However, it should be noted that this effect was influenced by session, with results showing the effect at session 1, but not at session 2. A possible reason for this is that after action observation, instead of inferring reaching capability only from body posture, participants rather used the observed reaching capability information that they acquired during action observation, which then prevailed over the posture cue information.

When considering the effects of postures in the stimuli, for both reachability judgements and distance estimates, as hypothesized, we found similar effects but in opposite directions. In line with previous research suggesting a close link between the two behaviors (Grade et al., 2015; Morgado et al., 2013; Osiurak et al., 2012), the present study brought additional evidence for an inverted relation between reachability and distance estimation, where increased reachability judgements were associated with reduced distance estimation, and vice versa. This relation between both behaviors might suggest that there is a common mechanism underlying the two behaviors when perceiving altercentric space.

One final effect of (perhaps subtle) interest was that in the very far distance category, action observation had an impact on distance estimation in session 2, causing distances to be estimated as smaller compared to prior action observation (session 1). It seems that after the observation of the actor's reaching actions, the environment was rescaled and compressed through the acquisition of a more accurate model of the actor's reaching capabilities. This modification re-calibrated the environment similar to that observed in egocentric distance estimations (Linkenauger et al., 2015; Morgado et al., 2013; Osiurak et al., 2012; Witt & Proffitt, 2008).

Concerning participant 17 investigations, results showed a clear difference in the reachability judgements in comparison to the controls before action observation (in session 1). Participant 17 judged almost all targets as being reachable by the actor, thus greatly magnifying the reaching capabilities of the actor beyond that which is possible. It seems that since participant 17 had a very small reaching capability, she might have exaggerated the reaching capabilities of the actor due to the contrast between herself and the actor. However, after participant 17 observed the actor in motion, she greatly reduced the amount of targets that she judged as reachable, so that her response profile was no longer different from the controls. This suggests that participant 17, despite having short arms, had no difficulties to extract meaningful information from action observation (Vannuscorps et al., 2013). This supports the idea that action simulation might not always be tied to the simulator's body proportions and action capabilities, but can actually go beyond these, and be modified to the body proportions of others, probably benefitting from the observation of actions performed by other people (Fischer, 2003; 2005).

For distance estimation, participant 17 also showed a difference from the controls, but in an opposite direction compared to reachability judgements, again showing an inverted relation between the two behaviors (Morgado et al., 2013; Osiurak et al., 2012). Participant 17 showed great underestimation of distances before action observation compared to controls, but this was no longer significantly different after action observation. Overall, it seems that spontaneous altercentric reachability and distance estimations performed by participant 17 were unusually inaccurate, possibly due to her reduced upper limbs motor repertoire, suggesting that motor repertoire information may be more useful for estimating reachability and distance when no action information is available. In the controls, this simulation would be largely accurate as the controls had intact motor representations. However, participant 17 would have seen the actor, simulated action with their own motor system, and then based on the actor having longer limbs, made the error of estimating that almost all targets were reachable, (or that all the targets were placed closer to the actor). For participant 17, the gain provided

by action observation to calibrate and improve the scaling of space in the environment vastly improved performance, replicating the more subtle improvement demonstrated in the control participants, suggesting that action observation provided more accurate information about the actor's space than perception of the actor's static body.

Overall, the present study brings evidence for the implicit use of other's action capabilities when processing external space (Fini et al., 2015). Similar to what is observed in egocentric distance processing (Grade et al., 2015; Linkenauger et al., 2009; Morgado et al., 2013; Osiurak et al., 2012), the perception of reaching capabilities of another actor seems related, and even contributes to the estimation of a distance separating the actor from an object. These cognitive processes allowing for the simulation and prediction of other's reaching capabilities seem malleable, taking into account the context (e.g., posture of the actor), adjusting according to observed reaching movements or even going beyond the simulator's body capabilities. Our observations therefore suggest a flexible nature of embodied action simulation processes (supporting Fischer, 2005), which are not necessarily anchored and limited to the simulator's body size and capabilities, but could also rely on a common coding for perception-action coupling, and the mirror neuron system in order to predict and understand others actions (Lamm et al., 2007). Such mechanisms of action simulation could contribute to scale external space perception, calibrated from information about the reaching space extent by the self (Bourgeois & Coello, 2012; Coello & Delevoye-Turrell, 2007), and by others (Fini et al., 2014; 2015). These processes could also be implied in social interactions (e.g., when maintaining appropriate distance between self and conspecifics to avoid social awkwardness and discomfort; Coello & Iachini, 2015), where it is suggested that reaching space boundary is related and possibly used for the scaling of adequate interpersonal distances (Iachini, Coello, Frassinetti & Ruggiero, 2014; Quesque et al., 2016).

In conclusion, the present study brings evidence for the cognitive processes underlying altercentric or third person-centered space perception. The results suggest that action simulation using one's own motor repertoire may

provide a calibration metric for the perception of space in the absence of action observation information, but still adjustable by static body posture information. However, the presence of observable reaching actions performed by the actor provided a more accurate calibration of space perception. Nevertheless, both of these processes demonstrate a flexibility, whereby the observer's simulation appears able to be modified by the arm length of the other person. Interestingly, the effects were observed for both reachability and distance estimation tasks, suggesting a common cognitive process for the two estimations of space. These results, for the first time suggest that action simulation mechanisms used for space perception may be grounded on the observers own motor repertoire. However, this motor repertoire can be adapted by other information such as the postural context or the information gained through the observation of other's movements that can modify this representation. This might imply that action simulation mechanisms are not strictly tied to the observer's own body dimension, but rather can be adapted to the observer's own body, or the body of another in the same environment.

CHAPTER 5:

DYNAMIC VIRTUAL SPACE EMBODIMENT: MODIFYING ACTION CAPABILITIES MODERATES PERCEIVED DISTANCE AND REACHABILITY

Abstract

Space perception is believed to benefit from embodied action simulation, where the represented capabilities of our body scale and calibrate the perception of the environment. Recently, it has been shown that modifying a user's body size, arm size or action capabilities using virtual reality (VR; among other techniques moderates distance estimation, or other spatial cognition tasks. In the present study, these effects of body and action augmentation on space perception were investigated in depth by assessing both reachability and distance perception in adults immersed within a virtual environment (VE). We induced three different manipulations of action capabilities using a VR system equipped with a head mounted display (Oculus rift) and a motion capture devise (Leap motion). Experiment 1 showed that virtually translating hand position further in depth caused an increased subsequent estimation of reachability (is this virtual object reachable? yes/no), but decreased subsequent estimation of distance (how many centimeters are there between you and the virtual object?). Experiment 2 revealed that virtually increasing the amplitude of movements by doubling speed did not affect perceived reachability, but similar to Experiment 1, induced a decrease in distance estimates for very far distances. Experiment 3 showed that the virtual augmentation of hand size affected none of the tasks. Altogether these results suggest that participants prior action experience had an active contribution on reachability estimation, suggesting the use of simulation for the perception of space. The results also demonstrate than reachability representation and distance estimation were negatively related, but that distance estimation can be influenced independently of reachability representation, possibly through effort or easiness, in the virtual interaction.

* *This chapter is an adapted version of:* Grade S., Tournadre M., Salvaggio S., Pesenti M., & Edwards M.G. (In preparation). Dynamic virtual space embodiment: modifying action capabilities moderates perceived distance and reachability

5.1. Introduction

When perceiving the space surrounding one's own body, the extraction of egocentric distance information (i.e., relative to the self) is essential for accurate and adaptive action behaviors such as reaching or walking towards an object while avoiding obstacles (Foley, 1978). The cognitive processes underlying the perception of distance in space depend upon different weightings of ocular and visual cues (e.g., Cutting & Vishton 1995). Space is also seen as a multimodal percept (Andersen, Snyder, Bradley & Xing, 1997) that relies upon sensory-motor coupling processed within the dorsal stream of the brain (Milner & Goodale, 1995; Gallese, Craighero, Fadiga & Fogassi, 1999). This multimodal construct is thought to partly define space from the representation of the perceiver's body, its action capabilities, and the use of mental action simulation or spontaneous action imagery, without any overt behavior (Coello & Delevoye-Turrell, 2007; Gallese, 2007; 2015). Therefore, the cortical motor system not only plans and controls action, but it also provides a calibration metric for perceiving space through internal action simulation processes (Fadiga et al., 2000; Jeannerod, 2001), that is anchored on the perceiver's body dimension and capability (Grade, Pesenti & Edwards, 2015; Witt, Proffitt & Epstein, 2005; Witt & Proffitt; 2008; Proffitt, 2013).

Space perception does not emerge as a single percept of whole space, but rather as multiple sub-spaces partly delimited by the body's action capabilities and functions. A neuropsychological based model states that the portion of space surrounding the body and within arm's reach (i.e., near, peripersonal space) is perceived and processed differently than the space outside arm's reach (i.e., far, extrapersonal space(s); Previc, 1998). Evidence for this comes from neuroimaging (e.g., Weiss et al., 2000; Committeri et al., 2007; Quinlan & Culham, 2007; Brozzoli, Gentile, & Ehrsson, 2012), and from behavioral and neuropsychological studies focusing on visual scanning, object affordances, navigation, reachability judgements, protective behavior (Coello & Delevoye-Turrell, 2007; Coello et al., 2008; Gross & Graziano, 1995; Rizzolatti et al., 1997; Previc, 1998). For example, Longo and Lourenco (2007) found different results for

performing a line bisection task in near versus far space. Line bisection performance in near space showed leftward biased bisections, while performing line bisections in far space showed rightward biased bisections. Furthermore, the results showed that the transition between bisection biases was determined by the participant's arm length (from the transition between leftward and rightward line bisection biases).

Some studies that have investigated the perception of near or peripersonal space have used a reachability judgement task. In this task, participants typically view an object, and are asked to decide whether the object is reachable or not without making an overt action. Interestingly, these studies show that decision times increase (i.e., participants are slower) and accuracy decreases (i.e., participants make more incorrect responses) as the object approaches the boundary between near and far space, defined by the participant's arm length (Bartolo et al., 2014; Coello et al., 2008; Fischer, 2000; Gabbard, Ammar & Lee, 2006; Gabbard, Ammar & Rodrigues, 2004; Grade et al., 2015; see also Chapter 3 in the present thesis). Using this task, there have been several experimentations that have demonstrated the important role of action in peripersonal space perception. Firstly, the perceived boundary of reachable space has been shown to be influenced by different constrains that reduce the ability (or easiness) to make actions (Carello, Grosofsky, Reichel, Solomon, & Turvey, 1989; Fischer, 2000; Gabbard, Cordova, & Lee, 2007; Rochat & Wraga, 1997). Secondly, disruption of action, either using Transcranial Magnetic Stimulation (TMS) applied over the left hemisphere's hand motor cortex, or using a concurrent hand squeezing dual task was shown to increase response latencies of reachability judgements, particularly for stimuli positioned near the boundary of peripersonal space (Coello et al., 2008; Grade et al., 2015; see also Chapter 3 in the present thesis). Finally, reachability perception was shown to be dependent on action outcomes within the environment, with distorted visual feedback of pointing movements (i.e., the pointing endpoint presented closer or further away from participants) reducing or extending perceived reachable space. These three manipulations demonstrate that the perception of near or peripersonal space appears derived from motor processes and pre-reflective representations of body-action capability at the

time of perceptual judgement (Bourgeois & Coello, 2012; Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015).

In a parallel stream of research (and somewhat independent to the research on reachability), the perception of space has been measured using distance estimation. As for the perception of reachability, distance estimation is also thought to be derived from action processes, scaled on metrics from the representation of the body capabilities (Witt & Proffitt, 2008; Philbeck & Witt, 2015; Proffitt, 2013). For example, Witt, Proffitt and Epstein (2004) demonstrated that throwing a heavy compared to a light ball towards a target caused participants to estimate the distance between the thrower and the target to be greater. This suggests that the effort by which the action was performed caused the participant to believe that the distance must have been greater. Therefore, the processing of the action caused a moderation in spatial processing, suggesting that action representations is used for the perception of space (Proffitt, 2006, 2013).

In Grade et al (2015; see also Chapter 3), we demonstrated that a concurrent hand squeezing motor dual task not only increased response latencies of reachability judgements for stimuli positioned near the boundary of peripersonal space (as described above), but also that the dual task slowed response times for egocentric distance estimation. This was not the case for allocentric distance estimation, where participants judged the distance between two objects. This replicates the study described in the previous paragraph, suggesting that the perception of egocentric near or peripersonal space for both behavioral tasks appeared dependent (at least for efficient responses) on motor processes. This common disruption effect for distance estimation and reachable space perception could indicate a common embodied cognitive process or mechanism that underlies both tasks (Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015; Philbeck & Witt, 2015; Proffitt, 2013). Support for this latter view arises from findings suggesting a negative relationship between reachability and distance estimation, where participants who have increased reaching capabilities, perceived targets as less distant (Osiurak, Morgado & Palluel-Germain, 2012).

One interesting manipulation of action capabilities presented in the literature comes from the use of tools (like rakes or rods), where following tool use, the perception of near peripersonal space extent, size or boundary has been demonstrated to increase (Bourgeois, Farné & Coello, 2014; see also Longo & Lourenco, 2006). In Bourgeois et al., (2014), participants were asked to judge the reachability of visual targets in reference to their right hand in a session occurring before and after having performed 50 reach and retrieve movements (i.e., casino rake used to collect poker chips). Results showed that the percentage of targets judged as reachable increased following tool use, as if the tool was incorporated in the body schema of the participant's body. Similarly, experiments investigating distance estimation have also demonstrated that participants who used tools, later perceived targets as closer than when no tool (or a shorter tool) was used (Osiurak et al., 2012; Witt, Proffitt & Epstein, 2005; Witt & Proffitt, 2008). Conversely, the presence of tall transparent obstacles in the scene that participants had to reach over (i.e., preventing the use of direct reach, but with no impact on vision) caused target distance to be perceived as more distant than when the obstacle was smaller (Morgado, Gentaz, Guinet, Osiurak & Palluel-Germain, 2013). These latter experiments also nicely demonstrated a negative relationship between reachability and target distance estimation.

In the present study, we were interested in extending these effects of tool use by manipulating the size of participant's bodies using virtual reality, first in an action interaction task, and then in the behavioral perception tasks described above. The emergence of virtual reality as a tool for experimental psychology research has provided new possibilities to study space perception, body representation and perception-action coupling (Bohil, Alicea & Biocca, 2011; Spanlang et al., 2014). In the field of space perception, several studies have investigated how the perception of distance is calibrated by body dimension and action capability by measuring how modifying the participant's body (perhaps only possible in VR) and actions change the perception of different spatial magnitudes (e.g., size and distance; Banakou et al., 2013; Linkenauger et al., 2015; Mohler et al., 2004). For example, Mohler et al. (2004) showed that modifying the relationship between walking speed and visual optic flow motion when

using a treadmill-based VR influenced subsequent distance estimation. When participants experienced slower (or faster) virtual optic flow associated with a constant walking speed, they showed over (or under) estimation of distance.

The effects of moderating VR on the perception of space provides further evidence that spatial information is partly derived and acquired through perception-action coupling or calibration. That is to say that the perception of space is determined by the last experience of interaction in space, whether that be by using the hand, or using a tool. For example, studies investigating locomotion and space perception using VR have shown that participants were more accurate in distance estimation tasks after compared to before having explored the virtual environment by walking (Kelly, Donaldson, Sjolund & Freiberg, 2013; Richardson & Waller, 2007). In this case, interaction inside the VE leads to a rescaling and calibration of perceived distances. In the studies reviewed above, the virtual environment was manipulated relative to a fixed action performance. However, other studies using VR have focused on how users integrate and represent a virtual body (i.e., avatar) as their own body (e.g., González-Franco, Peck, Rodríguez-Fornellis & Slater, 2014), and how changing the size of the entire, or parts of the virtual body influences the perception of different spatial magnitudes (e.g., size and distance; Banakou, Groten, & Slater, 2013; Linkenauger et al., 2015; Van der Hoort & Ehrson, 2014; Van der Hoort et al., 2011). These experiments show that it is possible to embody participants into virtual bodies, eliciting a sense of body ownership, even if the virtual body is very different from the real body (so long as there is intermodal matching, e.g., visuomotor, visuotactile or visuoproprioceptive matching) (Kilteni, Normand, Sanchez-Vives & Slater, 2012; Kilteni, Maselli, Kording & Slater, 2015; Kokkinara & Slater, 2014 Slater, Perez-Marcos, Ehrsson & Sanchez-Vives, 2014).

These observations are analogous to previous work investigating the embodiment of false or reflected limbs, known in the literature as the "rubber hand illusion" or "mirror box illusion" respectively (Botvinick & Cohen, 1998; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). Both

phenomena rely upon re-afferent mechanisms (Held & Schlank, 1959; Von Holst, 1954) characterized by sensory stimulations from touch, or resulting from self-produced actions being adopted to sensory-motor representations of the body. For example, the sight of the rubber limb is congruent to the expected perceived location of where the true hand would be for the person; Fourneret & Jeannerod, 1998; Held & Schlank, 1959). A visible rubber hand is placed parallel to the hidden real hand, and both are synchronously touched with a brush (Botvinick & Cohen, 1998). Intermodal matching of visuo-tactile congruency leads participants to believe that the fake rubber hand is their own hand. A similar illusion appears with the mirror box illusion. Here, the participant has a mirror placed between the two limbs, along the participant's sagittal axis. The participant sees one hand and then a reflection of the seen hand in the place of where the other hand should be (for example, they see their left hand and a reflection of the left hand in the place of the right hand). When the participant moves their left hand, they see bimanual action, and perceive that the mirrored hand is their right hand (Lamont, K., Chin, M., & Kogan, 2011; Ramachandran & Rogers-Ramachandran, 1996; Rothgangel et al., 2011). In both these examples, participants experience embodiment, whereby they perceive the illusory limb as their own.

With VR, it is possible to induce the same illusions. Entire body swapping has been created by putting 3D cameras on the top of a rubber mannequin (Petkova & Ehrsson, 2008). For example, in Van der Hoort and Ehrson (2011; see also Van der Hoort, et al., 2014), a camera was placed on the top of different sized mannequins, having from very large to very tiny sizes (the smallest was a Barbie doll). The camera was positioned so that the body to toes view was seen by a participant. While viewing the body view from the camera, the participant's foot was stimulated, and they viewed the same foot of the mannequin being stimulated. With the congruent stimulation, the mannequin was embodied by participants. Interestingly, their results showed that the illusion worked for all mannequin sizes, but that embodiment of a small body caused participants to estimate sizes and distances as greater compared to when they embodied a large body. This suggests a negative

relation between perceived body size and the estimation of magnitudes contained within the environment.

In some more recent studies, Linkenauger et al. (2015; see also Kilteni et al., 2012) demonstrated that embodiment of different virtual arm was possible for participants immersed in VR, for both smaller and larger arm lengths compared to the participants own arm length. In this case, participants moved their hand, but saw the virtual hand move synchronous to the real hand. In this experiment, they asked participants to perform reaching movements in order for participant to embody the virtual arm, and then they performed a distance estimation task (toward virtual targets). The study showed that the size of the virtual arm had an influence on distance estimation, with the smaller arm leading participants to estimate target distance as further away compared to the larger arm. Most importantly, the study clearly demonstrated that for the effect to emerge, it was necessary to have participants execute and experience reaching actions with their modified virtual upper limb, rather like in the mirror box illusion. No effect of virtual arm size was found when participants did not perform reaching movements prior to estimating distances.

In the present study, we extended the study of Linkenauger et al. (2015) by testing how manipulation of the correspondence between virtual arm length, speed and size, and the true arm length influenced space perception in both distance estimation and reachability tasks. In the study of Linkenauger et al. (2015), it was unclear whether the moderation of distance estimation was due to the virtual change of action reaching capability caused by moderated upper action amplitude or by the limb size. That is, by manipulating arm length, other changes in the limb occurred in addition to length. For example, giving participants longer than real arms would also result in potential differences in the observed speed of the action, and a reduced hand size. Here, we manipulated each factor independently: Experiment 1 manipulated action reaching range, Experiment 2 manipulated action amplitude and therefore speed, and Experiment 3 manipulated effector size (i.e., global size of the hand). The goal was to understand the impact of these three parameters on distance and reachability estimation. Participants

were tested within a virtual environment where they first performed virtual actions that were either normal (matched approximately to the same arm length as their real arm) or augmented by *reach-range* (Experiment 1), *amplitude-speed* (with larger amplitudes of movements appearing to move faster; Experiment 2) and *hand size* (Experiment 3).

Following each interaction with the environment, the participants performed the estimation tasks, measuring the perception of reachability and distances within the same virtual environment. Both behaviors were tested as we wanted to test whether distance estimation and reachability relied on similar cognitive processes. Linkenauger et al. (2015) suggested that reaching capabilities could serve as a perceptual ruler or a defining component for distance estimation. If the cognition for the two tasks is common, then the manipulations should have an impact on both measures. If, however, the cognitive processes underlying the two behaviors are different, the effects of the manipulations may differ. Concerning Experiment 1, the augmentation of reaching capabilities between actual and virtual action, we expected that this manipulation should influence both tasks. For reachability judgement, increasing arm length should increase the perceived boundary of peripersonal space, and cause participant's to over-estimate their action capability (relative to the true physical length of their arm). That is to say that the perception of reachability will be derived from the prior experience rather than on a long-term representation or knowledge of actual arm length. For distance estimation, we expect that an increase in arm length will cause participants to decrease the perceived magnitude of the distance (replicating Linkenauger et al. 2015). We therefore expect opposite effects, with the manipulation expanding reachable space, but retracting distance estimation (Grade et al., 2015; Morgado et al., 2013; Osiurak et al., 2012). In Experiment 2, we expect that the augmentation of action amplitude and speed will have similar effects to that with the augmentation of reaching range. In this condition, an actual 10 cm amplitude reaching action will be displayed in VR compared to 20 cm of physical amplitude movement (causing apparent speed). We expect that this will lead to an increase in perceived reaching capabilities and a decrease in distance estimation. Finally, concerning Experiment 3, we expect that the augmentation of hand

size will have no impact on distance and reachability estimation, as hand size is unrelated to peripersonal space boundary. This predicted absence of effect in the size augmentation condition would demonstrate that it is perceived action capabilities and not perceived body size that is used as a referential metric to calibrate distance perception.

5.2. Method

5.2.1. Participants

Sixty-two healthy participants (aged between 19-29 years, M = 20.7, SD = 1.6; 7 males; 5 left-handed) took part in the experiment. The data sets of two participants were excluded before conducting the analyses, as one participant didn't complete the experiment, and a second participant failed a stereopsis test. The remaining 60 participants had normal or corrected-to-normal visual acuity, and they gave their written consent prior to taking part in the study. Participants were not informed of the action augmentation that occurred during the experiment, and all participants were naïve to the purpose of the study. Participants were randomly assigned to one of three possible action augmentation experiments (i.e., reach, amplitude and size; Experiments 1-3), with 20 participants in each experiment. There were no significant differences in terms of age between the groups ($F(2, 58) = 2.1$, $p > .1$) and the balance of males and left-handers was globally matched for the three experiments (i.e., Experiment 1: 4 males, 2 left-handers; Experiment 2: 2 males, 2 left-handers, and; Experiment 3: 1 male, 1 left-handers). The experiment was non-invasive, and was approved by the ethics committee of the Institut de recherche en Sciences Psychologiques of the Université catholique de Louvain, in accordance with the ethical standards established by the Declaration of Helsinki.

5.2.2. Apparatus and stimuli

The experimentations were carried out in a research laboratory (4 m x 3.5 m x 2.5 m), equipped with an Oculus Rift DK2 head mounted display (v0.4.4, Oculus VR, LLC, USA; field of view approximately 110°; 960 × 1080

pixels per eye) and a position tracking camera to record head movements. This apparatus allowed for the stereoscopic visualization of a 3D virtual environment and 360° exploration through performing head and body rotation movements. Participants sat on a height-adjustable chair with a backrest that was positioned 35 cm from a table edge (dimensions: 150 cm length, 80 cm width and 70 cm high), and eye height was adjusted to 120 cm height from the floor. The participants were seated facing the Oculus position tracking camera. A Leap Motion (v2.2.2; USA) device was used to capture hand movements using infra-red optical tracking and positioned on the center of the table, 35 cm from the table edge.

An experimental environment was created using Unity3D. This same software was also used to integrate and interface the different equipment allowing for interaction within the VE. This environment consisted of a squared virtual room, with walls measuring 5m long and 3m high, with a centered virtual white table (220 cm long, 120 cm wide, and 70 cm high). The virtual camera position corresponding to participant's point of view in the virtual environment, and was placed just in front of the table edge, at a height of 120 cm from the floor. Prior to experimentation, virtual head position was calibrated using a chin rest to synchronize the head positions in the real and virtual environments, ensuring that all participants viewed the virtual environment from the same location in space. Two experimental tasks created: an interaction task and an estimation task.

During the interaction task, virtual boxes appeared on the table (35 cm from participants' virtual location). One box was large, and contained a total of 9 cubes (3 cubes of three different colors), and three boxes were smaller, and further away from the participant than the large box, one centered, one slightly to the left and one slightly to the right. Each small box was empty at the beginning of the interaction task, and each box was marked with a different color (corresponding to the colors of the cubes; see Figure 5.1.A). During this interaction task, participants were requested to grasp the cubes one at a time from the large box, and to move and drop them into the color-associated small boxes (e.g., placing a red cube into the box with the red mark). Real hand position was measured using the Leap Motion, and

corresponded to synchronized virtual hand action within the VE. The three different small box positions were used so that participants performed movements in different radial directions within the virtual space. Participants had to grasp and displace all nine cubes from the large to the small boxes twice, resulting in 18 reach, grasp, displace and release movements. Three action augmentation conditions were created for the purpose of the three different experiments: (1) reaching capabilities were doubled by displacing the participants virtual hands and boxes 35 cm further away in depth from participants virtual seated location; (2) the amplitude of participants hand reaching movements were doubled so that a movement of 1 cm in the real world would appear as 2cm in the virtual world, with all other aspects remaining the same (i.e., the real and virtual hands moving in the same direction, resulting in apparently faster movements, but requiring the same physical effort for execution), and; (3) the size of the virtual hand could be increased by 50% leading to participants experiencing virtual hands 1.5 times bigger than their actual size. For this latter manipulation, the participants real hand size was recorded by the Leap Motion, and manipulated to display the virtual hand.

In the estimation task (see Figure 5.1B) a single red rectangular cuboid (5cm length, 2.5cm height and depth) appeared at 12 different distances along participants' sagittal body-midline axis (15; 25; 35; 45; 55; 65; 75; 85; 95; 105; 115; 125 cm), repeated 4 times each, leading to 48 estimation trials that were randomly presented. A red rectangle was also placed just in front of participants, in the center of the table edge and used in order to provide participants with a reference mark when estimating distances (for similar set up, see Linkenauger et al., 2015).

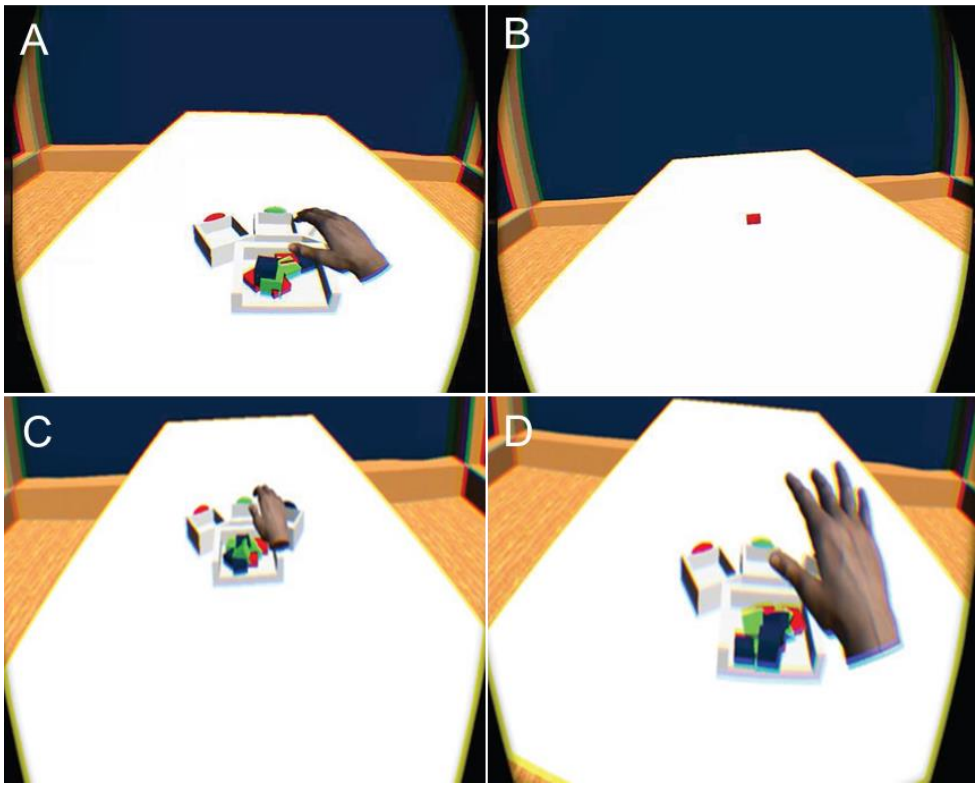

Figure 5.1: *Images extracted from the Oculus rift visual outputs, with* ***(A)*** *depicting the interaction task, where participants had to perform 18 reach to grasp, displace and release movements,* ***(B)*** *showing the estimation task where participants had to estimate 12 possible target distances, ranging from 15 to 125 cm, in steps of 10 cm,* ***(C)*** *depicting the action range augmentation and* ***(D)*** *depicting the hand size augmentation occurring during the interaction task.*

5.2.3. Procedure

For each experiments, participants came to the laboratory on two different days (always separated by seven days), and each time they started by performing the interaction phase, and then immediately performed the estimation phase. The augmentation of the interaction task was manipulated on the different days, with the participant either performing the task with no augmentation (i.e., where real and virtual actions corresponded to each other) or with augmented actions. The day when the manipulation occurred was counterbalanced across participants.

Participants were randomly assigned to one of the three virtual action augmentation experiments (i.e., reach-range, amplitude-speed or hand-size), with 20 participants in each experiment. Upon arrival to the laboratory, participants first completed a consent form and a cyber sickness questionnaire (Bouchard, Robillard, & Renaud, 2007). This was performed outside of the laboratory room. Then, participants were blindfolded, and with the help of the experimenter, guided to the testing laboratory and seated in front of the testing table, and the head mounted display put onto the participant's head. This procedure was done in order to immerse the participant in the virtual room, without them seeing or having any knowledge of the look of the actual laboratory and it's dimensions. Throughout the experiment, participants were asked to keep their back against the chair backrest, and they also wore a safety belt to ensure that they did not fall from the chair during the immersion. Once the head mounted display was worn by the participant, they were asked to open their eyes, and they were immediately faced with the virtual environment. They were invited to look around and discover the virtual environment by moving their head and their trunk. After visual immersion, they were then asked to complete the interaction task by performing the 18 reach, grasp, displace and release movements (either with or without the augmentation). Following the interaction task, they were asked to rest their hands on their upper legs, and the estimation task began.

For each trial (12 x 4 possible distances), participants were first asked to judge if the target was reachable or not by saying "yes" or "no" aloud, and immediately after, to estimate the number of centimeters separating the target from the reference mark placed in front of them, within the virtual environment. At the end of each trial, the experimenter encoded the responses and launched the subsequent trial by a pressing a key on a keyboard. After completing the 48 trials, participants were led outside of the room, again with their eyes closed, and they were then asked to again complete the cybersickness questionnaire. The aim of this was to measure if participants experienced any increased discomfort during the experiment due to the immersion. A second questionnaire was also given that measured virtual presence; the engagment of participants within in the virtual

environement (Robillard, Bouchard, Fournier, & Renaud, 2003). Finally, at the end of the second session, participants were given a basic stereopsis test in order to evaluate their ability to perceive 3D using the same visual cues used by the Oculus Rift to create the 3D virtual environment[2] (Nongpiur & Sharma, 2010). Participants' height, arm length and maximum reaching capability on the table were also measured. Finally, participants were questioned about their impression of the experiment, and all questions were answered.

5.2.4. Data analysis

In order to investigate the impact that the different types of virtual action augmentation had on space perception, several analyses were conducted on both reachability and distance estimation responses separately, for the three action augmentation experiments; reach-range, amplitude-speed or hand-size. To assess accuracy of egocentric distance estimation independently of the distance magnitude of the target to be estimated, an error rate was computed by dividing the difference between estimated and actual distance by the actual distance (i.e., [participant's response - actual distance]/actual distance; positive values of this error rate indicate overestimation, negative values indicate underestimation, and a value of 0 indicates perfect accuracy; for a similar index, see Crollen et al., 2013; Grade et al., 2015). Data from outlier responses (on which error rate was above or below 2.5 standard deviations from the overall mean) were excluded from the analyses (2.1 % of the total data). These error rates were submitted to a 2x4 repeated measure analysis of variance (ANOVA) with action augmentation (i.e., normal or augmented) and distance (averaged into four distance categories; very close with distances 15; 25; 35; close with distances 45; 55; 65; far with distances 75; 85; 95; and very far with distances 105; 115; 125) as within-subject factors. The same 2x4 ANOVA was used on "yes" response

[2]The experimenter put a pen just in front and a little below the nose of the participant who had to try to touch the pointed end of the pen with a second pen and using both eyes. There were 5 trials, if participants failed all of them the test was considered as failed and the participant removed from data analyses (only one participant failed the test and he also declared having bad stereoscopy due to an eye condition).

percentages as the dependent variable to investigate the impact of the experimental conditions on reachability judgements. For all analyses, Bonferroni corrections ($_{BC}$) were applied where multiple post hoc comparisons were used. To assess whether the virtual action manipulation moderated the perceived boundary of participant's peripersonal space, reachability judgement responses were also submitted to a logistic regression model. This model was used to fit the "yes/no" response occurrence to target distance, using the following equation:

$$y = e^{(\alpha + \beta X)} / (1 + e^{(\alpha + \beta X)})$$

Here, y is the participant's "yes" response probability, X is the target distance and $(-\alpha / \beta)$ is the estimated value of x at which targets are no longer considered as reachable anymore, delimiting the boundary of reachable space (for similar procedures see Bourgeois & Coello, 2014; Bourgeois, Farné & Coello, 2012; Coello et al., 2008). Then, separately for each participant and each action augmentation condition, bisection points were calculated by taking the value of x when y = 0.5, thus providing the extent of participant's peripersonal space in cm for normal and augmented virtual action conditions. Finally, bisection point means of the two conditions where compared using a paired sample *t*-test.

5.3. Results

5.3.1. Action range/reach augmentation condition

For the group of participants who experienced reach augmentation in their virtual actions, the analysis of error rate in distance estimation revealed a significant main effect of the action augmentation condition ($F(1, 19) = 6.2$, $p < .05$, $\eta_p^2 = .24$), with lower error rates in the augmented condition ($M = -0.16 \pm 0.21$) compared to the normal action condition ($M = -0.12 \pm 0.20$). There was no significant main effect of distance categories ($F(3, 57) = 1.8$, $p > .05$, $\eta_p^2 = .11$) and no significant interaction ($F(3, 57) = 1.8$, $p > .05$, $\eta_p^2 = .08$; see Figure 5.2). For reachability judgements, the ANOVA examining the percentage of yes responses showed a main effect of action

augmentation conditions ($F(1, 19) = 7.8$, $p < .05$, $\eta_p^2 = .29$), with higher yes response percentage in the augmented ($M = 63.6 \pm 9.1$) than in the normal ($M = 57.9 \pm 8.2$) action condition. There was a main effect of distance categories ($F(3, 57) = 289.6$, $p < .001$, $\eta_p^2 = .93$), with the far category being significantly lower than the very near and near categories and the very far category being significantly lower than the 3 other categories (all $p_{BC} < .05$). A significant interaction between distance categories and action augmentation conditions ($F(3, 57) = 6.7$, $p < .01$, $\eta_p^2 = .26$) was decomposed by contrasting normal and augmented action conditions for each distance category using paired *t*-tests. The only significant difference between normal and augmented action conditions was within the far distance category ($t(19) = 2.8$, $p_{BC} < .05$).

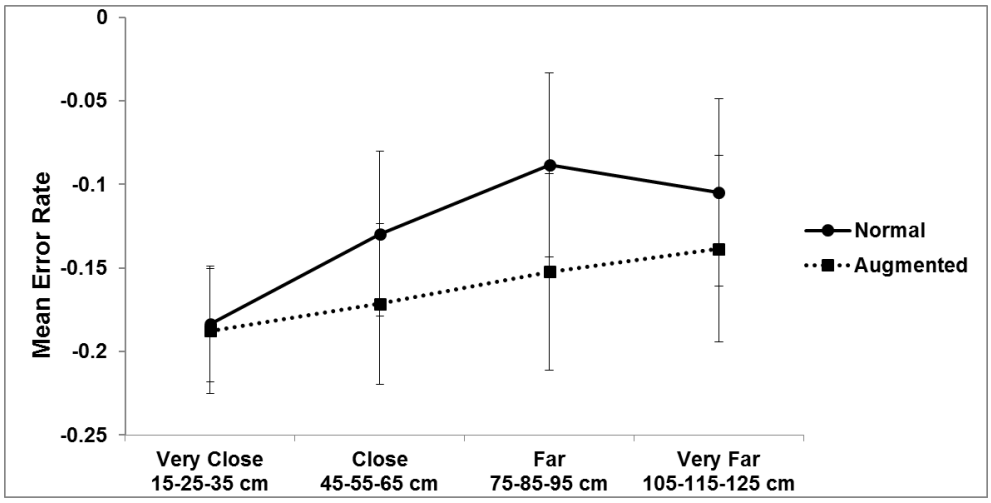

Figure 5.2: *Mean error rate of the distance estimates as a function of virtual action conditions (normal vs augmented) and distance categories (very near, near, far, very far) in the reach augmentation group.*

To assess the impact of virtual action augmentation condition on the perceived boundary of reachable space, bisection points were extracted from reachability judgement responses using a logistic regression model. The mean value of participant's bisection points was significantly larger in the augmented ($M = 85.6 \pm 10.9$) compared to the normal ($M = 79.01 \pm 10.3$) virtual action condition ($t(19) = 2.7$, $p < .05$; see Figure 5.3).

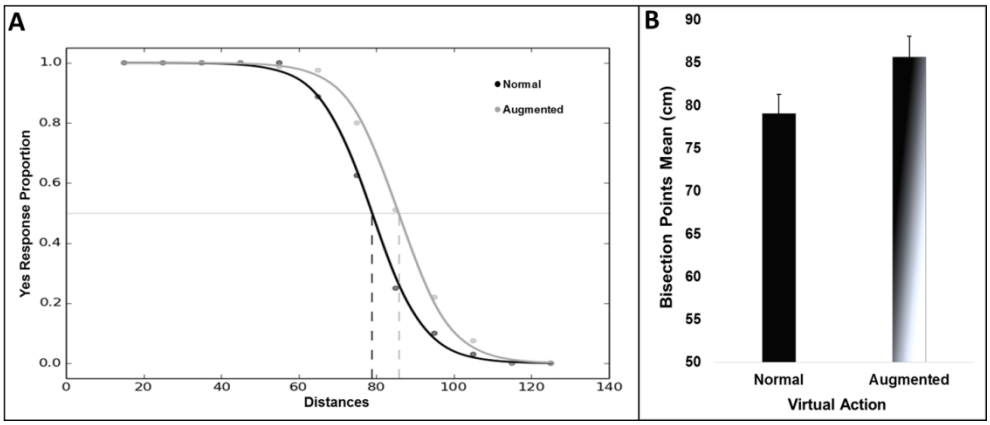

Figure 5.3: (A) *Yes (reachable) response proportions as a function of target distance and virtual action condition (normal, augmented).* ***(B)*** *Mean values of bisection points as a function of virtual action condition in the reach augmentation group.*

5.3.2. Action amplitude/speed augmentation condition

For the group of participants who experienced amplitude augmentation in their virtual actions, the analysis of the error rate in distance estimation revealed no significant main effect of the action augmentation condition ($F(1, 19) = 2.7$, $p > .05$, $\eta_p^2 = .24$). There was a significant main effect of distance categories ($F(3, 57) = 7.4$, $p < .05$, $\eta_p^2 = .28$), with the very near distance category being significantly lower than the three remaining distance categories (all $ps_{BC} < .05$), while no other pairwise comparisons showed significant differences. A significant interaction between virtual action conditions and distance categories ($F(3, 57) = 7.3$, $p < .05$, $\eta_p^2 = .28$) was decomposed by comparing normal and augmented action conditions for each distance category using paired *t*-tests. Mean error rates were lower in the augmented compared to the normal action condition, but only within the very far distance category ($t(19) = -2.8$, $p_{BC} < .05$; see Figure5.4). The remaining distance categories did not show significant differences between action conditions (all $p > .05$). For reachability judgements, the ANOVA examining the percentage of yes responses showed no significant effect of virtual action conditions ($F(1, 19) = 0.2$, $p > .05$, $\eta_p^2 = .01$). There was a main effect of distance categories ($F(3, 57) = 135.7$, $p < .001$, $\eta_p^2 = .93$),

with all categories being significantly different from each other (all $ps_{BC} < .001$), except for the difference between the far and very far categories. No significant interaction was found between distance categories and action augmentation conditions ($F(3, 57) = 0.03$, $p > .05$, $\eta_p^2 = .002$).

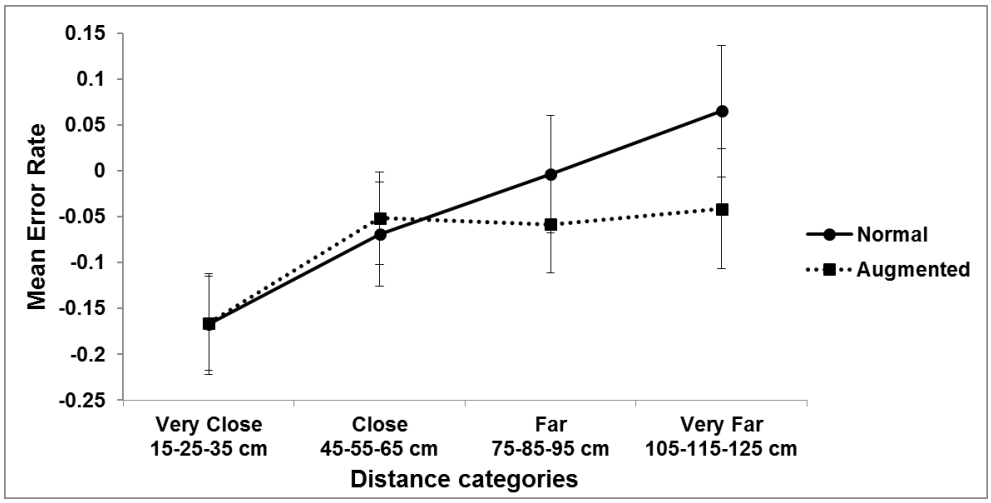

Figure 5.4: *Mean error rate of the distance estimates as a function of virtual action conditions (normal vs augmented) and distance categories (very near, near, far, very far) in the speed/amplitude augmentation group.*

To assess the impact of virtual action amplitude augmentation condition on the perceived boundary of reachable space, bisection points were extracted from reachability judgements using a logistic regression model. There was no significant difference between bisection points mean values in the normal and augmented virtual action conditions ($t(19) = 0.4$, $p > .05$; see Figure 5.5).

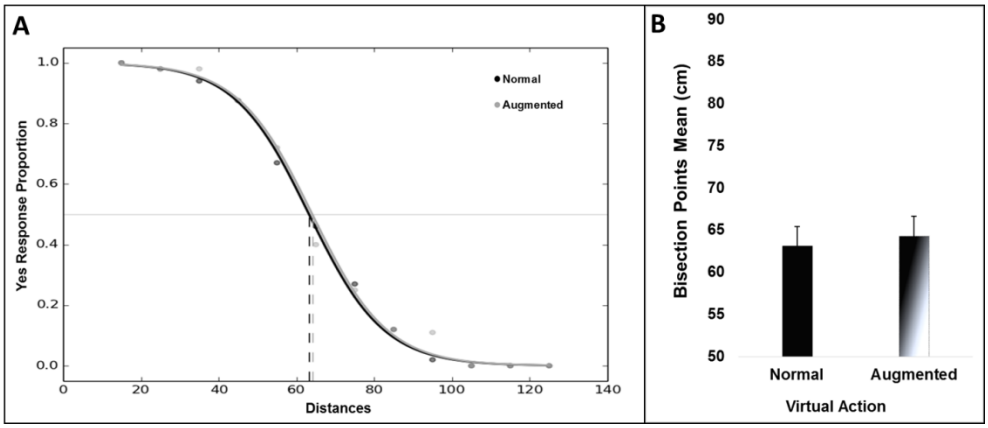

Figure 5.5: (A) *Yes (reachable) response proportions as a function of target distance and virtual action condition (normal, augmented).* ***(B)*** *Mean values of bisection points as a function of virtual action condition in the amplitude/speed augmentation group.*

5.3.3. Hand size augmentation condition

For the group of participants who experienced virtual hand size augmentation, the analysis of the error rate in distance estimation reveal no significant main effect of the action augmentation condition ($F(1, 19) = 0.1$, $p > .05$, $\eta_p^2 = .01$), no significant main effect of distance categories ($F(3, 57) = 2.5$, $p > .05$, $\eta_p^2 = .11$), and no significant interaction ($F(3, 57) = 1.4$, $p > .05$, $\eta_p^2 = .07$; see Figure 5.6A). For reachability judgements, the ANOVA examining the percentage of yes response show no significant effect of virtual action conditions ($F(1, 19) = 0.3$, $p > .05$, $\eta_p^2 = .02$), but there was a main effect of distance categories ($F(3, 57) = 127.7$, $p < .001$, $\eta_p^2 = .87$), with all categories being significantly different from each other (all $ps_{BC} < .05$). No significant interaction was found between distance categories and action augmentation conditions ($F(3, 57) = 0.8$, $p > .05$, $\eta_p^2 = .04$; see Figure 5.6B).

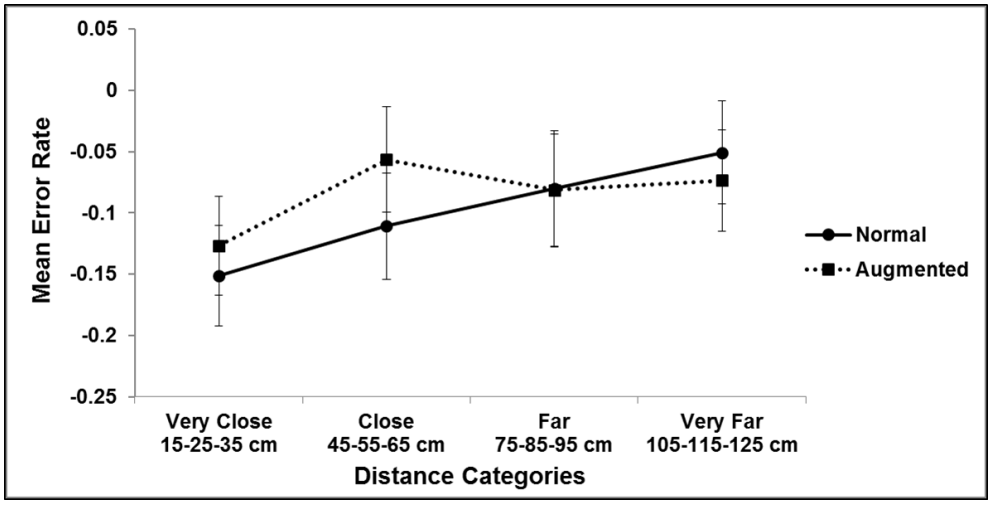

Figure 5.6: *Mean error rate of the distance estimates as a function of virtual action conditions (normal vs augmented) and distance categories (very near, near, far, very far) in the hand size augmentation group.*

To assess the impact of virtual hand size augmentation condition on the perceived boundary of reachable space, bisection points were extracted from reachability judgements using a logistic regression model. There was no significant difference between bisection points mean values in the normal and augmented conditions ($t(19) = 0.6$, $p > .05$; see Figure 5.7).

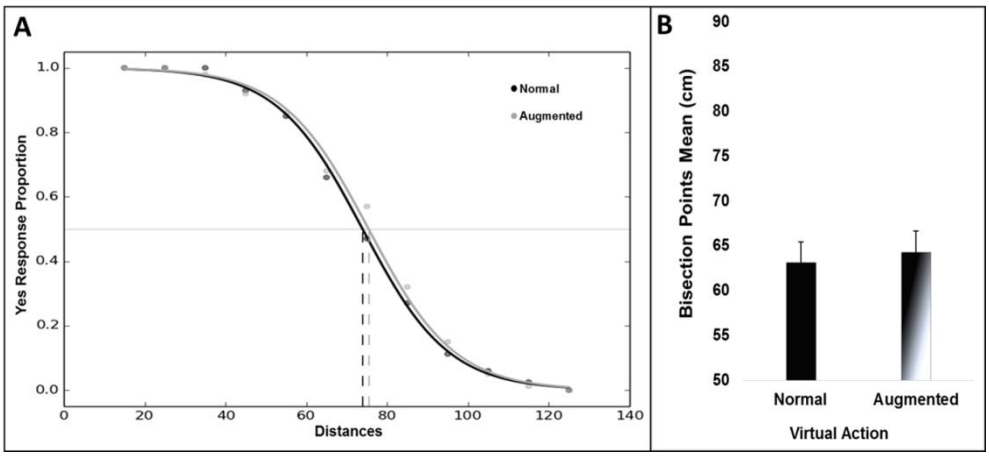

Figure 5.7: (A) *Yes (reachable) response proportions as a function of target distance and virtual action condition (normal, augmented).* ***(B)*** *Mean values of bisection points as a function of virtual action condition in the amplitude/speed augmentation group.*

5.4. Discussion

Recent literature demonstrated that changing the size of a user's arm within VR influenced distance estimation, but only if the user had previously experienced acting with a shorter or longer arm inside a VE (Linkenauger et al., 2015). The aim of the present study was to determine more precisely which component of body and action augmentation within VR was detrimental in affecting both egocentric distance estimation and reachability judgement. Both behaviors were investigated within the same group of participants, and therefore concomitant effects of the VR manipulation were expected. Three different types of augmentation were investigated. The augmentation of reaching range (Experiment 1), as expected, expanded perceive reaching capabilities while retracting distance estimation. In Experiment 2, where movement amplitude-speed was manipulated, the results were more ambiguous. Similar results to Experiment 1 were expected, but instead, the augmentation of amplitude-speed only affected the estimation of very far distances. Finally, for Experiment 3, there was an absence of hand size augmentation influence on both reachability judgement and distance estimation tasks, as predicted.

Experiment 1 showed that having performed movements with an augmented action reach range increased participant's perceived reaching capabilities. Analyses showed that more targets were considered as reachable, and that the reachable space boundary was extended following the interaction task performed with an augmented reaching range. As previously shown in the literature, participants adapted to the new action parameters, and they calibrated their reaching space as a function of the adaptation (Bourgeois & Coello, 2012). For distance estimation, having augmented action range led participants to underestimate distances more compared to having normal reaching capabilities, replicating previously reported literature (Linkenauger et al., 2015; Osiurak et al., 2012; Witt et al., 2005; Witt & Proffitt, 2008). The virtual manipulation of action range therefore had a clear influence on both estimation task performances, but in opposite directions, as an increase was found for reachability judgements, but a decrease was found distance estimates. This first set of findings clearly supports the assumption that

reachability and distance estimation might exploit the same perceived reaching capabilities as a calibration metric (Linkenauger et al., 2015; Grade et al., 2015; see also Chapter 3), further supported by the negative relationship between the two behavioral measures (i.e., as perceived reachability increased or decreased, estimated distance decreased or increased, respectively; see Morgado et al., 2013; Osiurak et al., 2012).

In Experiment 2, results showed that reachability judgements were not affected by prior interactions with amplitude-speed augmented actions, as the augmented amplitude-speed of the movements did not affect the perceived boundary of peripersonal space. Although unexpected, this absence of effect could be due to the fact that whatever the action condition (i.e., normal *vs*. augmented), the area of space where the virtual cubes appeared was the same for both conditions (while this was not the case in Experiment 1, since the cubes and boxes moved with hand position). Even if participants had bigger action amplitude, and therefore could act in a larger area, they did not need to, as the interaction task only required them to grasp and release the virtual cubes in the areas of the boxes. On the other hand, results showed that distance estimation was influence by the action augmentation condition, albeit for the very far distances (i.e., the amplitude-speed augmentation effect was restricted for the very far distances; 105; 115; 125 cm). When having performed actions with doubled amplitude (moving twice further and faster than the real movement), participants estimated very far distances as closer than when having performed normal action. This effect could be due to the difference between real hand position and virtual hand position increasing with time and speed of the movement. This is in line with a study demonstrating that an increase in amplitude (and/or effort) of reaching actions diminished perceived distance if distance estimation occurred during action planning (Kirsch and Kunde, 2013).

This amplitude-speed augmentation in Experiment 2 did not impact both measured behaviors as observed in Experiment 1, perhaps suggesting different mechanisms in the effects of the two types of augmentation. In the amplitude augmentation of Experiment 1, the effect could be more similar to the perceptive-motor recalibration of speed that was previously observed

when manipulating walking speed and optic flow (Mohler at al., 2004). An additional factor to be taken into account is the implication of more or less effort in the movements, as several findings point out that increased effort in actions (toward a goal) can induce participants estimations of distance (of that goal; Kirsch & Kunde, 2013; Witt et al., 2004). Yet, with twice more amplitude, the movements to be performed were twice less effortful, and this reduction in the effort might have caused the reduction of distance estimates that was observed. As for the effect of effort on reachability judgement, previous work show divergent findings. For example, wearing weights on the wrists reduced reachability judgements (for 1 vs. 3 kg; Rochat & Wraga 1999) or had no effect (1.5 kg Bourgeois & Coello, 2009). The reason for this inconsistency might reside in differences in postural stability requirements between the two studies, as participants were standing up in one experiment (Rochat & Wraga, 1999), while in the other experiment, head and body were maintained mechanically, and no movements were possible (Bourgeois & Coello, 2009). From this difference, we might assume that the effect of weights on wrist and reachability judgements might therefore arise only if postural stability is involved, as weights on extended arms can impact balance (Rochat & Wraga, 1999). In our experiment, participants were sitting, attached to a chair, and had no concern for their balance. This would suggest that in our experiment, postural stability was not an issue, and therefore a reduction of effort did not impact reachability judgements, somewhat replicating the results of Bourgeois and Coello (2009).

Finally, for the augmentation of hand size (Experiment 3), results were clear cut, as no influence was observed on reachability judgements and on distance estimation. As predicted, hand size was not used as a calibration metric in the scaling of distance perception. Still, it has been shown that hand size might be used in the scaling of graspable object size. (Linkenauger, Leyrer, Bulthoff & Mohler, 2013; Linkenauger, Witt & Proffitt, 2011). This would suggest that graspability (almost entirely determined by hand size) might contribute to size estimation, while reachability (determined by arm length, and also the rest of the body; whole body engagement; see Fischer, 2000) would contribute to distance

estimation (Linkenauger et al., 2015). This is further in line with research on visuomotor transformation along two separate (but linked) visuomotor channels implied in the processing of size (object-centered coordinates) for grasp execution and in the processing of distance (body-centered coordinates) for reach execution (Jeannerod, 1994).

The results presented here, along with others results reported in the literature (e.g., Kirsch & Kunde, 2013; Linkenauger et al., 2015; Morgado et al., 2013; Osiurak et al., 2012; Witt et al., 2005; Witt & Proffitt, 2008), provide evidence that perceptual metrics derived from the body capabilities could be exploited to scale spatial information in the environment. Still, it remains unclear what is the precise nature of these metrics (between being derived from body size or action capabilities; Linkenauger et al., 2015), and although represented reachability is assumed to contribute to this metric, it has not been directly measured together with and in relation to egocentric distance estimation (except in Grade et al., 2015, and the present study). Therefore, here we bring support for an online simulated representation of action capabilities involved in perceiving distance, as well as for a negative relationship between the two behaviors or reachability and distance estimation (Morgado et al., 2013; Osiurak et al., 2012).

Previously, it has been proposed that the perceptual metrics involved in distance estimation might not be derived from a representation of the body proportions or size, but rather might be derived from action capability representations, even though the two are highly related (Linkenauger et al., 2015). This was suggested by the fact that if no reaching actions were performed in VR, the size of the arm (still visible) had no subsequent impact on distance estimation (see Linkenauger et al., 2015) The present study casts additional light on this uncertainty, as we showed that the acting range of the hand had an impact on estimation measures, while hand size augmentation had no impact. Our results therefore suggest that a calibration metric for distance perception was derived from dynamic representation of action capabilities, rather than a structural representation of the (static) body. These results also strengthen the idea for the importance of having a virtual body for good perception of space in the virtual environment. Being

able to use the body in the virtual space was probably crucial for the effects (Kelly, et al., 2013; Linkenauger et al., 2015; Richardson & Waller, 2007).

The results in the current study suggest that dynamic action interaction calibrates space rather than calibration coming from a long-term fixed representation of body dimension. This calibration may seem obvious if one considers the constant need of our action system to compute or simulate on line to better adapt to surprises or obstacles in the environment that would influence our maneuverable potentials (Bartolo et al., 2014; Bourgeois & Coello, 2012; Bourgeois et al., 2014; Coello & Delevoye-Turrell, 2007). Depending on the context of an obstacle or an effector (e.g., danger; postural stability; use of tools), our action system adapts to all possible environments. Therefore, reaching capability representation might be stored in a long-term representation that would need to be flexible and adapt constantly to the possible diverse parameters of the environment. This would lead to a dynamic representation that is permanently generated by online action simulation mechanisms (Gallese, 2015). Qualitative evidence for this is provided by how fast participants adapt to changes (i.e., re-afference mechanisms; Held & Schlank, 1959; Von Holst, 1954), or distortion in perceptual-motor feedback, for example with the use of rubber-hand illusion (Botvinick & Cohen, 1998; Longo, et al., 2008), mirror box (Bourgeois & Coello, 2012) or virtual reality (Kilteni et al., 2012).

In conclusion, the present study brings further evidence that space perception benefits from embodied action simulation processes, where represented reaching capabilities contribute to distance perception by providing a calibration metric (Gallese, 2016; Grade et al., 2015; Linkenauger et al., 2015). The results of the present study highlight the dynamic contribution of reachability representation when visually perceiving if an object is reachable and estimating the amount of distance separating ourselves from an object (Bourgeois & Coello, 2012; Coello & Delevoye-Turrell, 2007; Proffitt, 2013).

CHAPTER 6: GENERAL DISCUSSION

In this thesis, my aim was to build on the current literature, and investigate the contribution of motor and magnitude processing for the perception of space to better understand the underlying mechanism involved in distance perception and in the delimitation of subspaces. In Chapter 1, I reviewed the literature arguing that space perception is represented using multiple sources of information, including body action capability, sensory motor (simulation) processes, and number magnitude processing, all of which rely upon dorsal-stream parietal and prefrontal networks. From this review, I suggested a possible functional reason for the proximity of the neural processing for these different sources of information, with the idea that at the heart of space representation, there might be a common or overlapping magnitude coding mechanism for the representation of space that uses body action capability simulation (sensory-motor). I tested this by investigating relations between number, magnitude, body action (simulation) and space in four empirical chapters.

Chapter 2 investigated the interactions between egocentric (near-far) space and numerical processing. The aim was to investigate the role of the body action capability on number space processing, and whether action simulation contributed to a calibration of external space perception. In Chapters 3, 4 and 5, the same standard measures of space perception were used; reachability and distance estimation (always with the same group of participants). Chapter 3 tested whether the same action simulation process was used in reachability judgement and distance estimation by using motoric dual tasks that would interfere with dynamic action simulation processes, leading to a disturbance in spatial processing. Chapter 4 tested the relation between action simulation and altercentric (other-centered) space perception, and the relative contributions of static and dynamic body and action information. Finally, Chapter 5 stretched simulation by augmenting body length, speed and size within a virtual environment. It was predicted that an increase in reaching action capabilities would impact on

the perception of the virtual environment's space, and that the effect would be equal for reachability and distance estimation, suggesting a common underlying representation for space perception.

In this General Discussion, I will discuss the findings of these empirical chapters by grouping their common findings, in relation to the general literature review of Chapter 1. Rather than repeating the discussion of each chapter, I will focus the discussion around three main themes: (i) how space is calibrated and delimited through body simulation capability; (ii) whether action simulation is based on dynamic or long-term learned body representations, and; (iii) whether magnitude coding of perceived distance arises from sensorimotor experiences. I will then discuss the thesis limitations, and finally, I will end with a discussion of future perspectives.

6.1. The calibration and delimitation of space through the body

One of the main objectives of the present thesis was to test whether distance estimation and reachability judgement relied on a common body action simulation mechanism to calibrate and delimit space (Bourgeois & Coello, 2012; Bourgeois et al., 2014; Carello et al., 1989; Morgado et al., 2013; Osiurak et al., 2012; Rochat & Wraga, 1997; Witt & Proffitt, 2008). Some support for this already existed in the literature, for example with studies having shown that increasing (with tools use) or decreasing (with obstacles or other action constraints) action capability, influenced distance estimation hence, space perception (Morgado et al., 2013; Osiurak et al., 2012). I therefore hypothesized that space perception would be calibrated and delimited by a common reach capability simulation process, and I tested this by measuring both processes together with the same participants and manipulations. From Chapters 3, 4 and 5, I found support for this hypothesis. The results presented in Chapter 3 showed that reachability and distance estimation appeared to share a common action simulation process, as the ball-squeezing dual task interfered with both measures in a similar way. Chapters 4 and 5 extended this, as the results clearly demonstrated that both behavioral measures benefited from calibration scaling that exploited

the static and dynamic representations of the body. Furthermore, Chapters 4 and 5 showed a clear negative relationship between the two measures, showing that if reachability estimation increased, distance estimation decreased, adding supplementary support that distance estimation and reachability judgements appeared to be derived from a common underlying process. I will discuss each of these chapter findings in more detail below.

In Chapter 3, I showed that repeatedly squeezing foam balls with both hands slowed down responses in reachability and distance estimation tasks. I suggested that the motoric dual task recruited motor resources, which competed and reduced the motoric resources available for the internal simulation of actions, slowing performance. This finding replicated the TMS of hand area motor cortex effects (Coello et al. 2008). The interference observed in the dual-task had similar impact on both reachability and distance estimation speed. This suggests that the two tasks rely on common motor resources, and a shared or overlapping action simulation mechanism. Despite response speed slowing, the dual task did not modify the response profile or accuracy of participant response. Therefore, even with reduced motor resources, the simulation of their represented body capabilities remained unchanged by the mobilization of the motor system. This may suggest that simulation uses the motor system as a purposeful space perception mechanism, but which uses non-motoric information (such as body knowledge) to perceive space. Here, the mechanism was slowed by the dual task, but the non-motoric information remained uncompromised. I will return to this point later in the discussion.

In Chapter 5, body capabilities were virtually changed using a virtual reality system composed of a head-mounted display and a motion capture device. Participants' hand reaching range was increased during prehension movements, leading them to experience new modified body capabilities. Due to this virtual manipulation, I showed that participants perceived an increase of subsequent reachability judgements (i.e., more targets were reported as reachable), and a decreased magnitude of egocentric distance estimates (replicating and extending previous findings; Linkenauger et al., 2015). These empirical findings sharpen the idea of a close relationship

between reachability and distance estimation, with a negative relation between distance magnitude estimation and perceived reachability.

Interestingly, this negative relationship was not only observed under an egocentric perspective but, in Chapter 4, it was also observed for altercentric spatial perception. The perceived reaching capabilities of a third-person external agent, and the estimation of distances separating the same agent from the targets were both influenced by the agent's body posture, but in opposite directions. Having the actor in a high compared to low posture led the participants to judge the agent's reachability as larger, and the distances between the agent and object as shorter (and vice versa). Moreover, accuracy in both tasks was improved by the observation of the actor performing reaching movements. This suggested that dynamic representations of the body in action were more informative than static posture for the perception of the surrounding space, though both static and dynamic body cues played a role in the calibration of external space.

As discussed in the previous paragraph, the results from Chapter 4 suggest that the simulation of other's body action capabilities, perhaps anchored on self body representation, were used to calibrate space. However, as an alternative, one might consider that the simulation of the agent's action capabilities would be based on postural cues and not on the observer's body proportion. The model proposed by Cutting and Vishton (1995) already pointed out the importance of size-distance consistency, stating that prototypical size of objects (or other elements in the environment) provides a crucial visual cue to extract distance or depth information (i.e., personal, action or vista subspaces; Cutting & Vishton, 1995). For example, one can benefit from the presence of a car versus a drinking bottle in the environment, as their "actual" size is known, and the two objects can be compared to their current situation size in order to extract an estimation of distance. The body size of other people probably offers similar visual-spatial scaling mechanisms, perhaps demonstrated using the famous Ames distorted room optical illusion (Gehringer & Engel, 1986; Runeson, 1988). This illusion consists of a room where the back wall appears normal and flat, but in reality one of the corners is more distant than the other causing the

illusion of body shrinking or enlarging depending on the corner where the person is located. With the idea that knowledge of other's bodies can be exploited to calibrate external space, we could expect that knowledge of body size (relative to the room or table size) could provide depth information. In this case, a simulation of the agent's action capability from static posture may not be necessary. However, this suggestion leads to problems. Estimating the reachability of the agent or the distance between the agent and object without body action simulation would require storing knowledge of how different body postures fit with the surrounding space. This seems unlikely, as one would need to store all of the different characteristics of body postures. Also, if this was the case, the retrieval of a body posture and associated space should be equal irrespective of object location. The results in Experiment 4 do not support this. For example, in reachability estimation, response time was slowed the more the object was place towards the boundary of peripersonal space (replicating Bartolo et al., 2014; Fischer, 2000; Fischer, 2005; Gabbard, et al., 2006; Lamm et al., 2007; see also Chapter 3). Therefore, to explain these results, it seems likely that postural information was combined with a body action simulation manipulation.

Overall, the present thesis suggests that space perception along the sagittal axis is calibrated by current state of body dimension and capability, supporting similar proposals in the literature (Coello & Delevoye-Turrell, 2007; Proffitt, 2013). In order to code visual information and spatial intensities, the perceptual system needs an anchor, an origin, a reference. I support these previous proposals, and with the data from the present thesis, I suggest that the current state of the body and its action capabilities in both first- and third-person perspectives are used in action simulation for perceiving space. The finding that virtual extension of reach capability (Chapter 5) changed space perception suggests that the calibration of space (through simulation) is a dynamic process that is constantly updated. As advocated by previous authors, visual information is constantly calibrated using eye-centered, head-centered, trunk-centered and world-centered frames of reference within the parietal cortex (Andersen et al., 1997; Gross & Graziano, 1995). I propose that these dynamic processes are used to

calibrate the current state and position of the body, or perceived other bodies, for the perception of space in reachability and distance estimation tasks.

This finding and suggestion provides a starting point to investigate other factors of how the brain codes current body state for actively simulating body capabilities, or for predicting future body states, and furthermore, how these simulations impact the perception of the environment (see section 6.2. for further discussion of the contribution of static and dynamic body information in space perception). As stated in the introduction, space perception can be seen as a multisensory-motor construct (Brozzoli et al., 2012; Coello & Delevoye-Turrell, 2007; Previc, 1998), where different actions such as gazing, grasping, reaching, and walking, as well as multiple visual and oculomotor cues, can be used together to segregate spatial cognition into different subspaces (Rizzolatti et al., 1997; Gallese, 2016; Grusser, 1983; Cutting & Vishton, 1995). In the following four paragraphs, I discuss how different possible delimitations of space could be defined by different types of bodily action.

In Chapters 3, 4 and 5, I tested the contribution of body action simulation on the delimitation of peripersonal space perception. However, as discussed in the literature review presented in Chapter 1, there is good evidence for segmentation of different subspaces that extend beyond peri-personal space (Brozzoli et al., 2012; Coello & Delevoye-Turrell, 2007; Cutting & Vishton, 1995; Grusser, 1983; Previc, 1998; Rizzolatti et al., 1997; Saj & Vuillemier, 2007). Moreover, these different subspaces would interact, as they serve complementary roles in spatial behaviors. If spatial cognition is calibrated and categorized according to different (current) body and action representations, then one might expect multiple different types of body action representations that provide the reference point for different sub-space perception.

In the current thesis, I focused on reach action capability being the delimiting factor of peripersonal space perception. In Chapter 3, I showed that hand based but not arm based motoric dual task interfered with

peripersonal reachability and distance estimation. I argued that these effects were driven by the fact that the hands may be central for goal directed action. This is somewhat supported by the coordination model of reach and grasp proposed by Jeannerod et al. (1995), where the purpose of reach is to transport the acting hand to the location of an object. Moreover, from the literature review, there is evidence of hand-centered reference frames for controlling and perceiving the moving hands within peri-personal space (Brozzoli et al., 2010; Brozzoli, Ehrsson & Farné, 2014; Brozzoli, Gentille & Ehrsson, 2012; Brozzoli et al., 2012; Brozzoli et al., 2009; Grazianio & Gross, 1993; Gross & Graziano, 1995).

Based on the action simulation proposal, one might expect that the simulated representation of hand action forms a hand-centered perception of space that is independent of reach-centered perception of space. Evidence for this is found in a study by Brozzoli et al. (2010; see also Brozzoli et al., 2009). They used a cross-modal visuo-tactile interference paradigm where participants wore tactile stimulators placed on their index finger and thumb that could be stimulated during the execution of reach to grip movements made towards a cylinder. The cylinder contained lights situated on the top and bottom parts of the object, and the congruence between light position (top *vs*. bottom) and finger stimulation (index *vs*. thumb) interfered with tactile perceptual discriminations. Interestingly, this interference was stronger when the hand was situated near the cylinder, at the end of the reaching phase, compared to when situated near the body (Brozzoli et al., 2010). This suggests that the spatial perception of touch was influenced by light location on the target object depending on the hand position during the action. Assuming that action simulation follows the same principals as action execution, one might also assume that simulation can use a hand-centered action simulation to the object, and that this type of simulation may be also used for within object spatial perception.

Grasping objects allows for subsequent object manipulation. For example, with an object in one's hand, one can perform various manipulations such as rotating the object within our hand. This type of action may provide spatial coding of tactile and orientation features of objects that can be combined

through multisensory integration and binding (Ernst & Bülthoff, 2004). Based on this point and the arguments of the previous paragraph, one might expect that within object spatial perception might be grounded on simulated grasping action, whereas peripersonal spatial perception might be grounded on simulated (goal directed) reach and grasp action (Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015). In this sense, the term peripersonal space could represent the dynamic and movable aspect of hand-centered grasping space.

Beyond peripersonal space; extrapersonal space(s) extend up to the limits of vision (Grusser, 1983; Previc, 1998). Previc (1998) described three different extrapersonal spaces: (i) the focal extrapersonal or oculomotor space that relies on vision, eye movement and attentional cognitive mechanisms to provide a movable fixation window for visual search and object recognition; (ii) the action extrapersonal space that relies on visual, auditory, vestibular and olfactory sensory systems, as well as eye, head and trunk actions allowing for orientation and navigation in any direction around the body (360°), and; (iii) the ambient extrapersonal space that is involved in postural control and locomotion, and related to lower limb action, as well as vestibular, somatosensory and visual sensory processes. Although, these three different extrapersonal spaces seem well defined, particularly by their actions, some of their functions could be further segregated. For example, orientation, navigation and scene memory, or postural control and locomotion, could be considered as different factors, and each factor may have particular pairings. For example, the perception of navigation space might be delimited by walking capability, whereas the perception of orientation might be delimited by vestibular processes of balance. The notion of representational or mental spaces seem important in navigation or wayfinding tasks, as well as the interplay between egocentric and allocentric perspectives (Ekstrom et al., 2014), suggesting that these space perception processes may be grounded on more processes than action simulation alone. Furthermore, the area of space behind our back (i.e., back space; Saj & Vuillemier, 2007) would require a grounded representation independent of action, as no direct motor behavior can be performed in the area of space

directly behind us (i.e., if one rotates or moves backwards, the space that was behind is no longer back space).

From this discussion, it seems apparent that the perception of space may go far beyond being grounded on body action capability simulation. It is more likely that a range of different information sources are used for each category of space, perhaps providing the defining features of the space categorization. Interestingly, this multiple source account might also be possible for peripersonal space perception. While my work supports a role of body reach action simulation for peripersonal space perception, there are also other body representation factors that may contribute to the perception of peripersonal space and personal space. For example, the current state of the body can be experienced internally through visceral perception (interoception) and muscle state perception (proprioception; Barrett & Simmons, 2015), or through an integrated combination of visual, tactile and vestibular information (Azañón et al., 2016). Mechanisms occurring within the limits of the body have previously been described as contributing to the perception of a personal, self or ego space inner sense (Kant, 1796, in Grusser, 1983), with the distinction between ego (or self) space and body space being that ego space would not represent the visual perception of one's own body parts.

From the previous point, it seems more likely that the external perception of the body through vision is integrated with inner state and other sensory processes (Azañón et al., 2016; Ernst & Bülthoff, 2004; Fadiga et al., 2000; Longo, Azañón & Haggard, 2010; Longo & Haggard, 2012). For example, support for visual-tactile integration was provided by investigations of bimodal visual-tactile neurons in the monkey brain (Fadiga et al., 2000). These neurons were shown to discharge when a stimulus entered an area of space close to a body part (i.e., reference field), even if there was no physical contact with the skin (Graziano et al., 1997; Gross & Graziano, 1995; Rizzolatti et al., 1981). Here, the space between the stimulus and body was represented by the neuron. Moreover, synchronous tactile stimulation of an invisible real hand coupled with the visual stimulation of a fake rubber hand (situated close to the hidden real hand) can cause a

misattribution illusion, whereby the rubber hand becomes perceived as part of the body in the place of the real hand (Longo & Haggard, 2012; Longo et al., 2008). The role of visual-tactile binding with body representation likely has the purpose of perceiving personal space for incoming harmful threatening stimuli, with the aim of damage prevention. The personal or body space must be kept secure since a threatening intrusion of the body space could result in damage to the organism (Coello, Bourgeois & Iachini, 2012). The perception of personal space (body representation; Azañón et al., 2016; De Vignemont, 2010; Grusser, 1983; Longo et al., 2010) could be based on multisensory (internal and external modalities) coding of the static or actual body rather than dynamic action simulation. This suggests another type of grounding reference for the perception of tactile space. In the next section of the discussion, I return to the data of the thesis, and I discuss the new idea that peripersonal space perception is derived from dynamic online simulated interactions with the environment.

6.2. Dynamic versus long-term body representation for online action simulation in space perception.

As already discussed above, Chapters 3, 4 and 5 suggest that an online action simulation mechanism is likely used for the perception of reaching space boundary and egocentric distance estimation. Support for this was first provided in Chapter 3, where the hand squeezing dual-task (but not arm lifting) interfered with response latencies of egocentric reachability and distance estimation. The absence of the arm lifting dual-task effect was discussed under goal directed reaching and grasping and hand-centered space accounts (Jeannerod, 1997; Brozzoli et al., 2012; see previous section). From the hand dual-task data, I suggested that the motor processes involved in space perception were probably slowed due to motor resources used for action simulation being mobilized by the concomitant execution of foam-ball squeezes. This suggests that action simulation was used for perception. However, the presence of this interference was not sufficient to inform of whether the action simulation retrieved a long-term representation

of body, or whether action simulation was based on very recent experiences of interaction in the environment.

The effect of VR manipulation in Chapter 5 was not a concomitant or interfering effect as in Chapter 3. Instead, new body capabilities (e.g., increased reaching range) were experienced through active (motor) manual exploration of the VE. After the interaction task, the previously experienced body capabilities were reshaped and recalibrated, causing changes in the perception of space that was observed in both perceptual tasks. These findings suggest that online simulation of reaching capabilities (see previous section) was dependent on recent previously experienced reaching movements (Bourgeois & Coello, 2012), rather than a long-term representation of the body. Indeed, there are now multiple sets of evidence showing that reachability judgements and distance estimation are influenced by modifications of immediately prior experienced reaching movements (Bourgeois & Coello, 2012; Linkenauger et al., 2015; Chapter 5), or from the use of tools that extend body reach limits (Bourgeois et al., 2014; Osiurak et al., 2012; Witt & Proffitt, 2008). These effects suggest that the internal representation of the body and reachability is therefore not rigid, but instead seems to be based on a flexible representation of the body that adapts to the current situation or context (Coello & Delevoye-Turrell, 2007; Coello & Iachini, 2015). This flexible mechanism may be useful when faced with uncertain or threatening situations, allowing for the perceived extent of peripersonal space to be modified in order to adopt a more conservative peripersonal space (Bourgeois & Coello, 2012; Coello et al., 2012).

In Chapter 4, I showed that both static and dynamic body information influenced altercentric spatial perception. The static body posture of the agent was taken into account in altercentric reachability and distance estimation, but the observation of the agent performing reaching actions had a calibration effect on estimation accuracy. Additionally, the data observed with participant 17 showed large differences for space perception accuracy from posture information alone (i.e., prior to action observation), which was corrected after observation. This suggests that action simulation must be possible beyond the action capabilities of one's own body capability, where

participant 17 could estimate altercentric space despite having a greatly reduced reaching capability. In some ways, this is perhaps not surprising. In hindsight, it seems logical to be able to predict the reach capability of others, irrespective of whether they have short or long limbs. This might suggest a flexible action simulation process, or the possibility of different types of action simulation mechanisms (Fischer, 2003). The profile of flexible simulation mechanisms defined by body posture might allow for recalibration, or a second, more refined simulation may operate following action observation. As for perception of egocentric space, one might also predict that the dual task presented in Chapter 3 would also interfere with concomitant altercentric reachability judgements, irrespective of any differences in body representation used in the simulation.

The findings of the present thesis are in line with the neurocognitive model proposing that internal action simulation processes participate to the perception of peripersonal space localization, organization and boundary extent (Coello & Delevoye-Turrell, 2007). My results also demonstrate the complexity of motor cognition, which should not be exclusively seen as an output system, but rather as a dynamic action processor involved in other cognitive functions such as perception, attention, action representation, observation and imagery (Barsalou, 2008; Buccino et al., 2001; Fadiga et al.,2000; Gallese 2003; 2007; 2016; Gentilucci & Corballis, 2006; Rizzolatti et al., 1981; Rizzolatti et al., 1997; Rizzolatti & Craighero, 2004; Wilson & Knoblish, 2005). Further, action simulation should be seen as a unifying mechanism for motor cognition (Jeannerod, 2001), where this active/dynamic and embodied process contributes to several ventro-dorsal stream functions (Gallese, 2007; 2016).

The idea of embodied action simulation mechanisms (Gallese, 2016) that are involved in space perception can be related to perception-action coupling (Gottlieb, 2007; Hommel et al., 2001; Jeannerod, 1997), predictive Bayesian perceptual inferences (Clark, 2013; Barrett & Simmons, 2015; Kilner, Friston & Frith, 2007), or multisensory combination and integration (Ernst & Bülthoff, 2004). All these cognitive mechanisms use integrative neural processes, particularly using the associative parietal cortex (Anderson

et al., 1997; Freund, 2001; Gottlieb, 2007; Gross & Graziano, 1995). In fact, early work on embodied cognition suggested that embodiment was already implicated in many different types of cognition (Wilson, 2002). For example, embodiment is thought to play a role in cognitive functions where body representations would shape, structure and support perception, action understanding, memory, knowledge, language and mental imagery etc. (Anderson, 2005; Barsalou, 2008; Gallagher, 2005; Gallese & Goldman, 1998). This suggests that the mechanism of embodiment or body simulation might be used for many components of cognition, and not exclusively confined to the cognitive perception of space. This latter point is interesting when considering the idea of neural reuse, massive redeployment, neuronal and cultural recycling (Anderson, 2007; 2010; Dehaene & Cohen, 2007; Wilson & Knoblich, 2005). Here, cognitive processes that have emerged more recently in human evolution would benefit from a recycled use of older cognitive processes and structures (e.g., perception and action). In the original perception and action cognition, the location of an object is perceived relative to the body position, and a reach action planned and executed to transport the grasping hand to the object (Jeannerod, 1997). A reversal of this process may allow for the simulation of action to an object in order to perceive target location relative to the body (Coello & Delevoye-Turrell, 2007), a cognition reused from an earlier form.

In this discussion, I have so far proposed that embodiment consists of an online dynamic mechanism for perception that might have developed from perception and action cognitive processes. I also suggest that the simulation mechanism allows for flexibility by being able to simulate different body representations for action capability. From the results of Chapter 5, I suggested that body action capability representation might come from the most recent experience of interaction in the environment. Here, the perception of space changed with the manipulation of body reaching capability. However, one caveat of this suggestion is that this was the case for the experimentation here, where perhaps the situational context (or VR) was new and unfamiliar. It might be that in a normal or familiar context, learned long-term representations of body action capabilities might be used in online simulation (Bourgeois & Coello, 2012). The latter may require less

cognitive resources, providing a more efficient mechanism. I propose that either types of body action capability representation (immediate *versus* learned) likely uses the same (online) simulation mechanism. Moreover, the motor representation provided by the simulation mechanism might be coded in terms of end-state position of the hand rather than in terms of movement trajectory. This is in line with the proposal of a hand-centered reference frame for controlling and perceiving moving hands within peri-personal space (Brozzoli et al., 2010). Our results support the idea that action simulation might focus more on representing the hand final position following a reaching movement rather than the means to make a reaching movement to get to that final position. Indeed, Chapter 3 showed that only hand squeezing dual task slowed down reachability judgement responses, but not the arm lifting dual task. This is consistent with the hands being more important for goal end-state interaction than use of arm reach action. Additionally, in Chapter 5, an increase of reaching capabilities (hand range augmentation, translocating hand position) caused an enlargement of perceived peripersonal space. However, an increase in reaching movement amplitude (modifying movement trajectory) did not impact the perception of peripersonal space. It could therefore be argued that a motor representation focuses on representing the end-state goal of an action and the impact that this action has on the goal rather than dynamic components of movement trajectory to reach the goal.

However, it is possible that unfamiliar or new environments (like experimental laboratories) compared to familiar environments (like home), could require additional action simulation calibration mechanisms. Action capabilities are learned through interaction, and that they are developed and improved through life span, or during the acquisition of new skills. It is therefore also likely that long-term representations of body action capability also develop. It could be that a Bayesian approach (demonstrated for perception-action; Clark, 2013; Ernst & Bülthoff, 2004) is used to select immediate versus learned body representations based on whether the current situation of the 'space perceiver' is unfamiliar or familiar. In this Bayesian framework, sensory information would be weighted in comparison to prior knowledge, and a cost (effort) -gain (reward) function computed to guide

the simulation mechanism (Coello & Delevoye-Turrell, 2007; Ernst & Bülthoff, 2004). In this sense, the brain would constantly simulate and code body states, actions capabilities and the events occurring in space, between immediate and long-term body action representations in order to correctly interact with and perceive the spatial limits of the particular environment (Barrett & Simmons, 2015; Ernst & Bülthoff, 2004; Hommel et al., 2001).

6.3. Magnitude, numbers and space: The role of perception and action.

Magnitude coding of space and numbers, as well as their possible shared representations, were investigated in Chapter 2. My research extended literature showing that the processing of space and numbers was associated, with one component influencing the other when processed together. In the literature, these effects are mostly observed on the horizontal and vertical axes of space, but some recent studies have has also shown these effects on the sagittal axis. In Chapter 2, I demonstrated clear bidirectional associations between numbers and space on the sagittal axis, with small numbers associated to near space, and large numbers associated with far space. My experiments also showed that numerical magnitude had an influence on near *vs*. far spatial categorization but not on left-right categorization. Furthermore, the spatial location (on both left-right and near-far axes) influenced numerical magnitude categorization. My results suggest different possible mechanisms for horizontal and sagittal number space interactions, since the bidirectional effects were only observed for the sagittal axis. I proposed that these differential effects on the different axes could have been mediated by the processing of magnitude within both distance and number coding, leading to congruency facilitation/interferences pairings (Chen et al., 2015). This would be in accordance with a generalized magnitude processing system being involved in both spatial and numerical processing (Walsh, 2003).

In the literature, different accounts to that discussed in the previous paragraph have been proposed for the underlying mechanisms driving space number associations and interactions. My results challenge many of these

alternatives. For example, the idea that an analog magnitude representation solely adopts the form of a horizontal mental number line (Dehaene, 1992) is not supported. A horizontal line alone would be insufficient to characterize how numbers and magnitude could be internally represented on the three dimensional axes of space (Chapter 2). The alternative to a uniquely horizontal orientation mental number line could be the existence of a mental map or mental 3D space that contains all three spatial axes, where the relevance of one axis could be selected for a given situation (Gevers & Lammertyn, 2005; Grade et al., 2013; Holmes & Lourenco, 2011; Winter et al., 2015).

However, the suggestion in the last paragraph does not require that number space interactions are derived from a generalized magnitude processing system, which experiences interference when processing incongruent magnitudes (Chen et al., 2015; Walsh, 2003). Recently, it was proposed that two different but complementary accounts could be used to explain the observation of different types of number space interactions. Numerical magnitude could be visuospatially coded on a horizontal medium (the mental number line; Dehaene, 1992), or imply a verbal-spatial coding on conceptual similarities between dimensions (e.g., associations between concepts like “small”, “near”, “down”, “left”, “early”; Gevers et al., 2010; Proctor & Cho, 2006; Santens & Gevers, 2008). The first account considers numerical magnitude to be represented on a mental visuospatial medium and would exploit attention orientation mechanisms (Fischer et al., 2003; Gevers et al., 2010; Ranzini et al., 2015, 2016). The second account points out that magnitudes can be expressed on two opposing polarities (e.g., small versus large, left versus right, near versus far, light versus heavy, etc.). These polarities of different magnitudes could interfere in different stimulus-response mappings (e.g., categorize magnitude using lateralized response keys).

Considered further, these two accounts of number space interactions might be used to suggest that the number space associations observed in Chapter 2 could have appeared due to inter-magnitude correspondence (Proctor & Cho, 2006; Walsh, 2003), or due to visuo-spatial and attentional

mechanisms involved in number processing (Fischer et al., 2003; Grade et al., 2013; Masson & Pesenti, 2014, 2015; Ranzini et al., 2015, 2016). The first account in the previous paragraph could better match with the bidirectional findings on the sagittal axis (underlying mediation of magnitude processing), while the second account would better fit unidirectional findings on the horizontal axis (prior orientation of attention interferes with magnitude categorization). This dissociation could also be related to what was described by Stevens (1957), where distinctions between prothetic (nonlinear; length, area, numerousness, duration, heaviness, brightness, loudness, etc.) and metathetic (more or less linear; visual position; inclination, proportion and pitch) continua in the environment were made.

Additionally in the literature, the mental number line is also considered to be compressed in a logarithmic manner (Dehaene, 1992; Moyer & Landauer, 1967). This mental number line compression, from few to many, is analogous to space compression from near to far space. The more distant an object, the less useful binocular disparity visual cues are, and this leads to the compression of far space (Cutting & Vishton, 1995). While the compression of number representation is difficult to reconcile with a left to right horizontal mapping, it perfectly fits with a near to far sagittal mapping of number representations. In this sense, numerical magnitude representations might acquire some of their psychophysical properties from cross-over representations in different dimensions of space. However, as well as cross-over associations between axes, some differences in the mental number line may exist between the three axes of space (e.g., horizontal or interaural, vertical or rostro-caudal, sagittal or dorso-ventral). For example, horizontal and vertical axes can be coded retinotopically, while sagittal axis coding may emerge cognitively by the use of different visual or occulo-motor cues (binocular disparities, stereoscopy, accommodation…; Cutting & Vishton, 1995) and by the use of action simulation mechanisms (Coello & Delevoye-Turrell, 2007). It is also suggested that the vertical compared to horizontal axis is more implied in the coding of egocentric distance (height in the visual field cue; Cutting & Vishton, 1995). One could go further and suggest that the vertical and sagittal axes coding of distance may have

emerged historically, where in animals, the vertical axis corresponded to depth since their spinal column is oriented along the sagittal axis. By standing on their feet, humans realigned their spine along the vertical axis, and changed the orientation of their body regarding the three dimensions of space.

As already discussed above, the number space associations observed with the different spatial axes could appear for different reasons. One other proposal presented by Fischer (2012) was that the different types of number space associations for the different axes could be viewed from different hierarchical levels of grounded, embodied and situated numerical cognition. Here, vertical number space associations could be seen as grounded (where the ground is a natural 0, and more is up), whereas grasping-number associations could be embodied on sensorimotor experiences, while left-right gaze or head direction could be associated with situated number processing (Loetsher et al., 2008; Loetscher, Bockisch, Nicholls, & Brugger, 2010; Winter et al., 2013).

The idea that magnitude and number representation can be seen as embodied in sensorimotor systems has been proposed by several authors (Andres et al., 2008; Badets & Pesenti, 2010, 2011; Barsalou, 2008). Support for this comes from bidirectional influences between number processing and grasping execution (or observation; Andres et al., 2004; Badets & Pesenti, 2010; 2011; Grade et al., 2016; Lindemann et al., 2007; Moretto & di Pellegrino, 2008). These effects have also been demonstrated in studies of pointing movements, performed toward horizontally aligned targets, with results showing moderation by numerical magnitude (Ishihara et al., 2006; Song & Nakayama, 2008). From these data, I argue that both reaching and grasping imply embodied magnitude processing of distance and size; corresponding to reach and grasp coordination (Jeannerod, 1997; Walsh, 2003).

The correspondence between magnitude and space has already been discussed in reference to the body capability representation (Coello & Delevoye-Turrell, 2007). The idea is that in order to give meaning to a

coded sensory magnitude, the parietal cortex codes sensory information in reference to eye-, head-, body- and world-centered coordinates (Andersen, et al., 1997). Here, space and magnitude consists of angles, lines, distances and size that are scaled on the body (Linkenauger et al., 2015; Proffitt, 2013). Exploiting these grounded spatial representations, number representation and processing could emerge, where increasing magnitude is associated to a line of numbers. Observed number space associations could be the cognitive signature of this grounding, which would go deeper than a simple mental number line. These possibilities are currently being tested using computational models aiming to replicate, the cognitive architecture and algorithms implied in numerical cognition (Chen & Verguts, 2010). Furthermore, research exploiting humanoid robots equipped with moving eyes and artificial intelligence are showing how perception and action learning can lead to embodiment, and support for different aspects of the theoretical models (Ruciński, Cangelosi & Belpaeme, 2011).

In the first three Sections of this discussion, I have attracted the reader's attention to the importance of body representations in the scaling and delimitation of space. Within this discussion, I proposed that among these representations, dynamic/online simulation of body action capabilities would contribute to space perception, and those different representations of the body could be used with this online simulation mechanism. In Section 6.3, I discussed the different interpretations for observed interference and association between number and space processing, suggesting that a common magnitude processing system might underlie simulation, body representation and numbers as well as other processes associated with perception and action. In the next section, I will discuss some limit of the thesis, along with potential confounds that must be taken into account when discussing the impact of my findings, and I suggest new investigations to clarify uncertainties.

6.4. Thesis limitations

In this section, I will summarize the various limitations already presented in each of the empirical chapters, and I discuss possible improvements that

could be considered in future experimentation. Starting with Chapter 2 (see also Section 6.3.), although my study brought added knowledge to bidirectional space-number associations in sagittal and horizontal axes, I was not able to use my data to draw firm conclusions about the cognitive mechanisms underlying space-number associations. The previous discussion supports the potential existence of alternative and complementary mechanisms for space and number processing (Gevers et al., 2010; Van Dijck, Ginsburg, Girelli, & Gevers, 2014), and I proposed from this discussion that in my experimental set up, the visuo-spatial account may be more suitable for horizontal space-number associations, while the verbal-spatial account may be more suitable for sagittal space-number associations (Gevers et al., 2010). More research is needed to test this proposal.

In Chapter 3, hand based but not arm based concurrent motor activity interfered with egocentric space perception. I already discussed why arm based concurrent motor activity perhaps had no influence, but I concede that further testing may be required. One alternative reason explaining the difference between arm and hand dual tasks could be that the actions involved different continuity/discontinuity. The same rhythm was imposed for both actions, but the duration of the action cycle differed. The grasp action was short and resulted in a discontinuous sequence of discrete actions. The arm movements however were long, causing the sequence of actions to be continuous. This difference may have caused different level of interference on spatial cognition. Despite this alternative suggestion, I maintain the importance of hand-centered space in peripersonal space perception, as other data exists that support this possible explanation (for reviews see Brozzoli et al., 2012; Brozzoli et al., 2014). One other limitation in Chapter 3, was that we did not investigate the impact of the dual-task on the estimation of allocentric distances oriented on the sagittal axis. This manipulation would have refined the investigation by showing that only the dual task influenced the perception of egocentric space (as in the current study), but not the perception of allocentric space within the same axis (i.e., measuring both horizontal and sagittal allocentric space).

In Chapter 4, the impact of body posture and action observation was tested within a single experiment. It may have been better to investigate the two manipulations separately to ensure that the effects were not caused by a conjunction of manipulations (although arguably, the pre-action observation estimation session could be considered as independent from action observation). The single case investigation was unexpected and unplanned, explaining the absence of a clinical description of the case. The results were interesting and complementary to the main experiment for understanding the role of body posture and observed action on the perception and calibration of space. I propose that further studies should replicate these findings with a larger group of participants, perhaps additionally contrasting participants born with limbs of reduce length and participants with limbs of reduce length due to amputation. This manipulation could be used to understand the role of long-term learned body representation and capability of space perception. Finally, one other limitation of this experiment was that we performed the study on a computer screen, requiring participants to recreate an accurate spatial representation of a photographed environment, possible increasing inter-individual variance, even though it was clearly specified that they had to estimate "real" distance rather than the screen distance.

Finally, for Chapter 5, I did not evaluate whether participants had prior experience with virtual reality immersion using head mounted display. This may have led to variance on our data, with participant differences in interaction easiness and speed of adaptation to the virtual settings. Additionally, about 40% of participants reported having noticed the difference in the action virtual augmentation (in range and hand size manipulations) between the two days of testing, despite testing being separated by a week (though no participant was aware of the speed/amplitude manipulation). This may have caused experimental bias, where participants adapted their response to meet expected effects. Evidence against this was that the hand size augmentation showed no effects of the augmentation of space perception. I propose that future studies use alternative or more implicit measures of space perception (e.g., production of distance; reproduction of distance; cross modal interactions; Linkenauger et al., 2015; Brozzoli et al., 2010), or the augmentation of reach and size

could be reduced to a level that is not explicitly detected, but the behavioral effect of increased space perception remains (Bourgeois & Coello, 2012).

Overall, the different empirical chapters could have tested larger samples of participants allowing for correlational investigation of the negative relation between reachability judgements and distance estimation. These additional analyses would allow to test if inter-individual differences in reachability judgement accuracy could predict inter-individual differences in distance estimation accuracy (i.e., a participant underestimating their own reach capability would estimate distance as bigger than someone overestimating their own reach). In relation to this, in Chapters 4 and 5 the order of the two tasks was fixed in the sense that participants performed both tasks on the same stimulus, always first providing a reachability judgement, followed by distance estimation. This was mainly done to reduce the duration of the testing, but we cannot exclude a direct influence of reachability judgements on the subsequent distance estimation. Future studies might disentangle this limitation by assessing reachability and distance estimation separately, investigating the links between reachability and distance estimation, or testing more explicitly the causal role of motor simulation on distance estimation.

Another important aspect in our empirical chapters for distance perception is the origin point on the body used by participants to perform distance estimation. More specifically, to what referencing origin (or zero-point position) did participants refer to in order to judge their estimations. In the instructions, an emphasis was made to the participants that they could use the table edge in contact with their trunk as a referent (providing a non-ambiguous origin point) to make their estimations. Despite these instructions, we cannot rule out that participants used eye or head position as a referencing zero-point for their egocentric distance estimations. Future research should investigate the role of the origin point on space perception accuracy and variance of response.

Another general limitation across all of the empirical studies was that no real or virtual identifiable objects were used. In all of my empirical

investigations, I used basic rectangles, cylinders and prisms as stimuli. This was an attempt to exclude potential influences that ventral stream (vision for identification; semantic processing; Goodale, 2014) or object-based affordance mechanisms (Gibson, 1979) would have on distance and peripersonal space perception. However, this makes the results and interpretations only valid for non-descript objects. In normal behavior, for example when drinking a beer (as presented in Chapter 1 of this thesis), dorsal and ventral streams are used in perception and action (Goodale, 2014). If body action simulation uses perception and action processes, it is likely that familiar object information might be (somehow) integrated into simulation mechanisms. In relation to this, object processing for action uses affordance mechanisms, and these mechanisms could also be implied in space perception (Coello & Delevoye-Turrell, 2007; Gibson, 1979; Philbeck & Witt, 2015). Future studies should investigate the complementary roles of ventral and dorsal stream perception in body action simulation and space perception (Kalénine, Wamain, Decroix & Coello, 2016; Wamain, Gabrielli & Coello, 2016).

One final limit of this thesis is that space perception uses a Cartesian geometrical coordinate system, where three spatial axes (x, y, z) originate from the body. These axes would go through three planes (horizontal, median, frontal) that separate the body into two parts depending on the plane (under-above; left-right; front-behind). The body is at all time positioned or oriented within these different planes, and movements of the head or the body in three-dimensional space would be partially coded by the vestibular system. In this sense, the vestibular system would also contribute to body, body orientation and space representation (Angelaki & Cullen, 2008; Azañón et al., 2016; Coté, 2011; Klam, 2003; Lopez, Halje & Blanke, 2008; Lopez et al., 2012). However, it should be noted that the head and trunk can move independently from each other, and therefore other sensorial information in addition to the that provided by the vestibular system would be certainly implied in body (and body part) orientation perception. In line with this, a differentiation between peri-hand, peri-head and peri-trunk representations was recently proposed (Serino et al., 2015). These representations provide distinct sub forms of peripersonal space, not entirely

independent from each other, and all referenced/anchored on the trunk. Future research might consider the role of vestibular processing in perception and action, in different subspaces perception, as well as its potential role in action simulation.

In the next and final section of this General Discussion, I will propose various research projects that I would be interested to complete in the future. I will propose these studies around three main themes. First, I propose an investigation of how body position representation influences space perception, in particular, implying the vestibular system. In the next section, I suggest future investigations of body calibration on space(s) perception. Finally, I will discuss possible future work investigating the representation of numerical magnitude arising through sensorimotor experiences in space.

6.5. Future perspectives

In the first three sections of Chapter 6, I discussed my findings from empirical Chapters 2, 3, 4 and 5 using three main themes. These were that space perception is anchored on body representation, and more specifically, that peripersonal space perception results from dynamic/online hand-centered reaching simulation (Brozzoli et al., 2012). Second, I discussed how different body-hand representations, dynamic and adaptable versus long-term learned, could be used in the calibration of space (Bourgeois & Coello, 2012). Third, I summarized the possible reasons for the observation of diverse number and space associations, as well as the contribution of the sensorimotor systems in the processing of magnitudes (and vice versa) (Walsh, 2003). In the three following sections of this Chapter 6, I will develop some future directions. First, I will discuss how body representation could be further investigated in order to understand position coding for three-dimensional space perception. I will then discuss possible manipulations of context (social; emotional; virtual) that may influence perception of action capabilities. Finally, I will propose some experiment to investigate number space association differences on the three spatial axes, as well as the contribution of embodied mechanisms in numerical magnitude processing.

6.5.1. Perception of body and space in different contexts: Coding body position and orientation

As mentioned in the discussion above, the body evolves in three-dimensional space, allowing for space representations to be oriented along three possible axes, but also through three rotational angles. Action interactions within three-dimensional space can be obvious, such as with reaching and grasping, or walking. However, some actions can be discrete, such as postural stability or balance. These types of actions are usually made in correspondence to visual perception, and encode space in terms of orientation (i.e., standing up-right). This raises the question of whether the orientation of space is represented in terms of simulated action posture. Based on the findings in the current thesis, and on the discussion above, I hypothesize that orientation perception is possible through simulation of action posture, which perhaps represents an additional simulation mechanism.

As demonstrated in Chapter 5, VR can be used to test how action simulation is used in space perception. Using VR, it would be possible to move the body without the participant experiencing visual motion, and likewise, the participant could experience visual motion without making any body movements. In these cases, one could evaluate the participant's perception of orientation in space. Moreover, the different rotational axes of azimuth, elevation and tilt, as well as optic flow, could each be manipulated independently in order to determine the relative role of separate vestibular sensory input for perceiving position in space. I would therefore investigate the role of the vestibular system, also mediated by the parietal and premotor cortices (Lopez et al., 2008), on body and space representations. I predict that body position would influence space perception through vestibular perception simulation. For example, when lying on the floor, the vestibular system detects that the body is realined with the sagittal axis, causing a change in perceived orientation. This in turn impacts action capabilities from the new body position, with reaching arm actions now more difficult, as the move in opposition to gravity. With virtual reality, body position can be physically versus visually manipulated, where for example, physically

lying on the floor in the saggital could appear virtually as standing upright. In this case, I could investigate the role of vestibular sensation on the perception of space orientation for action, and whether these manipulations influence the perception of space.

Manipulations of orientation have immediate applicable clinical value for patients suffering from tinnitus and vestibular deficits (Whitney et al., 2009). It could be possible to develop a new diagnosis measure of space orientation using VR in the manner already discussed above. Furthermore, I could also investigate the role of vestibular function on VR Cybersickness (or motion sickness). This is typically caused during interactions within virtual environments where visual changes occur, but they do not correspond to body movements (Bouchard et al., 2007). These uncomfortable mismatches between what the eyes perceive, and what the vestibular system encodes, is thought to form the basis of the sickness. It seems that the notion of agency is crucial here, as the user needs to be the cause of visual change that is experienced in VR. If the user undergoes visual change that is not elicited by their own movements, or not predictable, motion sickness will most likely occur. A future project could investigate how mismatch along the different spatial and rotational axes influence motion sickness induced by visual and vestibular incongruence. I hypothesize that mismatched orientations in the three planes or three rotational axes could elicit different degrees of motion sickness and balance impairments. Investigating separately the different spatial axes will also allow the investigation of their relative contributions to different frames of reference testing, for example, whether vertical and horizontal rather than saggital axes are more involved in world-centered balance maintenance, and maintaining a perpedicular body position in relation to the ground. In turn, I could investigate how these representations influence posture simulation for space perception.

6.5.2. Scaling the environment with body action capabilities.

The research presented in this thesis is clearly not the first nor the last to investigate how space perception is calibrated from body representation and action capabilities. In order to explain the findings of Chapter 5, I have suggested that body representation must be highly malleable to adapt to different situations, such as in VR, but also when using different tools. But how far can this flexible body representation adapt? In VR experiments, it has been observed that when experiencing two or three times longer arms than their own arm length, participants still consider the virtual hand as their own (Kilteni et al., 2012). However, having an arm four times longer greatly reduced the sense of body ownership, despite visuo-tactilo-motor congruency. This suggests a limit to the flexible body representation. By using these types of experimentation, it could be possible to define the characteristics of the flexibility of body representation. It should be noted that there may be differences in how these limits are coded. For example, Kilteni et al. (2012) suggested that flexible body limit might allow for arm lengths of up to three times actual length, but some tools may extend action capabilities beyond three meters (e.g., construction crane, telepresence, car, skis), and be embodied into the flexible body representation. VR can provide infinite reaching capabilities to participants by using a joystick function developed to test how far extrapersonal space can be remapped into the peripersonal space. Embodying participants into unconventional body dimensions and proportions might help understanding the limit of visuomotor adaptation. Overall, VR will prove a powerful tool to investigate the dominance of vision over proprioception in the determination of body position, and using VR, researchers will be able to investigate how far body representations can be adapted (Bourgeois & Coello, 2012; Fourneret & Jeannerod, 1998).

Peripersonal space delimitation is one of the signature explanations of space being segmented according to action behaviors in external space (Coello & Delevoye-Turrell, 2007; Previc, 1998). However this peripersonal or reaching space should not only be seen as the area where goal-directed hand

actions take place. Indeed, the representation of peripersonal space could be implied in protective and defensive behaviors (Coello et al., 2012), as peripersonal space is the last rampart before personal or body space (that must be protected), and it is the area where hands can be used to block or repel incoming threats. In support of this role of peripersonal space, recent work has shown an influence of fear and threat on reachability judgements (Coello et al., 2012). In our own research, we have begun to extend this research by investigating how the context of fear, danger or threat can influence space perception and represented action capabilities.

Peripersonal space is also believed to be exploited as a reference for calibrating interpersonal distances in social interactions (Coello & Iachini, 2015; Quesque et al., 2016; Iachini et al., 2016). In this sense, being able to discern the peripersonal space boundary of the self and of others in the same environment would be necessary for the establishment of an appropriate interpersonal distance. Research has shown that there could be an overlap between peripersonal space measured with reachability judgements, and interpersonal spaces measured by comfort social distance judgements (Coello & Delevoye-Turrell, 2007; Hall, 1966; Iachini, et al., 2016). In support for this, it has been shown that extending peripersonal space with a tool, also extended interpersonal space (Quesque et al., 2016). Interestingly, other research have also shown that the anxiety trait of participants, as well as perceived morality of an approaching virtual avatar could moderate the perceived size of peripersonal and interpersonal spaces (Iachini et al., 2015; Iachini, Pagliaro & Ruggiero, 2015). Recently, we extended these investigations by measuring the impact of participant anxiety and aggressiveness levels when making interpersonal (comfort) and peripersonal (reachability) judgements to walking virtual avatar stimuli (Marichal, 2015). Preliminary findings showed that both participant's anxiety and aggressiveness caused differences in perceived peripersonal and interpersonal spaces.

Finally, as discussed earlier, the body of others can also be perceived in order to calibrate the perception of the environment, including a possible social scaling of space (Fini et al., 2014, 2015; see also Chapter 4). I would

like to propose an experimental plan to test that body size and movements serve as a more efficient scaling cue than object size and movement (Cutting & Vishton, 1995). Participants would be immersed in a virtual environment where they would be asked to estimate egocentric and allocentric distances. To calibrate this environment, either virtual avatar body cues, familiar object cues (e.g., drinking can vending machine) or unfamiliar object cues (a blue cylinder) could be present in the environment. Using a trial-by-trial or block fixed experimental design, I would present these different cues and test whether familiar cues improve the accuracy of distance estimation in comparison to unfamiliar object cue. Furthermore, I would present the cues static or in motion. I would predict that for the different cues presented in motion (e.g., walking or object sliding), body avatar movements would have the greater use for scaling the environment. This experiment would refine our understanding of how agents exploit both static and dynamic body information in order to calibrate their perception of space, and in contrast, how objects present in the environment could have a lesser role on the perception of space.

6.5.3. Reaching for numbers and magnitudes in 3D spaces

Research in numerical cognition and magnitude processing remains far from understanding how space, magnitude and numbers are internally represented and how their functioning could be embodied into sensorimotor systems. A new model is needed that proposes an englobing view of the relations between action and body representations, space perception and numerical magnitude, but in order to create validate the cognitive architecture of such a model, much work will be needed. In the following section, I will present different future investigations that could be used to test and understand how spatial and numerical representations overlap and interact, as well as how magnitude is involved and emerges from sensorimotor processes.

First, the near-small and far-large associations reported in Chapter 2 could be investigated using an altercentred frame of reference (merging Chapters 2 and 4). An actor could be present on the left or right extremities of space (e.g., by making horizontal flips of the stimuli used in Chapter 4), and a

number target could appear near or far from the actor. Depending on the actor position, near-far positions will be in a congruent or incongruent with left-right numbers-space configuration allowing for a direct contrast between egocentric horizontal and altercentric sagittal spatial axes. I predict an influence of number magnitude on altercentred near-far judgements that would override the horizontal number space association, since the task will not require the processing of the left-right dimension. This would allow me to demonstrate that the relation of near-far space to numerical magnitude representation is more robust and grounded than in horizontal associations (Fischer, 2012).

Second, as grasping actions influence or can be influenced by number processing (Andres et al., 2004; Badets & Pesenti, 2010), I argue that similar findings could be found with reaching actions. Some studies have already shown that pointing movements towards number targets (arranged horizontally; from leftward to rightward pointing) have their kinematics influenced by the numerical magnitude of the number stimulus (Ishihara et al., 2006; Song & Nakayama, 2008; see also Fischer & Campens, 2009). However, number targets could also be arranged along the sagittal axis in order to investigate whether near or far reaching movements can be influenced by numerical magnitude processing like grasping movements (Andres et al., 2004; Lindemann et al., 2007; Moretto & Di Pellegrino, 2008). Along with this, number processing could also show influences on reachability judgements, as it was also shown that number magnitude can have an impact on graspability judgements (Badets, Andres, Di Luca & Pesenti 2007). The observation of short or long range reaching actions (similar to that in Chapter 4) could show influences on number recall (i.e., encoding and retrieval; Badets & Pesenti, 2010) or random number generation (Grade et al., 2016). Finally, we could use virtual reality to change the reaching capabilities of a user, and test whether the extension of peripersonal space can affect near-small/far-large numbers-space associations. Altogether, these proposed experiments might bring evidence suggesting that number representation or meaning is grounded or embodied in spatial magnitude partly arising from sensory-motor experiences of reaching and grasping.

Third, and finally, VR would allow the confrontation of the three different spatial axes in number space associations (Gevers et al., 2006; Winter et al., 2015). Number targets could be displayed in any position within a VE, and numbers-space associations could be investigated on the three spatial axes independently, or in competition. This would allow the investigation of similarity, differences and influences between the number space correspondences on the three axes. For this, we could manipulate the tridimensional position of a 3D target number with the addition of floor shadows to control for distance-size consistency, also manipulating the physical size of numbers, thereby investigating different magnitudes within the same experiment (Dormal & Pesenti, 2012b; Henik & Tzelgov, 1982;). This will permit the specification of possible independent or shared cognitive mechanisms (attentional, verbal, magnitude coding) involved in the processing of each spatial axes (x, y, z) and spatial dimensions (e.g., distance, size, eccentricity, curves).

CONCLUSION

The aim of the present thesis was to investigate if representations of the body and body action capabilities, as well as cognitive mechanisms involved in magnitude coding, would influence environment space perception. I demonstrated that space and number processing could interfere with each other on different spatial axes (sagittal and horizontal), but that bidirectional effects were only observed on the sagittal axis. I demonstrated interfering impact of a hand-based motoric dual-task on reachability and distance estimation. I also brought evidence for a calibration benefit of body posture and action observation when perceiving space centered on others. Finally, when action capabilities of participants were amplified using virtual reality technologies, this caused participants to change their perceived reaching capabilities and their perception of virtual distances, suggesting the possibility of a flexible body representation.

Overall, the findings from the present thesis suggest that space perception results from coding sensorial information, motor capabilities and magnitude of spatial properties (distance, size etc.). It supports the proposal of a sensorimotor or embodied account of space cognition, where the action capabilities of the body segment space perception into several imbricated subspaces. Moreover, the active simulation or representation of action capabilities informs the different boundaries between the subspaces. Finally, magnitude representations and processing might emerge and develop from sensorimotor experiences, and these could serve as a non-symbolic reference or ground for the use of numerical symbols depicting magnitude.

Following this doctoral research, I would not pretend to be an expert in perception, action or their coupling, in body representation, or in magnitude, numerical, spatial and embodied cognition. However, by doing the present research, I hope to have clearly ‘put on the table’ the idea that space cognition relies on mechanisms or functions generated by means of internal simulation. Through this internal simulation, information is shared that constrains and feeds other cognitive processes. I suggested that our

cognitive system is capable of remembering previous experiences, as well as using accumulated experiences gathered over many years. This includes measures of the present by perceiving the current state of the body and its position in the current environment. Besides, it could also include retrieving long term representations of the body reenacted from previous sensory-motor experiences. Finally, the cognitive system could generate predictive simulations of body and space to anticipate short term changes in the present, or to imagine how life will be in 20 years. In this sense, the brain could recreate body-space patterns that were never experienced before, although based on previous knowledge.

Throughout this Thesis, I presented my own view and research about how grounded and embodied cognition theories could be used to understand of the incredible neuronal mechanisms occurring every millisecond of every day to provide a perceivable and understandable representation of the environment. We evolve, develop and act in this gigantic environment, but we also shape the environment to create new imagined possibilities. I will terminate this thesis by attempting to answer a question that people seem to frequently ask. Scientific research shows that the entire capacity of the brain is exploited (and not 10% or 50% as sometimes depicted in the movies). All brain areas appear to play several roles, and they collaborate with other parts of the cerebral cortex. However, we might not use 100% of its capabilities, as some individuals can learn more than five different languages (e.g., Java, C#, Python, Chinese), play five musical instruments, know hundreds of dance moves, or be able to multiply any two digit numbers by themselves in a few seconds. So stop asking yourself this question, and go explore, act, learn and shape your environment to expend and crystalize your spaces.

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