Tell it to the hand: Attentional modulation in the identification of misoriented chiral objects

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“I will never know how you see red and you will never know how I see it. But this separation of consciousness is recognized only after a failure of communication, and our first movement is to believe in an undivided being between us”

Maurice Merleau Ponty

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Preface

Research in the field of cognitive neuroscience and neuropsychology on spatial cognition and mental imagery has increased considerably over the last few decades. While at the beginning of the XX century studying imagery was considered an object of derision – a “sheer bunk” (Watson, 1928) – at the present, imagery researchers have successfully developed models and improved behavioral and neurophysiological measures (e.g., Kosslyn et al., 2006). Mental rotation constituted a major advance in terms of behavioral measures sensitive to imaginative operations executed on visual representations (i.e., Shepard & Cooper, 1982). The linearity of modulation between response times and angular disparity of the images allowed a quantitative estimate of imagery processes. The experiments described in the present thesis were motivated by the intent to continue and extend the understanding of such fascinating mental phenomena. The evolution of the present work took initial steps from the adoption of a behavioral paradigm, the *hand laterality judgment task*, as privileged tool for studying motor imagery in healthy individuals and brain-damaged patients. The similarity with mental rotation tasks and the implicit nature of the task made it the best candidate to test hypotheses regarding the mental simulation of body movements. In this task, response times are linearly affected by the angular departures the hand pictures are shown in, as for mental rotation, and their distributions are asymmetric between left and right hands. Drawing from these task features a widely held view posits that laterality judgment of rotated hand pictures requires participants to imagine hand-arm movements, although they receive no instruction to do so (e.g., Parsons, 1987a; Parsons, 1994). In Chapter 1, I provided a review of the relevant literature on visual and motor imagery. Particular aspects of the mental rotation literature are also explored. In Chapter 2, I examined the hand laterality task and the vast literature of studies that employed this task as means to test motor imagery processes. An alternative view to the motor imagery account is also discussed (i.e., the disembodied account). In Chapter 3, I exploited the hand laterality task, and a visual laterality task (Tomasino et al., 2010) to test motor and visual imagery abilities in a group of healthy aged individuals. In Chapter 4, I described an alternative view that has been proposed by others to explain the pattern of RTs in the hand laterality task: The multisensory integration account (Grafton & Viswanathan, 2014). In this view, hand laterality is recognized by pairing information between the seen hand's visual features and the observer's felt own hand. In Chapter 5, I tested and found evidence for a new interpretation of the particular configuration of response times in the hand laterality task. I demonstrated a spatial compatibility effect for rotated pictures of hands given by the interaction between the direction of stimulus rotation (clockwise vs. counterclockwise) and the laterality of the motor response. These effects changed by following temporal dynamics that were attributed to shifts of spatial attention. In the same chapter, I conducted other psychophysics experiments that confirmed the role of spatial attention and that ruled out the view of multisensory integration as the key aspect in determining the asymmetries of the response times' distribution. In Chapter 6, I conducted a study with patients suffering from Unilateral Neglect (UN) in which they performed the hand laterality task and a visual laterality task. The findings indicated that patients failed to integrate visual information with spatially compatible responses irrespective of the type of task, and depending on egocentric stimulus-response spatial codes. A general discussion is presented in Chapter 7.

1. Seeing with the mind's eye and doing with the mind's limb

In this chapter I will review and discuss empirical findings from neuroscientific studies in which visual and motor mental imagery has been investigated. This chapter constitutes the empirical and theoretical background of the issues developed in the following chapters.

1.1 The cognitive neuroscience of mental visual imagery

The most significant theorizations about visual mental imagery focused on specifying the exact format of these forms of mental representations. Depictive theories of mental imagery hold that visual images are a specific form of mental representation characterized by a format that preserves important aspects of a picture (Kosslyn, 1980). Non-depictive theories postulate that visual mental representations are “propositional” in nature (Pylyshyn, 1980, 2003). The format of visual images would correspond to the form of an abstract and symbolic code similar to language. The experience of visual images is seen as an epiphenomenon of this propositional code processing. It is important to note that questioning the format of mental representations generates a reductionist view of cognition that lacks a full comprehension of the real correlates of these mental phenomena. It has been demonstrated that for any theory defined by a group of assumption about depictive representations and their transformations, it is possible to create another theory with different sets of assumption that specify the propositional code and processes that mimic the depictive theory (Anderson, 1978).

More recently, visual imagery has been investigated by generating neural responses to real and imagined stimuli. Using positron emission tomography (PET), Functional Magnetic resonance imaging (fMRI), and Transcranial magnetic stimulation (TMS), it has been shown that visual imagery partially relies on the same brain areas activated during visual perception. These findings will we briefly reviewed together with data from brain-damaged patients and data from the literature on mental rotation.

1.1.1 Functional association between perception and imagery

Early visual areas of the human brain contain a topographical representation of the visual world. Adjacent points on the retina are mapped onto adjacent points in the lateral geniculate nucleus and in the visual cortex. These topographical maps become less precise in late visual areas (Felleman & Van Essen 1991) because receptive fields are larger. Neural cells in area V1 are maximally activated by small bars in a given spatial position defined in retinotopic coordinates while in the inferior temporal cortex cells activation depends on the combination of visual features such shape, color and texture of the stimulus presented anywhere in the visual field (Tanaka, 1996). Another important characteristic of the visual system is that there are diffuse feedback fibers connecting later visual areas with V1 and V2 (Felleman & Van Essen, 1991). These connections potentially allow areas such as the inferior temporal lobules to modulate patterns of activation in early areas.

Different studies have exploited the retinotopic organization of area V1 to investigate the functional association between visual imagery and visual perception. Using PET, it was found that mentally visualizing big or small capital letters recruits respectively more anterior or posterior parts of area V1 (Kosslyn et al., 1993, 1995). Given the retinotopic organization of V1, large images were involved in the activation of more eccentric regions, with smaller visual images involved in the activation of more central regions. Thus the spatial layout of a perceived visual stimulus in the striate cortex resembles that of its imagined counterpart in the same brain area. Similar conclusions have been obtained using fMRI. A study compared imagery and perception of horizontal and vertical stimuli by exploiting the retinotopic representation of polar angle (i.e., the angle between a spot and the center of the visual field relative to a horizontal line). As expected, the orientation of the visual stimulus determined differential activation as a function of polar angle in V1 for both the perceived and the imagined stimuli (Klein et al., 2004). Other neuroimaging studies have found that brain activity during visual perception overlap with brain activity during visual imagery by 70% (Kosslyn et al., 1997) or even by 100% (Ganis et al., 2004).

Converging evidence comes from TMS studies. In one study (Kosslyn et al., 1999), observers memorized four quadrants made of black and with bars in order to make judgments about the characteristic of the shapes presented. Repetitive TMS (rTMS) at low-frequency was applied to the striate cortex while participants were either imagining the quadrants or while they were perceiving them. Response times for shape judgments slowed down both during perception and imagery relative to the shame condition. In another study, paired pulse TMS was applied to the primary visual cortex to define the phosphene threshold (a measure of visual cortical excitability) during a visual or an auditory imagery task. Compared to a baseline condition, visual imagery decreased phosphene threshold thus increasing visual cortical excitability, while auditory imagery did not (Sparing et al., 2002).

A class of depictive theories such as the perceptual anticipation theory claims that visual mental images arise when trying to anticipate the vision of a visual object, so that a pictoric representation is activated in visual areas (Kosslyn, 1994; see also Neisser 1976). Shapes would be stored in the inferior temporal lobules and during visual imagery these would be made explicit by means of feedback connections that modulate the activations in topographically organized early areas (Tanaka, 1996). Differently from objects and visual scenes, spatial representations would be stored in areas of the parietal lobule and thus could be processed without activation of early visual areas (Sereno et al., 2001). Consistently with this notion, a meta-analysis of the neuroimaging literature (Kosslyn & Thompson, 2003) found that activation of the primary visual cortex was not consistent across all studies because tasks that required spatial processing and not shape judgments had been often used (e.g., Mellet et al., 1995; 2000). Indeed, spatial representations used for example in navigation or in reaching, are stored in regions of the parietal cortex that contain already a detailed topographic map of the visual space (Sereno et al., 2001).

The hierarchical organization of the cortical visual system comprises two parallel streams of information processing that begin in area V1 and V2, and that project one to dorsal areas in the occipital and parietal lobule, and the other to the ventrolateral regions between the occipital and temporal lobules (Ungerleider & Mishkin, 1982). The dorsal stream is implicated in encoding visual information to subserve spatial cognition and motor behavior (Goodale et al., 2004; Goodale & Milner, 1992). The ventral stream provides object vision functions necessary for a detailed perceptual representation of the visual world (Desimone & Ungerleider, 1989; Haxby et al., 1991). Within this network, it is possible to highlight the contribution of different extrastriate areas recruited during visual perception and imagery. With fMRI, it was demonstrated a double dissociation in visual imagery for different classes of stimuli with a striking correspondence between imagery and perception at the neural level (O'Craven & Kanwisher, 2000). When participants visualized faces, there were significant activations in the FFA (fusiform face area) on the occipito-temporal cortices but not in the PPA (parahippocampal place area). On the contrary, imagining indoor or outdoor scenes depicting a spatial layout was associated with activation of the PPA, while FFA did not show any activity. Moreover, this pattern of results paralleled brain activity during actual perception of places and faces, even though the activations were weaker during imagery than during perception. Another study demonstrated that the similarity between imagery and perception is valid also at the single-neuron level. The study involved single cell recording from patients undergoing brain surgery because of pharmacological resistant forms of epilepsy. A group of neurons in the medial temporal lobule responded to both visual stimuli and visual imagery of the very same stimuli (Kreiman et al., 2000), confirming a common neural underpinning for perception and imagery.

In recent years the view that vision for perception and vision for action are represented in two separate neural pathways (Goodale & Milner, 1992) has been challenged. Recent studies have shown representation of location in ventral areas (e.g., Carlson et al., 2011; DiCarlo & Maunsell, 2003; Kravitz et al., 2010; Schwarzlose et al., 2008) and object representation in dorsal areas (e.g., Lehky & Sereno, 2007; Janssen et al, 2008; Konen & Kastner, 2008). It is now accepted that object-selective neural responses can be recorded in ventral as well as dorsal brain regions, like the posterior parietal cortex: Object information such as size, and viewpoint are represented in exstrastriate areas at intermediate processing stages between the ventral and dorsal stream (V3, MT, V7), while in areas of advanced processing stages of the ventral (lateral occipital cortex), and dorsal pathway (intraparietal sulcus) response proprieties are size and viewpoint-invariant (Konen & Kastner, 2008). Moreover, the notion that action is immune to visual illusions (e.g., Aglioti et al., 1995) has been proven wrong (Franz & Gegenfurtner, 2008; see also Dassonville & Bala, 2004). One of the most notable example of this shift towards an integrated view of dorsal and ventral visual processing is the finding that patient D.F. (e.g., Milner & Goodale, 2008) does not actually demonstrate dissociation of perception (visual agnosia) and action programming (grip-object scaling) when she is not allowed to receive aptic feedback after each interaction with the to-be grasped object (Schenk, 2012).

1.1.2 Data from neurological patients

As we have seen in the previous section, a substantial body of neuroimaging evidence suggests that neural computations subserving visual imagery strongly overlap with processing of sensory information. If the visual cortex actually supports visual imagery than patients suffering from focal lesions of these brain areas should demonstrate impairments in mental imagery tasks. Nevertheless, findings about the relationship between visual imagery and damages to the brain visual areas do not always go in the same direction, especially if we consider patients with cortical blindness. These patients have damages to regions of the primary visual area and report visual scotomas, namely decreased or degenerated visual acuity in corresponding portion of the visual field. One patient had one occipital lobule removed and was reported to have lost the ability to generate the contralesional half of his mental images (Farah et al., 1992). Butter et al. (1997), also investigated visual imagery capacities in patients with hemianopia (i.e., cortical blindness involving one-half of the visual field) using a mental scanning task. The authors compared the patients' imagery abilities in the functional hemifield with performance in the affected hemifield. Results showed that patients were impaired at mentally visualizing stimuli in the affected hemifield compared with imagery of stimuli presented in the intact hemifield. However, there are recent reports of patients with cortical blindness after damages to the primary visual area that do not show deficits of visual imagery (e.g., Bridge et al., 2012; Zago et al., 2010). One of them also showed a pattern of cortical activation during visual imagery (detected with fMRI) that was not different from that of healthy control participants (Bridge et al., 2012).

Thus, it is seems that from a neuropsychological point of view, the link between the primary visual area and visual imagery may be less strong than what one would expect from neuroimaging studies. Instead lesions of extrastriate visual areas are more robustly associated with problems in visual imagery. For example, Chatterjee and Southwood (1995) described two patients with bilateral damage to the occipital cortex who were able to generate visual images while being suffering from cortical blindness. However, a third patient with lesions extending from occipital areas to the left temporal lobule could not imagine visual forms. Similarly, another cortical blind patient that had damages to the primary visual cortex and also to the inferior temporal cortex experienced profound problems at mental visualization (Policardi et al., 1996). Lesions of the category-selective areas in the ventral extrastriate cortex offer a unique opportunity to study association between disturbance in visual perception and problems with mental images. For instance, patients affected by prosopagnosia (i.e., the inability to recognize known faces) parallel their perceptual deficits in visual recognition with problems at imagining faces (e.g., Young et al., 1994). Moreover, patients with object agnosia were also found to be impaired at mentally visualizing objects (Farah, 1984). Some clinical cases (Farah et al., 1988; Levine et al., 1985) have highlighted the distinction between the two visual streams in the imagery domain. In these cases it was possible to observe imagery deficits for structural element of the image or for visuo-spatial characteristic of the object. These neuropsychological conditions were accompanied by perceptual elaboration disturbances respectively of the occipito-temporal and of the occipito-parietal visual pathway.

Other case studies have shown some interesting dissociations. Servos and

Goodale (1995) described a patient with spared imagery functions in the context of visual agnosia. More recently, the opposite behavioral pattern has been documented in two patients with pure visual imagery deficits but spared perception and cognition (Moro et al., 2008). Both patients had their primary visual cortex intact but had extensive lesions of the left temporal lobule, a region implicated in the generation of mental images (see Tippet, 1992). These dissociations between visual imagery and visual perception may arise from damage to sections of cortical areas that have either perceptual or imagery functions. Indeed, in some fMRI studies (e.g., O'Craven & Kanwisher, 2000), the activations of visual areas related perceptual tasks are larger than the activations associated with mental imagery tasks. For example, some patients have been described with parallel deficits in visual perception and imagery of colors (e.g., Riddoch & Humphreys, 1987), but also with difficulties in perceiving colors (i.e., achromatopsia) and good imagery abilities for colors (Bartolomeo et al., 1997). Taken together, these data suggest that perception and imagery rely on partially overlapping brain resources so that brain damage usually affecting both functions can also manifest with more selective cognitive dysfunctions in the perceptual or in the imagery domain.

Also patients suffering from unilateral neglect may show imagery deficits. Representational neglect patients (or "imagery neglect") fail to mentally represent and imagine the contralesional side of mental images (e.g., Bisiach & Luzzatti, 1978). These imagery-related dysfunctions associated with unilateral neglect will be treated in Chapter 6.

1.1.3 Mental rotation

Several paradigms have been used to investigate quantitatively the subjective experience of mental visualization. In the classic mental scanning task (Kosslyn et al., 1978), participants memorize a picture of a map with different landmarks. They are asked to pay attention to a given landmark on the map, and then to respond as soon as they could “see” another landmark named by the experimenter. Response time typically increases with the distance between the two landmarks, and this result is taken as evidence of the structural isomorphism between mental images and corresponding objects in the physical reality. However, tasks like this can be criticized because they are cognitively penetrable. In other words, task performance can be influenced by beliefs, goals, expectation, and knowledge (Pylyshyn, 1981). An exceptional progress has been made in the study of visual imagery with the introduction of mental rotation tasks. In a seminal paper, Shepard and Metzler (1971) presented participants with pairs of three-dimensional solid objects (i.e., group of cubes assembled together to from 3D structures with different “arms”) and asked them to report if the pairs included the same objects or if they were mirror-reversed. Response times and errors were linearly proportional to the angular disparity between the two objects. The slope of the curve that described the relationship between response times and angular disparity was the same when objects were rotated in depth. It was argued that, in order to decide if they were the same or mirror-images, participants mentally rotated one of the objects until it matched the position of the other. The observer would imagine move the object in the space along the same trajectory as if it would be actually moved (Shepard & Cooper, 1982). These authors also demonstrated that, in a mirror image discrimination task of rotated letters, if before the test stimulus advance information about its orientation was shown, RTs diminished as a function of the stimulus onset asynchrony (SOA) between the advance information and the test stimulus (Cooper & Shepard, 1973).

Typically mental rotation is considered a mental spatial transformation operating on a holistic (and analog) visual representation. However, the idea that mental rotation operates on a holistic representation has been questioned (Just & Carpenter, 1985;

Pylyshyn, 1979) and has not yet received support from empirical data. Holistic mental rotation strategies seem to depend on the complexity of the visual stimuli (Folk & Luce, 1987), and on individual differences between good and poor imagers, with the former adopting holistic and the latter piecemeal rotation strategies (Khooshabeh et al., 2013). Recent findings indicate that given the limitations of the human visual system in keeping track of multiple features during mental rotation, holistically rotate a visual representation would be almost impossible (Xu & Franconeri, 2015).

Mental rotation processes have been invoked to explain important aspects of object constancy, namely the ability to recognize objects despite the tremendous variation in the image when they are perceived from different views. The linear increment of RTs is present in mirror-image discrimination tasks (or also handedness discrimination tasks) like in the study from Shepard and Metzler (1971), and in direction of facing tasks that consist in determining the direction (left versus right) an asymmetric plane-rotated object is facing if it would be seen upright (e.g., Jolicoeur, 1988). Similarly to these tasks, when participants have to name a familiar object (i.e., a recognition task with alphanumeric characters or common objects) that is shown with different angular departures, the time they take increases with the angle of stimulus presentation (Jolicoeur, 1985; Jolicoeur et al., 1998; Murray, 1995). Nevertheless, RTs in naming tasks of familiar stimuli tend to become flat over a period of practice (e.g., McMullen & Jolicoeur, 1992). Moreover, naming of misoriented letters (Corballis et al., 1978a), and classification of misoriented alphanumerical characters (Corballis & Nagourney, 1978) produced RTs effects that were either independent of stimulus orientation or were very small. One explanation of practice effects is that once the observer has encoded the objects over a substantial period of time, then recognition would follow by virtue of view-invariant stimulus features, and no mental rotation is required (e.g., Corballis, 1988; Jolicoeur, 1990). The question then arises as to whether mental rotation is necessary to recognize visual objects. Contrary to an involvement of mental rotation in the recognition of familiar objects is also the finding that naming of familiar stimuli presented with a larger number of angular departures (i.e., ranging from 0° to 180° at step of 30°) does not entail a monotonic relationship of RTs with the stimulus angle of rotation (Lawson & Jolicoeur, 1999). Thus, for familiar stimuli, the stimulus spatial normalization is either absent or cannot be inferred by the linearity of RTs. However, with such stimuli, handedness discrimination (discrimination of standard and mirror-reversed versions of familiar stimuli) always produced linear increments of RTs as the stimulus angle of presentation increased (e.g., Corballis et al., 1978a; White, 1980). There is wide agreement that handedness recognition necessarily involve mental rotation processes. However, it is hard to imagine an ecological situation in which we recognize visual stimuli by means of mirror-image discrimination. There are a few exceptions as, for example, when we wear the first glove or the first shoe and so we need to recognize on which hand or foot to wear these accessories, or when recognizing the laterality of misoriented pictures of body parts (e.g., Parsons, 1987b). Cooper and Shepard (1973) showed that in a task of handedness recognition (i.e., mirror-image discrimination) with letters, if given advance information about the angle of presentation of the stimulus, participants RTs still increased as a function of orientation. Hinton and Parsons, (1981) proposed that people do not have a representation of the handedness of misoriented stimuli. The need for mental rotation in handedness recognition would be the consequence of attributing intrinsic (i.e., object-centered) frame of reference to an object. For 2D stimuli, this means assigning top/bottom and front/back directions to the perceived object. The problem is that with misoriented stimuli we can know both directions but not the stimulus handedness directly. Thus in order to establish handedness the stimulus needs to be mentally transformed and compared with the observer left and right egocentric coordinates.

Object model verification theories state that object constancy is achieved by confronting the perceived object with stored representations in object sensitive areas of the ventral occipito-temporal cortices. A prefrontal-parietal network allows spatial transformation (i.e., mental rotation) necessary for object categorization (e.g., Schendan & Stern, 2007). A version of these theories, the multiple-views-plus-transformation account, foresees that object's representations from distinct view are stored so that if a similar view is shown it becomes directly matched. However, in order to match the visual input of an unfamiliar orientation with its stored representation the image has to be transformed through mental rotation processes (Bülthoff et al., 1995; Tarr and Pinker, 1989, 1990). This is proved by the evidence that with practice, the effect of specific orientations diminish but do not transfer to new orientations even in tasks that do not involve the assignment of handedness (2D stimuli: Tarr and Pinker, 1989; 3D stimuli: Tarr, 1995). The effects of orientation in object recognition are accounted for mental rotation because the response rates are similar to the rates found in classic mental rotation tasks. It is usually considered that an analog transformation is taking place whenever the rotation rates are not faster than 0,78ms/degree (1282°/s) (Tarr & Pinker, 1989). Thus, for objects we encounter very frequently, multiple-view representations allow direct recognition (Tarr & Pinker, 1989), while for other objects, relevant features can be enough to achieve recognition as well (e.g., Biederman & Gerhardstein, 1993). It has been proposed that, if the visual object differs in the way its parts are assembled along a single dimension then mental rotation is not necessary. If the object is defined by parts located simultaneously along two dimensions, then the object must undertake mental rotation, even though the task does not involve mirror-image discrimination (Tarr & Pinker, 1990).

The performance of patients with cerebral damages is usually impaired in performing mental rotation tasks after lesions of the right hemisphere (e.g., Ditunno &

Mann, 1990). Right hemisphere damaged-patients experience also more difficulties with depth rotations than plane rotations (Layman & Greene, 1988). Farah et al. (1988), reported a neuropsychological case as prove of dissociation between visual recognition and mental rotation. Their patient (R.T.) suffered from a large fronto-temporo-parietal brain damage to the right hemisphere and was impaired in performing mental rotation. At the same time R.T. was good in naming inverted figures. One of the tasks used to tap mental rotation was the Ratcliff manikin task (Ratcliff, 1979). In this task, a picture of a manikin with extended arms is showed either from the front or from the back. The manikin holds a disk in his left or right hand and the participant judge which hand the disk is been held. The problem with this study is that the task used does not merely tap mental rotation processes. The same task has been extensively employed to investigate the so called own-body transformation task (Parsons, 1987a), that is very often used as a perspective taking task (e.g., Zacks et al., 1999). Nevertheless, the way this task was employed it has been recently criticized because it is susceptible of spatial stimulus-response compatibility effects (Gardner & Potts, 2011; May & Wendt, 2013; cf. Parsons 1987a exp.2). Moreover, R.T. performance on visual categorization was defined “normal” when compared with a group of healthy participants that performed the same categorization task but with very short displays. Importantly, R.T. categorization of upright figures was impaired. Another group of researchers reported a patient that could not discriminate between mirror-image objects while performed good in discriminating objects with minor differences and also with objects rotated in the picture plane (Turnbull & McCarthy, 1996). Another patient, L.G., could not copy or draw objects from memory in their correct orientations, and also failed in matching the orientation of different objects unless they were shown upright. However, she could well name the objects that could not represent in their canonical upright version (Turnbull et al., 1995).

Converging evidence points to an involvement of motor processes for the mental transformation of visual images. Wohlschläger and Wohlschläger (1998) had participants performing a mental rotation task and a physical rotation task with the same 3-D figures that were rotated by moving a dial. In both tasks RTs showed the effect of angular disparity, thus highlighting similarities in the temporal dynamics of physical and mental rotations. Another study (Wexler et al., 1998), employed a dual task paradigm in which mental rotation was performed together with manual rotations with a joystick in a clockwise or counterclockwise direction. RTs in the mental rotation task were facilitated when the direction of mental rotation was congruent with the direction of manual rotation. In a recent study, mental and physical rotations were directly compared (Gardony et al., 2014). Participants used an handheld rotational sensor to rotate on a monitor the Shepard and Metzler 3-D figures in real-time. The RTs for these physical rotations were compared with RTs in the mental rotation condition revealing very similar pattern of results. Moreover, the data from continuous physical rotations showed that in mental rotation, people do not rotate figures to achieve a perfect match, and also that they use different strategies for same and different judgments. To date, a large number of neuroimaging studies on mental rotation have been reported. Many show significant activations of the posterior frontal cortex in areas related to action planning and execution during mental rotation (e.g., Carpenter et al., 1999; Cohen et al., 1996; Ecker et al., 2006; Kosslyn et al., 2001; Lamm et al., 2001; Richter et al., 2000; Tagaris et al., 1998; Vingerhoets et al., 2002). These findings have stimulated a debate regarding whether these motor activations reflected cognitive operations of spatial reasoning or if they were only due to spurious aspects of the motor demand of the task (i.e., pressing a response button). The activity in these areas likely reflects computations that are relevant to the spatial transformation of the image. For example, Richter and collaborators (2000), observed with time-resolved fMRI (see also Lamm et al., 2001) that activity in premotor areas were correlated with RTs in the mental rotation task of

Shepard and Metzler (1971). In another fMRI study participants were trained to imagine rotate the 3-D stimuli either by an external force or by the movement of their own hand (Kosslyn et al., 2001). The condition in which they imagined to turn the object yielded greater activation in the precentral cortex. Importantly, neuroimaging studies have found that the intraparietal sulcus (IPS) and the dorsal occipital cortex show a linear increase of activation as the angular disparity between stimuli increases (e.g., Carpenter et al., 1999). Comparable results were shown using event related potentials (ERPs) in the mental rotation task with a later posterior negativity that varied systematically with the amount of mental rotation performed and emerges at a latency of 300-600 ms (Perronet & Farah, 1989). In one fMRI study, the brain network supporting the host of cognitive processes reflected in mental rotation was mostly expressed by activity of the frontal eye field, the dorsal extrastriate areas (with V5/MT), and the superior parietal lobule (Cohen et al., 1996). The superior parietal cortex is known to construct a map of space organized retinotopically that is fundamental to represent the position of objects that can be gazed/reached. In the monkey, cells in the superior parietal lobule represent eye-centered spatial coordinates for eye movement and reaching (Colby, 1998; Colby & Goldenberg, 1999), but these cells can also be influenced by the monkey body's position (Snyder et al., 1998).

1.1.4 Spatial reference frames

Space representations allow organisms to locate things based on spatial coordinate systems: The spatial reference frames. Egocentric reference frames locate things with respect to the self and its relative axes such as front-back, up-down, and left-right. Egocentric reference frames can code the location of things relative to different body parts. There are brain cells that code eye-centered reference frames as well as head-centered reference frames, respectively in the lateral and ventral intraparietal area (Colby, 1998). These coordinate systems based on the self are fundamental for action execution. In order to grasp an object it is necessary to transform the frame of reference of the object from eye-centered coordinates to effector-centered coordinates, specifying the location of the object relative to the hand. This function is likely to be expressed in the superior parietal lobule and the posterior frontal cortex (Graziano & Gross, 1998). Spatial reference frames centered on the object locate things relative to the axes of an object independently of its position in the space. Environmental references frames locate thing relative to axes of fixed space like the cardinal directions north, sud, west, and est. These spatial reference frames define all possible forms of interaction an organism can have in its environment. Transformations of reference frames can be performed as well as imagined: perceptual reference frames for perception can be coded and transformed in correspondent representational frames of reference in mental imagery (see also Chapter 6). For example, mental rotation can be considered as the transformation of an object-centered reference frame: the reference frame of an object is transformed relative to the egocentric and environmental reference frame (see Zacks & Michelon, 2005). Egocentric mental spatial transformations are perspective transformations of the observer's point of view (e.g., answer where is located an object relative to a person). Egocentric transformations can be also effector-centered. In this case reaching and grasping movements are simulated.

Some researchers have investigated the subjective reference frame of mental rotation by manipulating the position of the observer's head. By tilting the head in either the left or right directions it is possible to dissociate the environmental from the retinal upright (Corballis et al., 1976; Corballis & Roldan, 1975). Therefore, if the upright orientation of the subjective reference frame is aligned to the environmental reference frame, then tilting the head will produce faster responses for stimuli that are shown upright relative to the environment. If the reference frame is aligned to the retinotopic reference frame then tilting the head will produce faster responses for stimuli that are shown as aligned with the head. Previous research has shown that different factors can influence the type of reference frame that is updated as a function of stimulus orientation. For example, familiar and sample objects are usually transformed within a reference frame that is aligned to the environmental reference frame (e.g., Corballis, 1976; Rock, 1974). However, complex and unfamiliar stimuli are transformed within retinotopically aligned frames of reference (e.g., Rock, 1986). The effects of head tilt can be influenced also by instructions (e.g., Corballis et al., 1978b; Rock, 1973), or the type of task (e.g., Corballis et al., 1976).

1.2 The cognitive neuroscience of motor imagery

Motor imagery can be defined as the simulation, or the rehearsal of a motor act without its actual execution, that is based on motor representations used to program and control actions (Decety, 1995). Likewise visual imagery, where phenomenological aspects of mental visual images relate to the activity of visual areas of the brain, motor imagery involves the work of brain regions relevant for preparing bodily movements (Jeannerod, 1994). Interestingly, motor imagery is a key tool in sport psychology for enhancing and learning specific motor skills (Weinberg, 2008), even for improving muscular strength (Yue & Cole, 1992). More importantly, motor imagery can improve rehabilitation of motor control after stroke (Jackson et al., 2001; Page et al., 2007; Sharma et al., 2006), and has also been employed to discern levels of awareness in vegetative patients (Owen et al., 2006). The focus of this section is on the cognitive and psychophysiological conditions that characterize the analogy between motor imagery and the control of actions together with an analysis of the literature concerned with studying the alterations of motor processing that affect motor imagery. In doing so, I will also evaluate the main available measures of motor imagery abilities, based on experiments with healthy individuals as well as patients with different sensorimotor impairments.

1.2.1 Motor images

According to Jeannerod (1995), motor images correspond to conscious motor representation, namely they are representations of actual body movements. A motor image “has the same functional relationship to the represented action, the same causal role in the generation of that action, and shares common mechanisms with motor execution” (Jeannerod & Decety, 1995). Motor images are processes, namely they are motor simulations: they involve changes that represents the unfolding of a real action obeying to the biomechanical constraints of the body and to the laws that govern actions. For example Decety and Michel (1989) showed that the time to imagine to write a sentence or to draw a cube mimic overall the time to actually perform these same action movements. Moreover, motor imagery conforms to the Fitts's law which states that the total movement duration of a rapid action is a logarithmic function of the ratio between target-effector distance and the target's width. Using virtual reality, Decety and Jeannerod (1995) instructed participants to mentally walk trough gates of different widths and at different distances. Participants took longer to mentally pass trough narrower gates presented at farther distances, thus confirming that Fitts's law applies to both actual and imagined movement. In one study (Sirigu et al., 1996) participants were asked to execute or imagine (in different conditions) sequential oppositions of the thumb with the other hand's fingers to the rhythm of a metronome. The metronome velocity was set to increase every 5 seconds and participants reported when it was no longer possible to follow the metronome with fingers opposition. The healthy participants' group showed a clear congruence between the maximum speeds of imagined and executed fingers opposition. Another task involved the execution and motor imagery of four hand gestures, each of which alternated between two hand postures that were selected to be progressively more difficult. In healthy controls the time for both imagining and performing these gestures increased from the simplest to the more complex gesture. A task that involved pointing towards targets of different width either by moving one hand or by imagining it was also used. For the healthy participants, pointing movements were slower as the target width decreased (Fitts's law) for both imagined and executed actions. A patient with damage to the mid-rolandic region of the right hemisphere could perform all tasks with comparable times between the imagined and the actually executed conditions, thus demonstrating a good capacity for generating motor images (Sirigu et al., 1995). Even though response times for the contralesional hand were significantly longer, this patient demonstrated the expected Fitts's relationship for imagined and executed actions in the pointing task. Patients with parietal lesions did not show Fitts's effect when performing the pointing task with the contralesional hand (Sirigu et al., 1996). These patients produced inconsistent contralesional responses between imagined and performed finger oppositions as well as between imagined and performed hand gestures. Damage to the motor cortex did not affect the generation of motor images that instead reflected the impairment for actual movements of the contralesional hand in the imagery domain. Moreover, lesions of the parietal lobule impaired the representation of the contralesional hand's movements, although two patients with left hemisphere damage were impaired with both hands (Sirigu et al., 1996). The selectivity of the impairment for hand actions was confirmed because when patients were tested for motor imagery of other body parts performance was normal.

The impairment in imagining movements of the contralesional hand after parietal brain damage support the notion that this region is crucial for monitoring the state of the motor representation by comparing the efferent copy of the action and multisensory reafferent signals with a stored model of the to be-imagined action. Moreover, their good ability to perform actions with the contralesional hand suggests that the evaluation of the reafferent signals may be impaired in these patients.

It is often found that impairments in overt movement execution are followed by slowing down of simulated movements of the corresponding limb. This seems to be true especially for explicit motor imagery tasks. For example, as for the patient with damage of the motor strip in Sirigu et al. study (1995), patients with lesions of the primary motor cortex and hemiparesis on one side of the body are slower at imagining (and execute) movements of their contralesional arm relative to the ipsilateral arm (Decety & Boisson, 1990; Malouin et al., 2004). Compared with healthy controls, Parkinson patients with asymmetric motor symptoms (Dominey et al., 1994; Thobois et al., 2000), patients with damaged basal ganglia (Li, 2000), or with damaged cerebellum (Gonzales et al., 2005) are slower when explicitly imagining movements with the affected hand, while patients with spinal cord injury are slower in movement execution but not in motor imagery (Decety & Boisson, 1990).

Motor imagery abilities can also be measured with self-report questionnaires. The most used motor imagery questionnaires are: The Movement Imagery Questionnaire (Hall and Martin, 1997), the Vividness of Movement Imagery Questionnaire (Isaac et al., 1986), and the The Florida Praxis Imagery Questionnaire (Ochipa et al., 1997).

1.2.2 Forward models

Within Jeannerod's framework, motor representations are compatible with “internal forward models” of the action goal (e.g., Wolpert et al., 1996). In this view the action goal is specified at different levels of the model hierarchy. The hierarchy is reflected in a sequence of different modules activated in sequential order: The higher level containing the complete internal model activates the action plan, which in turn activates the motor program that then activates the module for action execution. The model includes a control mechanism activated in parallel within the stream of information processing that corresponds to dedicated memory for each level of the model needed to store the operation performed. Reafferences of the ongoing behavior are matched to these motor memories as comparators in order to signal the degree of action completion. If the goal of the action is not reached, thus comparators detect a mismatch between the stored desired state and the reafference, then the memory will not be deleted. In this case an error signal will be sent to the program level. If changing the program will not be sufficient for reaching the action goal then an error will be sent to the plan module. While in condition of normal action execution the content of the motor representation cannot be experienced directly, motor imagery is usually accompanied by awareness of the motor image. This relates in the above described model with persistence of motor memories together with constant activation of the representational modules.

This model makes implicit the use of the so called “corollary discharge” and “efferent copy”. When a motor command is executed a corollary discharge is generated from which it is possible to predict the sensorial reafference that would flow back were the action being performed. So, in this way, it is possible to predict the sensory consequences of an action without actually performing it. The brain uses these mechanisms for example to produce stability in visual perception (Sperry, 1950), and for self-monitoring (Blakemore et al., 1998). The relevant information in the context of the present work is that the internal forward model can explain off-line processing during motor simulations (i.e., motor imagery). Following computational models of motor control and internal models of the brain (Wolpert & Miall, 1996; Wolpert & Ghahramani, 2000), a reaching movement with the arm starts with an internal inverse model that sends out the motor command to the muscles. At the same time an internal forward model predicts the actual state of the effector and the sensory consequences of the action from on-line sensorial afference and a copy of the motor command (i.e., the efference copy). When the predicted movement and the sensory feedback mismatch, then the movement is adjusted. During motor imagery the motor command is assumed to be blocked but the availability of the efference copy allows prediction of the future state of the effector. Therefore the brain would build neural networks that represent sensorimotor information and that also emulate these representations. In this way, internal models can solve the problem of delay of feedback information in action production, and can also explain mental imagery in terms of emulations of efference copies (Grush, 2004).

1.2.3 Neurophysiology of motor imagery

Another interesting phenomenon related to motor imagery is that, even though muscular activity is suspended, it is possible to detect changes in autonomic activity and in the excitability of the corticospinal tract. Respiration and heart rate increase significantly during motor imagery of pedaling or running at increasing rates (Beyer et al., 1990; Decety et al., 1991; 1993). These effects are ascribed to central activity related to the motor simulation. Supporting this notion, experimentally paralized individuals show increased of heart rate activity associated with attempts of muscular contraction (Gandevia et al., 1993). Finally, corticospinal excitability recorded as motor evoked potentials (MEPs), is modulated by imagery of hand movements (flexion/extension, opening/closing) in corresponding hand muscles (Fadiga et al., 1999;

Hashimoto & Rothwell, 1999; Rossini et al., 1999). The same type of MEP facilitation was obtained during observation, imagery and execution of hand gestures in a within-subjects experimental design (Clark et al., 2004).

At the brain level, motor imagery has been shown to recruit a network of structures implicated also in action planning and execution. These structures include prefrontal, premotor and parietal regions, the supplementary motor area, the cerebellum and the basal ganglia (Decety et al., 1994; Filimon et al., 2007; Grafton et al., 1996; Hanakawa et al., 2003; Johnson et al., 2002a). Some studies reported greater response during motor imagery than during action execution in the bilateral premotor, prefrontal, the supplementary motor area, the caudate, and the left posterior parietal cortex (Gerardin et al., 2000), the dorsolateral prefrontal cortex, the inferior frontal gyrus and the middle temporal gyrus (Stephan et al., 1995), or the posterior superior parietal cortex, the lateral premotor cortex and the pre-SMA (Hanakawa et al., 2003). It has been shown that the functional role of SMA within the motor imagery network is for suppressing actions (in M1) that increase activity of the motor system but that are not executed but imagined (Kasess et al., 2008). Other studies report significant activation of the primary motor cortex (M1) during motor imagery (Gerardin et al., 2000; Leonardo et al., 1995; Lotze et al., 1999; Nair et al., 2003; Porro et al., 1996; Roth et al., 1996) but only some have controlled muscular activity during imagery (Gerardin et al., 2000; Leonardo et al., 1995; Lotze et al., 1999). The primary motor cortex is usually significantly activated only at the group level analysis (Michelon et al., 2006), it seems that the posterior part of M1 retain spatial encoding rather than functions of motor execution (Sharma et al., 2008). Moreover, motor imagery of various body parts (i.e., hand, feet, and tongue) shows somatotopic organization in the primary, supplementary and premotor cortex (Ehrsson et al., 2003; Stippich et al., 2002) similarly to the somatotopic activation of the premotor cortex during action observation (Buccino et al., 2001).

Another important consideration relatively to the functions different brain structures play in action representation comes from neural prosthetics. Neural prosthetics allow tetraplegic individuals with spared brain functioning to steer a robotic arm. Activity of cells from chips implanted in specific brain areas is recorded while the patient imagined making a given movement. Previous implants centered on the primary motor cortex produced basic actions that were focused on the detailed reconstruction of single movements (e.g., Hochberg et al., 2006). Very recently, it has been possible to decode motor intentions in the form of action goals and action trajectories from two implants centered in the posterior parietal cortex (Aflalo et al., 2015).

1.2.4 Prospective action judgment

The studies discussed so far all employed explicit motor imagery tasks: participants were instructed to perform mental imagery and were thus aware of their motor representations. On the other hand, implicit motor imagery tasks activate motor representations through a perceptual decision while the subject is not necessarily aware of the motor components of the task. These types of tasks are considered a better way of studying imagery because in some cases judgment's accuracy can be measured, and because these tasks should not be influenced by the observer's expectation and knowledge. Two main implicit motor imagery tasks have been developed: prospective action judgments (Johnson, 2000a), and perceptual decisions about the laterality of body parts (Parsons, 1987a; Sekiyama, 1982). The latter task will be treated extensively in the next chapters. Here I will discuss prospective action judgments. In this task participants are shown with pictures of rotated dowels that are colored for one half pink and the other half tan. They are instructed to judge whether the thumb of their hand would be on the pink or on the tan area of the dowel if they were to grasp it with a power grip. At the beginning of each trial it was indicated on which hand (the left or right hand) they would have to base thr judgments. Results showed that grip selection (overhand versus underhand) is influenced by biomechanical constraints of the arms that are mirror image of one another (Johnson, 1998). The same effects were obtained with participants actually grasping a rotated dowel with a power grip. Moreover, prospective choices inversely correlated with awkwardness ratings about actual dowel's prehensions, and with awkwardness ratings about perceptual judgments of the same rotated dowel (Johnson, 2000a). Based on these results it followed that in order to make prospective action judgments participants relied on motor imagery, namely they mentally simulated the grasping movement. It was suggested that, contrary to the notion of motor imagery as the conscious experience of a pre-motor plan that is then inhibited, motor simulation would correspond to analog simulations that elaborate different motor plans before response selection, by anticipating the consequences of the to-be performed movement before its execution (Johnson, 2000a; Johnson et al., 2002a). Prospective action judgments are correlated with activations of the dorsal premotor cortex, intraparietal sulcus, the superior parietal lobule and the cerebellum (Johnson et al., 2002a). Coherently with the motor imagery hypothesis these areas are known to form a cerebral network for planning hand grasping actions (e.g., Grafton et al., 1996). Patients suffering from hemiplegia/hemiparesis after a recent vascular accident have been found to perform the task based on their impaired contralesional hand as accurately as based on their healthy ipsilesional hand. Only two patients were reported to show no correlation between their prospective judgments based on the ipsilesional and contralesional hand. Differently from the other patients they had damage of the frontal or parietal brain areas (Johnson, 2000b). Also chronic hemiplegic patients with impairments of the non-dominant hand perform prospective action judgments accurately for judgments based on their ipsilesional hand as well as their contralesional hand

(Johnson et al., 2002b). This was demonstrated also in a prospective action judgment task that elicited an object's precision grip. Performance was assessed by comparing prospective action judgments with actual motor performance executed with the unaffected limb. Moreover, the accuracy of densely hemiplegic patients did not differ from that of patients that had recovered their motor impairments. However, chronic hemiplegic patients were less accurate in representing nonprehensile proximal actions (i.e., arm posture) of either arm compared to recovered hemiplegic patients (Johnson et al., 2002b). By contrast, patients with ideomotor apraxia were impaired in performing prospective action judgments (Buxbaum et al., 2004).

Similar findings have been obtained by presenting a rotated object that could afford an easy or an awkward grasp. Responses relative to the ease of prospective grasp (i.e., easy versus difficult judgments) were a function of the angle of presentation of the object and were correlated with the time to actually grasp the object placed in that orientation (Frak et al., 2001).

2. The hand laterality task and the motor imagery account

As mentioned in the previous chapter, implicit motor imagery tasks constitute a privileged tool for studying analog mental representations. In the following section I will review the literature on the so-called hand laterality task (or hand laterality judgment task) as it is one of the most employed behavioral paradigms utilized in studies testing implicit motor imagery abilities in healthy individuals and neurological patients with different impairments. This research program began in the 70's/80's and has continued for several decades until now, giving rise to an impressive body of theoretical, experimental, and clinical studies. A common denominator to the majority of these studies is that laterality judgments of hands rely on mental rotation processes, and that task performance relates to the neuro-cognitive resources for action planning and motor imagery.

2.1 The inception of a theory

It is worth mentioning that Immanuel Kant had thought about the mirror-symmetry of left and right hands in his pre-critic phase, when he started to have insights into the problem of space representation (Kant, 1783):

> *“What can be more similar in every respect and in every part more alike to my hand and to my ear, than their images in a mirror? And yet I cannot put such a hand as is seen in the glass in the place of its archetype ; for if this is a right hand, that in the glass is a left one, and the image or reflexion of the right ear is a left one which never can serve as a substitute for the other. There are in this case no internal differences which our understanding could determine by thinking alone. Yet the differences are internal as the senses teach, for, notwithstanding their complete equality and similarity, the left hand cannot be enclosed in the same bounds as the right one (they are not congruent) ; the glove of one hand cannot be used for the other.”*

This was one of Kant's thoughts to support Newton's view of absolute space and time against Leibniz's view of space as dependent on the relationship among existing things. Kant's reasoning can be explained as follow: Left and right hands are symmetric (i.e., the relationship among their parts is the same but inverted) but they are not congruent (i.e., they do not occupy the same space surface); it follows that if the space would correspond to the relationship among an object's parts, then the space occupied by the left and the right hand (which have the same internal relationship even if inverted) should be the same, but this is not the case. Therefore, where there is the same relationship among object's parts, the space is not same. In Kant's vision, this would demonstrate that the space is not given by the relationship between parts but that the space comes before all things (that the space is absolute and is an independent aspect of objects reality) like in Newton's view.

The Russian neuropsychologist Alexander Luria employed laterality judgments' of left and right hand drawings as a test of visuo-spatial transformation of mental images (Luria, 1966). It was, however, only between the 70's and the 80's that the task was actually developed by psychologists, who were interested in different aspects of mental imagery. Cooper and Shepard (1975) were the first to rigorously investigate the effect of plane rotation on the recognition of left and right hand drawings depicted from the back or from the palm. RTs were modulated by the degree of stimulus's plane rotation like in mental rotation tasks. When participants were instructed to imagine a given hand (left or right) in a specific view (back or palm) at a given orientation (one of six angles in the picture plane) and the test stimulus corresponded with these instructions, then RTs were not affected by orientation and errors were absent. The authors concluded that in order to judge hand laterality participants imagined moving the “phantom” of one of their hands towardss the stimulus for comparison. Some years later, in 1982, Karou Sekiyama discovered a particular characteristic of the task: The relation between the RTs' function for the left hand and that for the right hand is mirror-reversed with an asymmetry relative to 180° of stimulus rotation. In other words, faster/slower RTs for clockwise (CW: from 0° to 180°) and counterclockwise rotations (CCW: from 180° to 360°) were inverted for trials with left hand stimuli and right hand stimuli. More specifically, the interaction between hand stimulus laterality and its angular departure showed that left hands were judged faster when presented with CW rotations than CCW rotations, while right hands were judged faster when presented with CCW rotations than with CW rotations (see Figure 1). This effect was then termed "Medial-Over-Lateral Advantage" (MOLA; Funk & Brugger, 2008) and describes the mirror-reversed configuration of RTs for left and right hand stimuli. Sekiyama noticed that this particular pattern of RTs closely mimicked the actual capability of left and right hands movements in the frontal plane. Participants' verbal reports also suggested that they mentally transformed the image of their own hand into the orientation of the seen hand stimulus. The author also claimed that since the mental representation of one's own hand is visual as well as kinesthetic, the mental transformation of this representation should be influenced by proprioceptive information. This would be described by the asymmetry of RTs that reflects the “manageable direction” of one's own hand movements. In this view, as soon as the stimulus is presented the observer forms an hypothesis about the left/right identity of the stimulus. According to this hypothesis, the observer generates the image of her/his hand in a canonical orientation (fingers pointing upward), and then transforms it into the same orientation of the seen hand stimulus. In doing so, RTs will be influenced by the “manageable direction” of hand movements. If the hypothesis matches the stimulus, the observer's response will correspond with her/his hypothesis, if it does not match with it then the response will be the opposite of the hypothesis. The author also noted that the hypothesis formulated upon stimulus presentation should be in most cases the correct one, in order to generate such a systematic relation between left and right hands' RTs and stimulus orientation. In the same study (Sekiyama, 1982) the author replicated the results of the first experiment by instructing participants to explicitly imagine the “feeling” of her/his own hand, and to rotate that “feeling” into the orientation of the hand stimulus in order to make the laterality judgment.

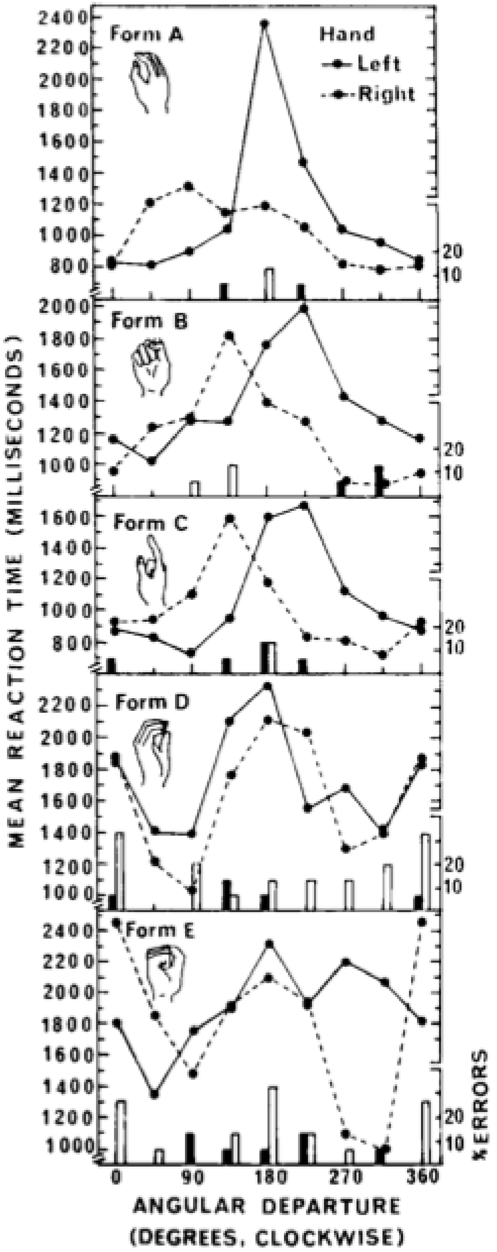


Figure 1. Mean RTs as function of the stimulus angular departures. Note the mirror-reversal of RTs for left and right hand stimuli on form A, B, and C. From Sekiyama, (1982).

Subsequent investigations (Parsons, 1987b; 1994) aimed at specifying the conditions under which laterality judgments of body parts operate. In experiment 1, Parsons (1987b) had participants perform laterality judgments of left and right hands' drawings showed from the back or from the palm rotated in the picture plane. In this experiment, similarly to Sekiyama's study, RTs were mirror-reversed for left and right hand stimuli. When hands were rotated with a lateral orientation (left hands in CCW and right hands in CW) RTs were longer than when they were rotated with a medial orientation (left hands in CW and right hands in CCW). However this effect was significant only for hands shown from the palm. In experiment 2 more hands' views were employed (see Figure 2).

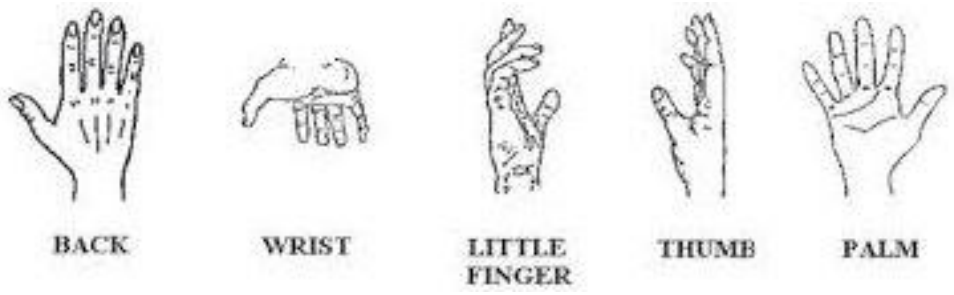


Figure 2. Stimuli employed by Parsons in his studies.

RTs were longer for laterally-oriented stimuli than for medially-oriented ones. Moreover, RTs correlated with awkwardness ratings made about the anatomical constraints of hand's movements in the displayed stimulus orientation. Experiment 3 consisted of laterality judgments of plane-rotated feet' drawings that led to similar results than experiment 2. In experiment 4 participants explicitly imagined their left or right hand (signaled before each trial) moving from its position towards the orientation of the stimulus shown. In experiment 5 Parsons employed feet instead of hands as stimuli. For both types of stimuli Parsons found that the time to explicitly imagine moving these body parts to match the stimulus correlated with the awkwardness ratings about assuming the same posture as the stimulus, and with the RTs for left-right body part judgments. The author concluded that people “make left-right judgments of body parts by imagining moving their hand/foot towards the stimulus orientation for comparison”. More specifically, people imagine moving the corresponding body part to the stimulus with the starting position of the imagined movement corresponding to their actual body parts' position. In other words observers seek confirmation rather than disconfirmation in their judgments. For example, they imagine their right hand if the stimulus is a right hand and their left hand if the stimulus is a left hand. This would be confirmed by the fact that the time to mentally simulate body parts' movements (explicitly), while knowing beforehand which hand to imagine, strongly correlates (despite a smaller effect of orientation) with the RTs for laterality judgments. Moreover, people would prefer to imagine their body parts moving towards the stimulus, and not the contrary, because it is convenient for them to exploit readily available processes used in the planning of similar physical movements. This would be supported also by participants reporting kinesthetic sensations during task execution (see also Cooper & Shepard, 1975; Sekiyama, 1982). Parsons considered also alternative hypotheses. If observers would seek disconfirmation they could either always imagine their dominant hand at the orientation of the stimulus, or they could randomly imagine their left or right hands or, else, imagine the hand for which the orientation of the stimulus is not awkward at the stimulus orientation (i.e., “likely guess”). In all these cases, when a mismatch occurs, the observer could infer that the correct response involves the other opposite hand. The first alternative hypothesis predicts that RTs pattern for left and right hands should be the same, and should differ only by a fixed time interval needed to infer a mismatch with shorter RTs for the dominant hand. This hypothesis is ruled out by the observed differences between the pattern of RTs for medial and lateral orientations of both hands. The second hypothesis predicts neither differences between left and right hand stimuli, nor between medial and lateral stimuli for left and right hands. This is obviously not the case. Parsons ruled out also the third hypothesis, because it does not explain why long RTs are observed for positions that are awkward for both hands (i.e., 0° or 180°). Moreover, given that the RTs difference between non-awkward and awkward orientations varies considerably, the tendency to imagine the wrong hand at an awkward orientation (for the correct hand) should be probabilistic. Finally, participants usually report that they imagine the correct hand at the orientation of the stimulus while the “likely guess” hypothesis predicts frequent reports of wrong first guesses.

After the study discussed above Parsons published another set of experiments (Parsons, 1994). In this study, new findings were presented that confirmed the motor imagery hypothesis for laterality judgments of hands. In experiment 1 it was demonstrated that RTs for left-right judgments about plane-rotated hand drawings were similar to the time taken to execute actual hand movements into the same hand postures as shown in the target stimulus. In experiment 2 the time to mentally simulate (explicitly) hand movements into the orientation of the stimulus was found to reflect the time to actually move the hand towards the stimulus. In experiment 4, participants carried out the hand laterality judgment task either with their hands with palms facing down (like in all other experiments) or with the palms facing up. Results showed that the time to make left-right judgments in the actual palms up position was parallel and always greater than in the actual palms down position. In experiment 5 participants executed actual hand movements into the stimulus orientation, having either with their own palms down or their palms up. The time to execute these movements closely mimicked the RTs for left-right judgments in the corresponding hand posture conditions (palms up versus palms down). Parsons had essentially shown that the kinematic of hand movements are represented in mental simulations of these movements and that laterality judgments of body parts show similar, if not the same, spatial and temporal proprieties. As in his previous study (Parsons, 1987b), in this one (Parsons, 1994) the author states that the exact match confirmation used in laterality judgments (the simulation of the left or of the right hand) is defined by preattentive processing of the hand stimulus (see also Gentilucci et al., 1998b). Thus, on each trial of the hand laterality task the observer 1) analyzes the orientation and handedness of the stimulus

2) analyzes the orientation of the internal corresponding hand 3) plans an hand movement towards the hand stimulus 4) mentally simulate the planned movement and 5) makes an exact match-confirmation of the shape of the hand stimulus with the shape of the internally represented hand. It has been proposed that left-handers rely more on the first implicit visual processing of the hand shape, while right-handers are concerned more with the confirmatory rotational process (Gentilucci et al., 1998a; Ionta & Blanke, 2009; see also Daprati & Sirigu, 2002). Another consistent results found across studies is that right-handers are usually faster with right hand stimuli than left hand stimuli, and that left-handers do not demonstrate such a difference (e.g., Funk & Brugger, 2008; Gentilucci et al., 1998a; Ionta & Blanke, 2009).

2.2 Functional imaging studies

What are the neural correlates of hand laterality judgment? Two PET studies from Parsons and colleagues (Parsons et al., 1995; 1998a) employed lateralized tachistoscopic presentation and showed increased cerebral blood flow in frontal, parietal and cerebellar regions implicated in the execution and imagery of bodily movements. These brain activations were contralateral to the stimulated hemisphere and relative to the handedness of the hand stimuli. Moreover, two commissurotomized patients performed the hand laterality task with hand stimuli randomly presented (150ms) either to the left visual field or to the right visual field (Parsons et al., 1998b). Patients judged stimulus handedness accurately (82% average accuracy) when its handedness was contralateral to the cerebral hemisphere that was stimulated (left hands in the left visual field – perceived first by the right hemisphere; right hands in the right visual field – perceived first by the left hemisphere). Accuracy dropped significantly when the stimulus handedness was ipsilateral to the cerebral hemisphere that was stimulated (left hands in the right visual field; right hands in the left visual field). Healthy control participants showed a similar pattern of results with slightly more accurate responses for stimuli contralateral to the stimulated cerebral hemisphere. RTs for both patients and controls reflected the RTs mirror-reversal showed in previous studies (Parsons, 1987b, 1994). Taken together, findings from these experiments were taken as evidence that, similarly to actual and imagined movements, judging the laterality of visually presented hands relies on limb-specific sensorimotor programs that are represented in the contralateral cerebral hemisphere (Parsons et al., 1995; 1998a; 1998b).

In addition to Parsons et al. (1995; 1998a), other researchers have tested the neural correlates of judging hand laterality using functional imaging techniques (e.g., Bonda et al., 1995; de Lange et al., 2005; 2006). Using combined PET and fMRI, Bonda et al. (1995) found increased blood flow in the superior parietal cortex, the intraparietal sulcus, and the inferior parietal lobule during hand laterality judgments, compared to a control memory task with the same hand pictures. The study of de Lange et al. (2005) involved the use of fMRI during laterality judgments of rotated hands and normal-mirror version judgments of typographical characters (i.e., letters). The authors could thus dissociate neural responses associated with the type of stimulus, with mental rotation and with the motor response. The middle occipital gyrus (consistent with the Extrastriate Body Area, EBA) showed selectivity for stimulus type. More specifically this area showed increased activation for laterality judgments of hands independently of rotation. The lingual gyrus was instead activated for both hands and letters. Activity related to mental rotation for both type of stimuli was found in occipito-temporal cortex (consistent with MT/V5), and in the left frontal eye field. The left posterior parietal and premotor (precentral) cortex showed increased activity with increasing rotational angle during laterality judgment of hands. The same parietal cluster was modulated by the angle of mental rotation for letters while the precentral cluster was not. Response-related activity was found in the primary motor cortex. In a follow up fMRI study (de Lange et al., 2006), hand laterality judgments were made with either arms extended, or with the left forearm flexed (in a CW orientation), or with the right forearm flexed (in a CCW orientation). Behavioral results showed longer RTs for laterally oriented (left hand in CCW and right hand in CW) than medially oriented (left hand in CW and right hand in CCW) hand drawings, namely the behavioral signature of the MOLA. When the left forearm was flexed in a CW orientation laterality judgments of left hands were longer when shown in a CCW rotation. When the right forearm was flexed in a CCW orientation laterality judgments of right hands were longer when shown in a CW rotation. At the neural level, the right dorsal premotor cortex (dPM) showed increased activity according to the biomechanical constraints of the left hand stimulus orientation. Similarly, the left dPM also showed modulation of activity as a function of orientation but independently of stimulus laterality. The intraparietal sulcus (IPS) also demonstrated variation of activity as a function of stimulus orientation, with the right IPS being sensitive to the left hand stimulus and the left IPS to both hand stimuli. There was also increased brain activity in the IPS for stimuli showed with lateral orientations when participants' own hand was flexed in a medial orientation. This effect corresponded to the functional correlate of the behavioral effect of hand posture. Thus, the parietal cortex contributed to integrate proprioceptive information with visual information and with the efferent copy of the motor command.

The studies of Kosslyn et al. (1998) and Vingerhoets et al. (2002) represent an exception because they did not use laterality judgments. In the former PET study the authors tested same-different judgments of pairs of hands' pictures and of pairs of solid abstract objects (as in Shepard & Metzler, 1971). A baseline was obtained using a task in which the pair of stimuli had the same orientation (i.e., no rotation). Their results showed increased activity of the parietal lobe and extrastriate visual areas (BA 19) for mental rotation of solid objects. Mental rotation of hands was correlated with increased activity of the primary motor cortex, the superior and inferior parietal lobules, the primary visual cortex, the premotor cortex, the insula and the dorsolateral prefrontal cortex. In the latter fMRI study, Vingerhoets et al. (2002) investigated the neural correlates of same-different judgments of rotated pairs of hands and tools. The control task consisted of same-different judgment of pairs of hands and tools that were not rotated. Superior parietal cortical regions were found to be active during both mental rotation of hands and tools. The right fusiform gyrus was activated during mental rotation of hands, while for tools the superior occipital gyrus was activated bilaterally. The cerebellum and the premotor cortex were also activated for both tools and hands. It is important to note that same-different judgments of hand pictures do not entail the mirror-reversal of RTs for left and right hand stimuli, and that this type of task is not affected by the observer's actual hand position (Hoyek et al., 2014). It is therefore difficult to interpret the results of Kosslyn et al. (1998) and of Vingerhoets et al. (2002) relative to the hand laterality task. However, these studies do support the notion of a domain-specific processes associated with the mental representation of imagined body parts' movements (transitive and intransitive) and imagined object's rotation.

A recent activation likelihood estimation (ALE) meta-analysis (Hétu et al., 2013) tried to identify common brain activations across different neuroimaging experiments on motor imagery. A group of studies (n=10) was referred to the “laterality judgment task” (LJT) and the activations found for this group were compared to the activations found in explicit motor imagery studies of the upper limb (MI). The regions that overlapped between the two types of tasks were fewer than expected. The LJT was found to be associated with right hemisphere activations and the MI with bilateral activations. Moreover, LJT studies showed increased brain activity in the middle frontal gyrus and in the superior parietal lobule. MI was found to consistently activate the supplementary motor area and the supramarginal gyrus. However, Hétu et al.'s (2013) selction of studies included in the LJT group was rather arbitrary: In this group they included studies that employed same-different judgments of rotated hands (i.e., Kosslyn et al., 1998; Vingerhoets et al., 2002) and studies that used completely different tasks (i.e., Johnson et al., 2002a; Wolbers et al., 2003; Wraga et al., 2005). Thus, the reported differences between LJT and MI in the Hétu et al.'s (2013) meta-analysis may be biased by the inclusion of tasks that did not test laterality judgment of hands.

A magnetoencephalography (MEG) study showed that hand laterality involves firstly activation of visual areas within 100-200ms from stimulus onset, and then activation of the inferior parietal lobe (after 200ms). Activity in the inferior parietal lobe was followed by premotor activity very closely in time. Activity in primary motor/sensorimotor areas was observed in some subjects. This process was interpreted as the transformation of retinotopic locations into a body-centered reference frame that is necessary for mental rotation (Kawamichi et al., 1998).

TMS experiments have shown that stimulation of the motor cortex (M1) slows down RTs performance on the hand laterality task (cf. Sauner et al., 2006) but not on laterality judgments of feet (Ganis et al., 2000), or letters (Pelgrims et al., 2010). Importantly, in all these studies the effect of TMS on motor cortex activity did not influence the MOLA effect.

2.2.1 Hand posture

In de Lange et al.'s study (2006) the participant's left or right hand was flexed medially, and influenced RTs for hand laterality judgments specifically by increasing RTs for hands rotated in the opposite direction of the actual hand position. When the left hand was flexed medially towards the body-midline (in a CW orientation) RTs for left hands showed in a CCW orientation were longer than RTs of left hands in a CW orientation. When the right hand was flexed medially towards the body-midline (in a CCW orientation) RTs for right hands showed in a CW orientation were longer than RTs of right hands in a CCW orientation.

Other behavioral studies have found an effect of hands' posture during the hand laterality task (Ionta et al., 2007; 2009; Parsons, 1994; Shenton et al., 2004). Different types of hand posture were adopted across studies. Parsons (1994) had participants holding their hands with palms up or palms down during the hand laterality task, during explicit simulation of hand movements, and also during actual hand movements towards the hand stimulus. When participants were holding their hands with palms up, there were longer response times for laterality judgments and explicit hand simulations that were paralleled by increased execution times for actual hand movements towards the hand stimulus. In the studies by Ionta et al. (2007; 2009) participants either held both hands behind the back, or held only the right hand behind the back. In the former study the authors found increased RTs for hand laterality judgments but not for feet laterality judgments, with both hands behind the back (Ionta et al., 2007). In the latter study, holding the right hand behind the back was associated with longer RTs for laterality judgments of right hand stimuli but neither for left hand stimuli nor for feet were found differences in RTs (Ionta et al., 2007). Moreover, left-handed subjects did not show such an effect of hand posture (i.e., the right hand behind the back). Finally, in the study by Shenton et al. (2004) the right hand could be either (in view) in a palm up or palm down position, or (out of view on the thigh) in a palm up or palm down position, or also (out of view on the thigh) in a palm up or palm down position while a fake hand was positioned in front of the subject, in correspondence of her/his right hand that was placed underneath on the thigh. When the right hand was out of view and it was held in a palm up position, laterality judgments of right hands in palm view were faster than judgments of right hands in back view. When the right hand was out of view and it was held in a palm down position, laterality judgments of right hands in back view were faster than judgments of right hands in palm view (see figure 3). The presence of a fake hand did not influence performance.

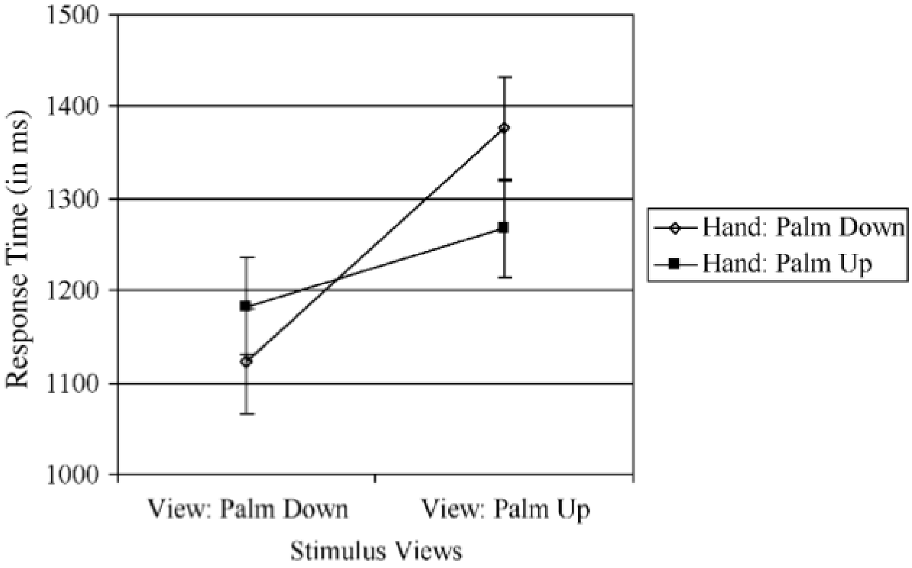


Figure 3. RTs for the two actual hand postures of the right hand (palm up; palm down) on laterality judgments of hands shown from the palm or from the back. Error bars depict standard error of the mean. From Shenton et al. (2004).

What are the neural mechanisms that allow the integration of visual and proprioceptive information responsible for the effect of congruence between hand posture and stimulus view (i.e., back-palm view)? Single-cell recording studies in non-human primates have demonstrated that vision of an arm and its proprioception are integrated at the neural level in area 5 of the superior parietal lobe. One experiment investigated the spatial congruence between the location of a fake arm, and the position of the real arm placed underneath. A good portion of neurons in area 5 responded more when the position of the two arms was spatially congruent (Graziano, 2000). Moreover, if an ipsilateral fake arm was used neural activity was not significantly increased (e.g., neural response to a right arm recorded from a neuron in the right parietal lobe). However, if a contralateral arm was employed neural activity increased (e.g., neural response to a left arm recorded from a neuron in the right parietal lobe) even when the fake arm was presented in a palm up posture, while the monkey real arm was in a palm down posture. The author concluded that the neuron in are 5 "knew" the laterality of the fake hand because responses were increased selectively for the contralateral fake arm independently from the view. Neurons with similar proprieties have been found in the monkey premotor cortex (Graziano, 1999). These cells code the position of the arm relative to a moving stimulus approaching the arm or to a static stimulus in the space near the tactile receptive field of the arm. When the position of a rubber hand was manipulated relative to the monkey's real arm like in the previous study, some neurons were more likely to respond relative to the position of the real arm, while other neurons responded more in relation to the position of the fake arm. These studies show that bimodal neurons in the parietal and frontal cortex contain convergence of visual and proprioceptive information that allows estimation of body position fundamental for guiding movements towards objects in the space within-reach. Neurons with bimodal tactile and visual receptive fields have been found in the ventral premotor cortex (e.g., Fogassi et al., 2006), as well as in temporal (Bruce et al., 1981), and parietal areas (e.g., Duhamel et al., 1998). In humans multisensory interactions between vision, touch, and proprioception have been studied with crossmodal congruency tasks, or with the rubber hand illusion (for a review see Maravita et al., 2003). These studies suggest that these multisensory representations can be modified with experience or also by using tools that can extend the bimodal receptive fields beyond the peripersonal space (Iriki et al., 1996).

It should be noted that the different hand postures used in the study of de Lange et al. (2006), and in the study of Shenton et al. (2004) had different effects on the performance of hand laterality discrimination. In the former study the lateral orientation of the hands (i.e., one hand is resting on the chest) affected the RTs distribution related to the orientation of stimulus presentation, namely if the stimulus was medially-oriented or laterally-oriented. In the latter task, changes in the horizontal orientation of the hand (held in a palm up posture) influenced the time to respond to visual stimuli displayed in a compatible view (i.e., hands seen from the palm). Unfortunately we do not know the exact cerebral correlates of the latter effect. However, de Lange et al. (2006) found that the lateral orientation of the hand posture modulated brain activity in the intraparietal sulcus and that the interaction between posture and stimulus orientation was represented in this brain area and also in the dorsal premotor cortex. These results are in line with the results discussed above about bimodal neurons present in the parietal and in the frontal cortex. Therefore, even if fundamental for action planning and execution, these bimodal neurons can allow pairing of some visual and proprioceptive signals relative to static images of hands, like those used in the hand laterality task.

2.3 The neuropsychology of the hand laterality task

The findings of Kosslyn et al. (1998) implied that mental transformation of body parts relies on cognitive processes that prepare motor actions, while mental transformation of objects is achieved through visual imagery and its related activity in visual areas. Such a dissociated view of the visuo-spatial representation of stimuli found confirmation in the results of some neuropsychological studies. Sirigu and Duhamel (2001) described one patient with bilateral infero-temporal lesions who could perform motor imagery tasks but demonstrated difficulties when performing mental rotation of solid objects. A patient with left fronto-temporo-parietal damage was instead impaired in judging hand laterality but showed good performances on tasks tapping mental rotation of objects (Rumiati et al., 2001; Tomasino et al., 2003a). In a group study, with five left-brain-damaged (LBD) patients and four right-brain-damaged patients (RBD), a dissociation between performance on the hand laterality task and on mental rotation tasks was found depending on the damaged hemisphere (Tomasino et al., 2003b). Patients with unilateral left brain damage were impaired on the hand laterality task with good performance on mental rotation tests, and patients with unilateral right brain damage performed poorly on mental rotation tests while having good results with the hand laterality task.

Subsequent investigations highlighted the contribution of top-down cognitive processing. In a PET study participants first observed and object rotating by means of an electric motor, or they actually rotated the object manually (Kosslyn et al., 2001). When in the scanner, pairs of pictures of this object were compared either by imagining the figures as if participants could touch and move them, or by imagining the object rotating by an external force, like they had seen before entering in the scanner (Kosslyn et al., 2001). The comparison between brain activity in the two conditions revealed that the motor system (including area m1) was involved only when participants imagined rotating the object as if they could move it with their hands. This led the authors to suggest that there are at least two qualitatively different ways of imagining rotating an object in space. Moreover, the type of processing adopted could be directed voluntarily in either way. The idea that, independently of stimulus type, mental spatial transformation would depend on the strategy chosen was then evaluated in a group of studies with brain-damaged patients. It was shown that LBD patients were impaired in mental rotation of hands, and of branching solid objects (as those used in Shepard and Metzler, 1971) when adopting a motor strategy, and that RBD patients were impaired in mental rotation of the same stimuli when adopting a visual strategy (Tomasino et al., 2004). For hand stimuli the motor strategy consisted in the classic hand laterality task, namely patients decided if a rotated hand drawing represented a left or a right hand. The visual strategy required patients to imagine the hand upright (i.e., with fingers pointing upward) and to report if the thumb was on the left or on the right of the hand. For solid objects stimuli, pairs of figures were presented and the motor strategy consisted in imagining rotating with the ipsilesional hand the rotated stimulus towards the upright one in order to decide if they were the same or different objects. The visual strategy consisted in reporting whether a small red cube present in the structure of the rotated object was on the left or on the right of the object. Patients responded by pressing one of two keys with the index and middle finger of their ipsilesional hand. In a recent study (Tomasino et al., 2011), another double dissociation was found between three patients with left hemispheric brain tumor resection of the hand sensorimotor representation (i.e., at the border with M1 and S1), and two patients with left hemispheric brain tumor resection of frontal regions of comparable lesion size that spared the hand sensorimotor representation. The experimental testing included in the first experiment a task of mental rotation of hands and a task of mental rotation of letters where pairs of figures were presented and same/different judgments were given. In the second experiment motor and visual strategies of mental rotation were employed for both rotated pictures of hands, and solid-abstract cubes. In the visual strategy participants indicated on which side a red dot that was present, on either the hand or the cube once it would be visualized with fingers pointing upwards. In the motor strategy, participants imagined which of their hands corresponded to the hand stimulus. For cubes stimuli, patients indicated which hand they would have used in order to touch with the thumb a red dot presented on the solid cube stimulus. The patients that had gliomas affecting the hand sensorimotor representation were impaired on mental rotation of hands in the first experiment, but not on mental rotation of letters, while the group of patients with spared sensorimotor hand representation performed well both tasks. The former group also performed pathologically on the motor strategy for both hands and cubes, while the group of patients with spared sensorimotor representation had good scores in both mental rotation strategies. However, in this study participants were instructed to perform the hand laterality task (i.e., the motor strategy on hand stimuli) by imagining their hand moving towards the stimulus (Tomasino et al., 2011). For this reason it would be difficult to compare these results with the literature on the hand laterality task in which an implicit motor imagery task has normally been used. In a different study, two groups of brain-damaged patients with either left or right brain damage (n=10 for each group) performed three tasks: the hand laterality task, a similar task where the laterality of visually presented pictures of gloves had to be determined, and a grip selection task with pictures of manipulable objects (Daprati et al., 2010). I will describe the results from the first two tasks as they are relevant to the current discussion on laterality judgments. The patients were included in the experimental group if they had brain damage of vascular origin that had resulted in motor impairment of the upper limb. They responded using the ipsilesional hand pressing one of two adjacent response keys. The results were not clear-cut and there were different significant interactions between side of brain damage, level of motor impairment, and characteristics of the stimuli (i.e., orientation and view). RBD patients performed less accurately than LBD patients and healthy controls on the hand laterality task. RBD patients with mild motor impairments were less accurate than controls and LBD patients with comparable motor impairments. RBD were also less accurate than LBD and controls in judging the laterality of hands shown in awkward orientation (i.e., lateral orientations) when stimuli were shown in palm view. However, LBD patients were slower in judging hand laterality than RBD patients and controls. Thus, it is possible that the two groups of patients traded accuracy and speed of response differently while performing the hand laterality task, hypothesis that was not directly tested by the authors. The second task consisted in determining if a visually presented glove could fit a left or a right hand. Patients' results were similar to their performance on the hand laterality task. Despite the different interpretation of Daprati et al. (2010), these results show that the effects of brain damage on left and right hemispheres are heterogeneous if one compares results between studies (cf. Tomasino et al., 2004), and may be only casually influenced by the level of motor impairments. As I have discussed in Chapter 2, patients affected by motor impairments of central origins are usually slower in performing explicit motor imagery tasks. For this reason, the results of Daprati et al. (2010) where patients with severe motor impairments performed better than patients with moderate motor deficits appear problematic. In another study that was discussed already in the context of prospective action judgments, chronic hemiplegic patients with lesions that did not involve premotor or parietal brain areas, and with motor impairments (hemiplegia) involving the non-dominant hand were tested also on the hand laterality task (Johnson et al., 2002b). Performance of chronic patients did not differ from that of patients that had recovered their motor impairments. Patients did not show any significant difference in judging left or right hand stimuli.

Two studies investigated the ability of judging hand laterality in patients with congenital hemiparesis (Mutsaarts et al., 2007; Steenberg et al., 2007). These researchers looked at the relationship between response times and angle of stimulus presentation as an index of motor simulation without considering the interaction of these two factors with hand laterality, namely the MOLA. In the former study (Mutsaarts et al., 2007) the authors found that, compared with left hemiparetic cerebral palsy (right congenital brain damage) and healthy controls, right hemiparetic cerebral palsy (left congenital brain damage) was associated with no significant linear relationship between response time and the angle of stimulus rotation. They concluded that patients with right hemiparetic cerebral palsy could not perform motor imagery and that this caused their known inability in anticipatory action planning (e.g., Steenbergen et al., 2000). Mutsaarts et al. (2007) employed a set of hand stimuli shown only from the palm. These stimuli were pictures that could depict either a closed hand or a hand grasping an hummer. When they employed drawing of hands seen either from the back or from the palm, the difference between left and right hemiparetic cerebral palsy patients disappeared: Also right hemiparetic cerebral palsy patients showed a linear increment in response time as function of the angle of stimulus rotation.

Patients suffering from focal hand dystonia were also found to perform the hand laterality task slower than healthy controls (Fiorio et al., 2006). Nevertheless, there were no differences in response times when patients judged the laterality of plane-rotated feet. On the other hand, Parkinson patients with right-lateralized motor symptoms were found to be slower in judging hand laterality when stimuli were shown in lateral orientations (i.e., awkward biomechanical constraints). These behavioral effects correlated with increased brain activity in the right EBA and in the right occipito-parietal cortex as was measured with fMRI (Helmich et al., 2007).

Conson et al. (2010) tested the effect of complete motor de-efferentation on judging hand laterality in patients suffering from locked-in syndrome. Results showed that, compared to healthy controls, patients carried out the hand laterality task less accurately, and they were not affected by the biomechanical constraints of the hand stimuli. It is however important to notice that in this study response times were not reported even if recorded, with the possibility that patients made very slow responses performing the task, making the analysis on accuracy almost pointless. Moreover, the average accuracy performance of locked-in patients was very low (around 60% of correct responses).

Another important research question that has been tackled using the hand laterality task is concerned with the characterization of action representation and motor imagery in amputees and aplasic individuals. Nico et al. (2004) recruited a group of patients (n=16) that had suffered amputation of the right or left upper limb. In performing the hand laterality task patients who lost their dominant arm made significantly more errors and responded slower than the group of healthy controls. These patients were also less accurate in judging hand laterality of stimuli shown from the pinkie-side and from the back with unnatural orientations. Amputees of the non-dominant hand did not differ from controls. In another analysis patients were grouped according to the habit of wearing or not wearing prosthesis. The former group performed less accurately and slower than controls, especially for amputees of the dominant hand when judging unnatural stimulus orientations but also for amputees on the non-dominant hand when judging natural and unnatural orientations. Amputees of the non-dominant hand not wearing a prosthesis did not differ from controls. Three patients with congenital limb absence were also tested. Surprisingly, they performed as controls on the accuracy measure. These patients were overall slower than controls but did not show an effect of orientation (i.e., the medial-over lateral advantage) for the absent limb, while they did so for the present limb. Note however that information regarding possible phantom limb was absent. Two patients with acquired peripheral loss of upper limb function (i.e., brachial plexus lesion) performed less accurately than all other patients. Their correct responses were fewer, especially for hands shown in unnatural postures. The authors concluded that loss of limb altered neural mechanisms that normally control movements and mental simulation. In the absence of one limb, predictive control of movement becomes hard to be achieved because even if the feedforward command is issued, information from periphery is not available. Thus, the longer RTs exhibited by patients may represent the use of alternative (visual) strategies. Alternative explanations, such as a disturbance of body schema given by the missing experience of visually perceiving one's own arm, or of the presence of phantom sensations which denoted a still compensating body schema were excluded. Indeed, patients that never experienced the feeling and the sight of one of their arm (i.e., the congenital absent limb patients) were slower to judge hand laterality corresponding to the affected upper limb and did not show the effect of biomechanical constraints. Similarly, the patients with brachial plexus lesion who lost the sensorimotor control of their arm while still perceiving it visually were also impaired in the task. Funk and Brugger (2008) tested unilaterally amelic patients (n=9 with absent left hand, and n=5 with absent right hand; none had phantom sensations), and two patients with bilateral amelia (A.Z., who has experienced phantom sensations, and C.L., who has never experienced phantom sensations) with a particular focus on the effect of biomechanical constraint (i.e., the MOLA) in the hand laterality task. A group of 24 normally limbed participants served as control. Patients responded pressing one of two adjacent response keys either with the stump or with the prosthesis. C.L., responded using his right foot. Right unilaterally amelic patients showed a significant MOLA only for right hand stimuli. However, the MOLA for left hand stimuli in this group was close to reach the significance level. The lack of a significant effect was probably due to the small group of patients and the lack of statistical power. Left unilaterally amelic patients showed a MOLA for both left and right hand stimuli. Thus, patients with only the right hand showed a MOLA for the hand they had and also for the hand they never had experience (i.e., the left hand). Note that this result is in contrast with Nico et al.'s study (2004), where the three left amelic patients showed a MOLA only for the hand that was present (i.e., the right hand). Overall, for unilaterally amelic patients, laterality judgments were faster when the stimulus depicted a hand that corresponded to their present hand respect to an hand that corresponded to the hand they missed. When checked for the factor prosthesis the authors did not find any significant difference. For the bilaterally amelic patients, performance was influenced by the angle of stimulus presentation.

However, A.Z., showed a MOLA for both left and right hand stimuli while C.L., did not exhibit this effect for neither hand. The presence of the medial-over-lateral-advantage in A.Z., but not in C.L., was associated to the presence of phantom sensation in A.Z., which for the authors made improve motor imagery of A.Z. Nevertheless, the absence of an advantage for C.L. might be due to a type II error, as also acknowledged by the authors.

2.3.1 The disembodied account

A single case study tried to disentangle the effect of phantom sensations from the occurrence of the MOLA studying a patient with congenital bilateral upper limb aplasia without phantom limb sensations (Vannuscorps et al., 2012). Patient D.C. performed the hand laterality task with comparable MOLA effect with healthy control participants. This result has been interpreted as strong evidence that the effect of biomechanical constraints (i.e., the MOLA) is not dependent on processes related to the planning and execution of arm-hand movements. Moreover, rating of awkwardness about the hand stimuli, but not of visual familiarity significantly correlated with RTs of hand laterality judgments. The authors suggested that knowledge of body biomechanical constraints is intrinsic to visual perception of body parts. In a more recent study, a patient (P.M.) with bilateral congenital amelia with no arms, no forearms, and no hands, with no history of upper limb prosthetics or phantom limb sensations has been reported (Vannuscorps & Caramazza, 2015). P.M. performed the hand laterality task with the same behavioral signature of MOLA as healthy participants. This case was taken as a demonstration that the influence of biomechanical constraints on body parts perception is not due to the recruitment of one's own body representation, and that instead the response profile on the hand laterality task follows the natural way the perceptual system processes bodies.

For the authors, these results do not conflict with evidence that performance of different motor-impaired patients slows down RTs or alters the MOLA. Vannuscorps and Caramazza (2015) support the classic explanation that hand laterality is first recognized by perceptual analysis and then confirmed by a simulation strategy (Parsons, 1987b; 1994). In this view, motor disorders interfere with the confirmation process, while patients such as D.C., and P.M., rely uniquely on the visual-perceptual analysis of the stimuli. Moreover, their view supports the notion that the hand laterality task and the MOLA effect cannot be attributed to forms of body representations (i.e., the body schema, the body image or the body structural description). I will discuss this alternative hypothesis in Chapter 6, where I will discuss the studies done on chronic pain patients and where I will also report my study on unilateral neglect.

3. The effects of healthy aging on egocentric and allocentric mental spatial transformations

The work presented in this chapter has been already published (De Simone et al., 2013). However, in the light of the subsequent studies that will be described in the following chapters, different aspects of the present work will be reconsidered. For this reason, I will describe the present work in line with the ideas and interpretations made in 2013, but I will also attempt an updated discussion of the present experiment in the light of the new results described in chapter 5. The re-elaboration of the present work can be found at the end of chapter 7.

In the present chapter, a study on a group of healthy aged individuals and a group of young participants will be presented. I compared performance of healthy elderly individuals in the hand laterality task with their performance on a visual laterality task. Performance of a group of young participants on both tasks was compared to the elderly participants' performance. The study was inspired to the idea that the hand laterality task relies on sensorimotor and multisensory components necessary to perform egocentric mental spatial transformations. The visual laterality task was employed in order to evaluate complementary abilities in performing allocentric mental spatial transformations. The latter task was held to tap the ability to locate stimulus's parts relative to the object-centered coordinate system, while the former task was assume to involve the recognition of handedness and, as such, to rely on egocentric spatial transformations.

3.1 Introduction

Substantial evidence indicates that aging affects cognitive as well as motor processing. Behavioral (e.g., Salthouse, 2000) and neuroimaging studies (e.g., Hutchinson et al., 2002; Reuter-Lorenz, 2002) have analyzed the aged brain under a variety of cognitive and motor tasks. Researchers are trying to clarify whether aging is associated with specific alterations in perception and action or whether a more general decline in cognitive functions produces diffuse deterioration (Reuter-Lorenz, 2002). For example, elderly individuals have been found to be slower than younger controls at explicitly imagining movements in a Fitts' like task (Personnier et al., 2010; Skoura et al., 2005), particularly when they imagined movements of the non-dominant hand (Skoura et al., 2008). This is consistent with their being less accurate and slower at executing movements with the non-dominant hand in highly demanding tasks (Francis & Spirduso, 2000; Mitrushina et al., 1995; Teixeira, 2008). At the same time, mental rotation seems to slowly degrade in elderly individuals. Importantly, age-related changes have been reported for mental rotation of objects and alphanumeric characters (Berg et al., 1982; Cerella et al., 1981; Dror & Kosslyn, 1994; Gaylord & Marsh, 1975; Hertzog & Rypma, 1991; Kemps & Newson, 2005; Puglisi & Morrell, 1986; Sharps & Gollin, 1987), and laterality judgment of hands (Devlin & Wilson, 2010; Saimpont et al., 2009). However it is unclear whether the age-related decline in mental imagery hides a more specific deficit in applying either an egocentric mental transformation or an allocentric mental transformation. In this chapter I will try to clarify the impact of normal aging in applying either an egocentric (i.e., the hand laterality task) or an allocentric mental transformation (i.e., the visual laterality task). As I have discussed in Chapter 1, tasks that require handedness discrimination involve the updating of the egocentric reference frame. Conversely, the visual laterality task tests the ability to locate part of the stimulus relative to its own coordinate system. Differently from previous research, the paradigm employed in the present study allowed us to directly compare the two complementary mental spatial transformations by holding constant the stimuli to be mentally rotated and the type of response required. If the two classes of mental transformation differently decline with age, then I expected the group of elderly participants to perform worse in one of the two tasks. Instead, if healthy aging generally affects the ability to perform mental transformations, then I expected impairments in both the egocentric and the allocentric task.

Since the functionality of the non-dominant hand changes with age (see e.g., Mitrushina et al., 1995; Francis & Spirduso, 2000; Teixeira, 2008), all our right-handed participants were asked to respond with their dominant hand (i.e., the right hand) irrespective of whether the response was left or right. This is at variance with Saimpont et al. (2009), in which elderly participants responded with the left hand or the right hand for left and right stimuli respectively. Thus, I also predicted that if normal aging specifically affects non-dominant hand sensory-motor programs, then our elderly participants' performance should be impaired for left-hand stimuli even when they respond with the dominant hand for both left and right handed stimuli. Based on previous studies, I hypothesized that judging the laterality of a visually presented hand relies on limb-specific sensory-motor programs that are represented in the contralateral cerebral hemisphere (Parsons et al., 1995; 1998a; 1998b). Left-right judgments are faster when right hands are presented to the right visual field and when left hands are presented to the left visual field (Parsons et al., 1998b). If elderly individuals were particularly challenged by engaging in sensory-motor programs to control their non-dominant hand during MI (Saimpont et al., 2009; Skoura et al., 2008), then they should be especially affected by the lateralized presentation of left hands. Furthermore, compared with young controls, elderly individuals may experience a greater interference when left hands are presented to the ipsilateral hemisphere (i.e., longer RTs for left hands presented to the right visual field), as well as a reduced advantage when left hands are presented to the contralateral hemisphere (i.e., longer RTs for left hands presented to the left visual field).

By computing linear regression lines (slopes and intercepts) on RTs it has been possible to differentiate between different components of the task. The slope represents the average RTs change produced by the stimulus angular departure reflecting the spatial transformational process, with steeper slopes indicating slower speed of rotation. The intercept is thought to be related to processes such as visual perception, decision making, and response preparation (Shepard & Cooper, 1982). If elderly individuals were slower in imagining proportionally longer spatial transformations their performance should highlight steeper slopes than the group of young participants. Moreover, if they were slower for more complex effector-centered transformations then the slopes for laterally-oriented stimuli should be steeper than the slopes for medially-oriented stimuli. Finally, if they were generally slower, differences should be found on the intercepts of the least square RTs/angle regression line.

3.2 Methods

3.2.1 Participants

Fifteen elderly (mean age = 71.9 years, SD = 4.2, 8 female) and 15 young volunteers (mean age = 26.5 years, SD = 2.1, 8 female), with no history of previous neurological or psychiatric disease took part in the experiment. All participants were right-handed (elderly = 96 ± 4.8; young = 93.3 ± 6.1) according to the Edinburgh Standard Handedness Inventory (Oldfield, 1971). The elderly participants were well preserved both physically and cognitively (CRIq = 126.3 ± 7.2, Nucci et al., 2011; MOCA = 27.4 ± 1.1, Nasreddine et al., 2005).

3.2.2 Stimuli and tasks procedures

Participants sat in front of a PC screen at a distance of 60 cm away. All participants responded with their dominant right hand by pressing a custom-made button box consisting of two pads located next to each other. Participants were told that the pad on the left was to be used for left responses and the pad on the right for right responses. Each image was a realistic picture of a hand and was the result of a rotation and/or refection of two basic hand postures (back or palm). Each hand stimulus (left or right) was presented in six different angular departures (45°, 90°, 135°, 225°, 270°, 315°), and at three positions on the screen (left, LP; right, RP; and center, CP) (see Figure 4a and 4b for an example of the stimuli) Each participant performed two laterality tasks, one requiring an allocentric transformation, and the other requiring an egocentric transformation. In the allocentric task, participants decided if a red dot was on the left or on the right side of the hand as it would be seen in the upright position (i.e., canonical orientation with fingers pointing upward), while in the egocentric task they were asked to decide whether the presented hand was a left or right hand. The red dot could be located either on the extremity of the little finger or ring finger, or of the index finger or thumb. The red dot was presented in both tasks however in the egocentric task it was not relevant. Two blocks of the egocentric task and two blocks of the allocentric task were interleaved for each participant, while the order of presentation was counterbalanced across participants. Each block consisted of 144 trials for a total of 576 trials. Each trial began with a central fixation cross (1500 ms), followed by the presentation of a stimulus that was shown on a white background. After, a stimulus appeared randomly to the left, the right or on the center in the screen, each trial was timed-out upon the participant's response. Participants were required to make the laterality judgment as quickly and accurately as possible, and they did not obtain any feedback about their performance. The stimuli were presented in a random order except that the same stimulus could not appear twice within three successive trials. To make sure that participants understood the instructions, they were asked to perform ten practice trials prior to each block. During these training phases they were instructed and monitored by the experimenter to focus their gaze on the central fixation cross.

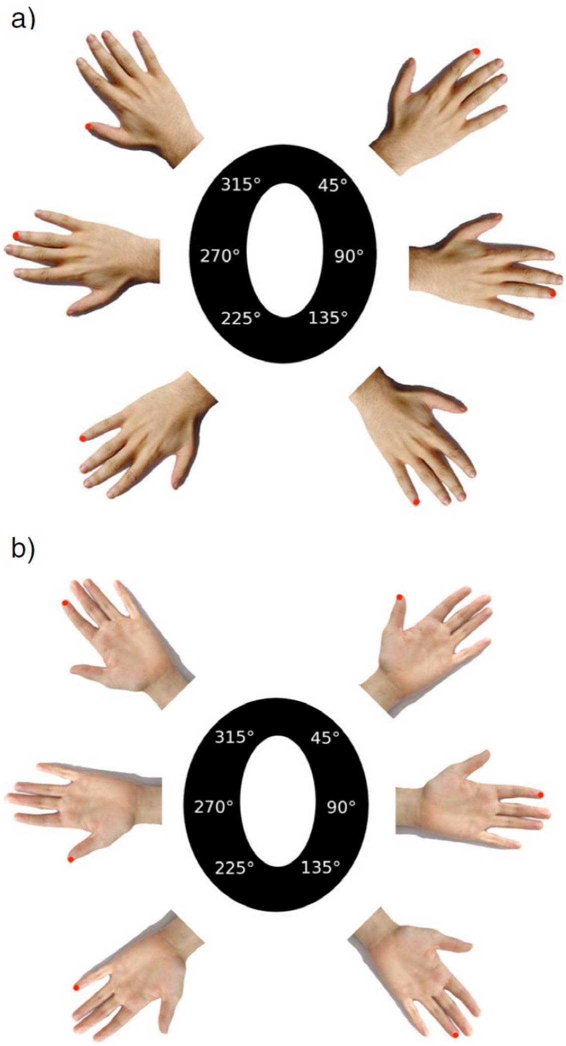


Figure 4a. Example of a right hand showed in back view at the different angles.
4b. Example of a left hand showed in palm view. From De Simone et al. (2013).

3.2.3 Data analysis

A first analysis was carried out to check that MR processes were effectively engaged during both the egocentric task and the allocentric task. In order to do so, two mixed design ANOVAs were conducted on RTs separately for the egocentric and the allocentric task. Each ANOVA had Handedness (left/right), View (back/palm), Position (LP/CP/RP) and Angle (45°, 90°, 135°, 225°, 270°, 315°) as within-subjects factors, and Group (elderly/young) as between-subjects factor.

To test the effects of aging on the MOLA effect, two mixed design ANOVAs on RTs and accuracy were conducted. Each ANOVA had Task (egocentric/allocentric), Handedness (left/right), View (back/palm), Position (LP/CP/RP), and Orientation (medial/lateral) as within-subjects factors, and Group (elderly/young) as a between-subjects factor. Lateral orientations correspond to hands rotated away from the participant's midsagittal plane (i.e., left hands when rotated counterclockwise and right hands when rotated clockwise), while medial orientations correspond to hands rotated towards the participant's midsagittal plane (i.e., left hands when rotated clockwise and right hands when rotated counterclockwise). Accordingly, medial orientations corresponded to the mean RTs of trials with 45°, 90°, and 135° of rotation for left hand stimuli, and with 225°, 270°, and 315° of rotation for right hand stimuli. Lateral orientations corresponded to the mean RTs of trials with 225°, 270°, and 315° of rotation for left hand stimuli and with 45°, 90°, and 135° of rotation for right hand stimuli. For each participant, and each combination of task, hand, view, position, and orientation, RTs were calculated as the average time of correct trials. RTs greater than two standard deviations above the mean and shorter than 500 ms were not included in any of the analyses (total loss, 6.8% of trials). Accuracy was calculated as proportion of correct trials before removing RTs outliers.

In addition, I computed linear regression lines (i.e., slopes and intercepts) on RTs. The slopes were computed from the average RTs among angular departures equidistant from 0° (i.e., 45° with 315°, 90° with 270° and 135° with 225°), separately for medial and lateral orientations (medial orientations: left handed stimuli with 45°, 90° and 135°, right handed stimuli with 225°, 270° and 315°; and lateral orientations: left handed stimuli with 225°, 270° and 315°, right handed stimuli with 45°, 90° and 135°). The slope represents the average RT change produced by the stimulus angular departure reflecting the spatial transformation process, with steeper slopes indicating slower speed of rotation. The intercepts were computed from the average RTs between angular departures equidistant from 0° (i.e., 45° with 315°, 90° with 270° and 135° with 225°). The intercept is thought to be related to processes such as visual perception, decision making, and response preparation (Shepard & Cooper, 1982). Earlier or later intercepts suggest that participants took shorter or longer time respectively to accomplish those processes. I then ran two ANOVAs on slopes, one for each task, with View (back/palm), Position (LP, CP, RP) and Orientation (medial/lateral) as within-factors and Group (elderly/young) as a between-factor. Even though RTs for medial orientations do not typically show a linear relation as a function of the rotational angle (Parsons, 1994; ter Horst et al., 2012), the slope analysis was planned to check if the laterally oriented hand stimuli were harder to be mentally transformed for the elderly group than for the young group. I also ran an ANOVA on intercepts of each participant with Task (egocentric/allocentric), Handedness (left/right), View (back/palm) and Position (LP, CP, RP) as within-factors and Group (elderly/young) as a between-factor. The alpha-level was set at 0.05; post-hoc comparisons were carried out using the Tukey HSD test. Partial eta squared (η^2) are reported where necessary.

3.3 Results

3.3.1 Angular departures

3.3.1.1 Egocentric Task

The main effect of angle was found significant, $F (5, 140) = 41.51, p < .001; \eta^2 = .597$. There was a significant interaction between handedness and angle, $F (5, 140) = 28.80, p < .001; \eta^2 = .507$, and a significant three-way interaction between handedness, angle, and group, $F (5, 140) = 3.74, p < .005; \eta^2 = .118$. Both groups showed the expected RT asymmetry between left and right hand stimuli, with a preferred direction of rotation modulated by stimulus handedness (see Figure 5).

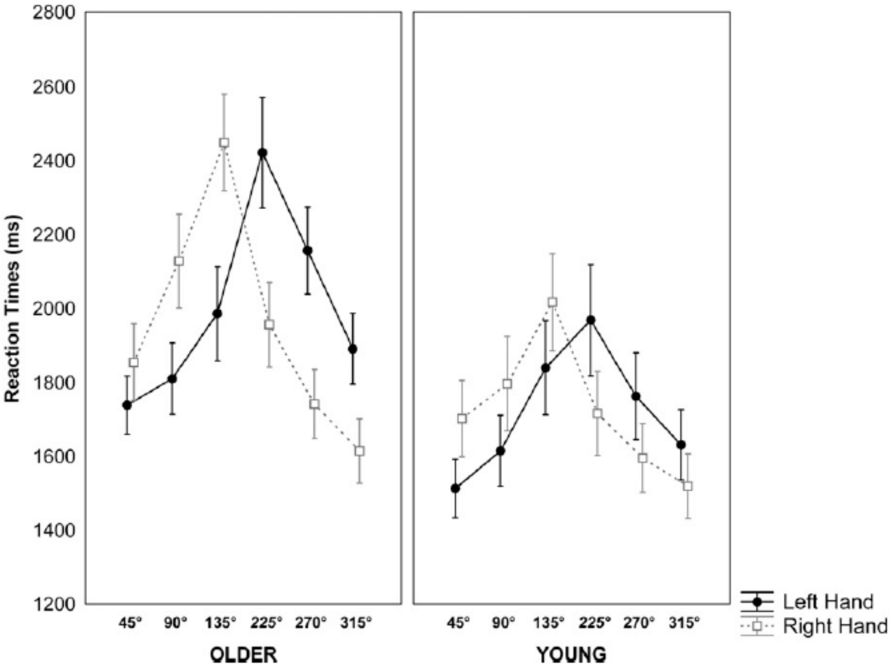


Figure 5. Egocentric task. Mean RTs at the different stimulus angular departures (45°; 90°; 135°; 225°; 270°; and 315°) for the two stimulus handedness (left hand–right hand) and the two groups (elderly–young). Error bars depict the standard error of the mean. From De Simone et al. (2013).

For the group of elderly participants, RTs were faster when left hand stimuli were shown with 45° and 90° than when left hand stimuli corresponded to 225° and 270° of angular departures (ps < .005), and RTs were faster when right hand stimuli were shown with 270° and 315° than when right hand stimuli corresponded to 90° and 135° of angular departures (ps < .001). For the group of young participants, RTs were faster when left hand stimuli were shown with 45° and 90° than when left hand stimuli corresponded to 225° of angular departure (ps < .005), and RTs were faster when right hand stimuli were shown with 270° and 315° than when right hand stimuli corresponded to 135° of angular departure (ps < .05). Moreover, elderly participants' RTs for left hand stimuli with a rotation of 225° were slower than young participants' RTs for left hand stimuli with a rotation of 45° (p < .05), and for right hand stimuli with a rotation of 315° (p < .05). Elderly participants' RTs for right hand stimuli with a rotation of 135° were slower than young participants' RTs for left hand stimuli with a rotation of 45° and 90° (ps < .05), and for right hand stimuli with a rotation of 270° and 315° (ps < .05). For the group of elderly participants, the differences between left and right hand stimuli, for each angle of rotation, were always significant(ps b .05), except that for 45° of stimulus angular departure (p > .05). The group of young participants did not show such difference between left and right hand stimuli for each stimulus angular departure (ps > .05). The main effect of stimulus view was significant, F (1, 28) = 12.05, p < .005; η^2 = .300. The view × angle, F (5, 140) = 6.03, p < .001; η^2 = .177, and the handedness × view × angle, F (5, 140) = 5.04, p < .001; η^2 = .152, interactions were also significant (see Figure 6).

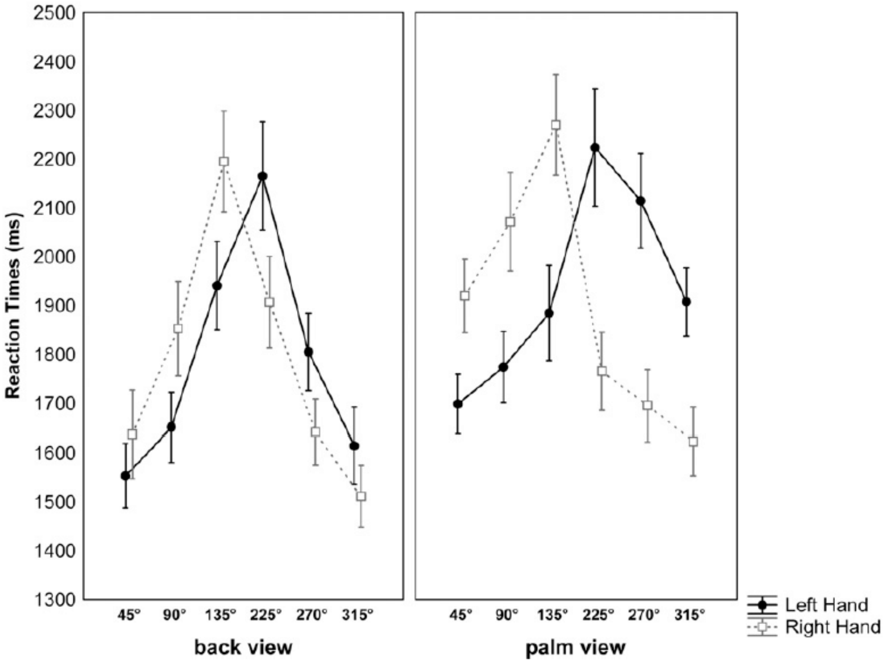


Figure 6. Egocentric task. Mean RTs at the different stimulus angular departures (45°; 90°; 135°; 225°; 270°; and 315°) for the two stimulus handedness (left hand–right hand) and the two stimulus view (back–palm). Error bars depict the standard error of the mean. From De Simone et al. (2013).

For stimuli showed in back view, RTs differed between left and right hands with faster RTs for left hands at 135°, and with faster RTs for right hands at 225° (ps < .05). For stimuli showed in palm view, RTs differed between left and right hands with faster RTs for left hands at 45°, 90° and 135° (ps < .05), and with faster RTs for right hands at 225°, 270° and 315° (ps < .05). The handedness × position × angle interaction was also significant, F (10, 280) = 2.15, p < .05; η^2 = .071. When stimuli were presented centrally (CP), the 45° and the 315° of angular departures did not differ between left and right hand stimuli (ps > .05). When presented on the left (LP), trials with 45° of angular departure did significantly differ between left and right hand stimuli, with faster RTs for left hand stimuli (p < .001). When presented on the right (RP), trials with 315° of angular departure did significantly differ between left and right hand stimuli, with faster RTs for right hand stimuli (p < .005) (see Figure 7).

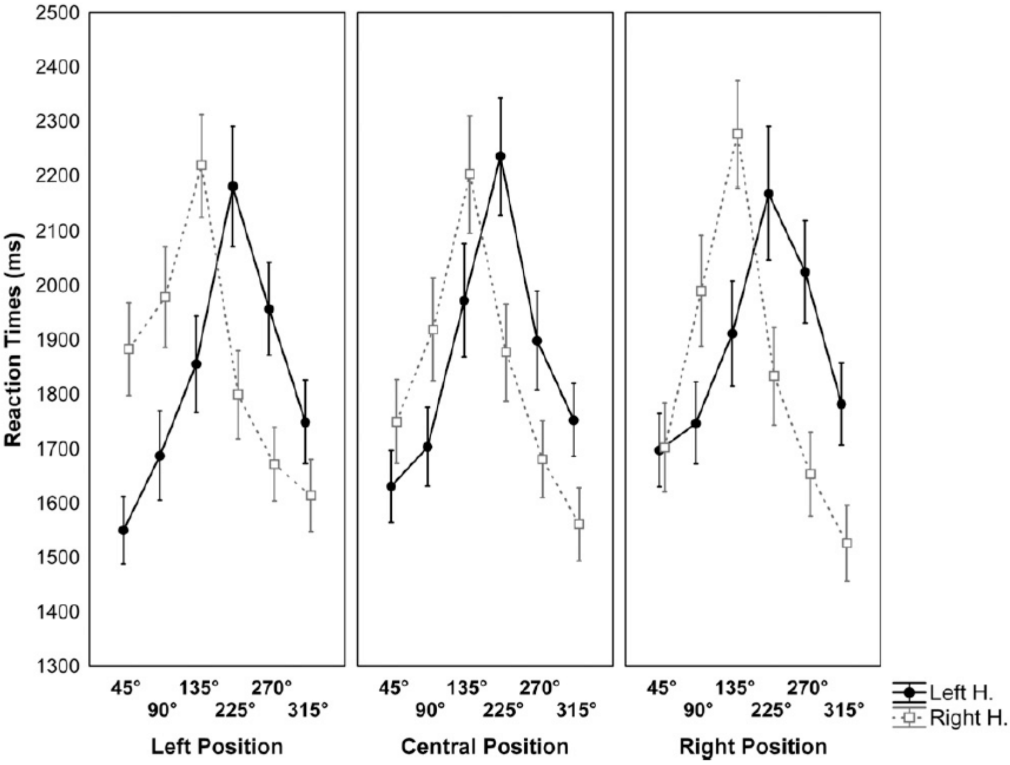


Figure 7. Egocentric task. Mean RTs at the different stimulus angular departures (45°; 90°; 135°; 225°; 270°;315°) for the two stimulus handedness (left hand–right hand) and the three positions of stimulus presentation (LP–CP–RP). Error bars depict the standard error of the mean. From De Simone et al. (2013).

3.3.1.2 Allocentric Task

The factor angle led to a significant main effect, F (5, 140) = 65.93, $p < .001$; η^2 = .701, with a significant angle × group interaction, F (5, 140) = 3.78, $p < .005$; η^2 = .119. The group of young participants did not show increase in RTs as function of stimulus angle of presentation. Differently from elderly participants, their RTs slowed-down only for 135° and 225° of angular departures. Elderly participant RTs showed a monotonic increment as angular departures were further from the upright (0°): trials with an angle of 45° were faster than all other angles (ps < .05), except for 315° (p = .999); trials with an angle of 90° were faster than 135° and 225° (ps < .005) but they were not different from 270° ($p = .999$); trials with an angle of 135° were slower than all other angles ($ps < .001$), except for 225° ($p = .994$). The group of young participants was faster for trials with 45°, 90°, 270°, and 315° compared to RTs for trials with 135° and 225° of angular departures ($ps < .001$), while RTs for trials with 45° and 90° did not differ from those with 270° and 315° of angular departures ($ps > .05$). RTs are plotted as a function of stimulus angular departures for each group in Figure 8. The handedness × angle interaction, $F(5, 140) = 5.16$, $p < .001$; $\eta^2 = .155$, revealed that RTs were modulated by the angular departures and by the laterality of the visual marker. When the visual marker was located on the left side of the stimulus, RTs significantly increased between 90° and 135° of angular departures ($p < .001$), while RTs between 135° and 225° of angular departures did not differ from each other ($p = .446$). RTs then decreased from 225° to 270°, and to 315° of stimulus angular departures ($ps < .001$). When the visual marker was located on the right side of the stimulus RTs significantly increased between 90° and 135° of angular departures ($p < .001$). RTs then decreased from 135° to 270° ($ps < .005$), while RTs between 270° and 315° of angular departures were not significantly different ($p = .127$). A direct comparison between left and right sided markers revealed a significant difference at 225° of angular departure, with right located marker stimuli faster than left located marker stimuli ($p < .001$).

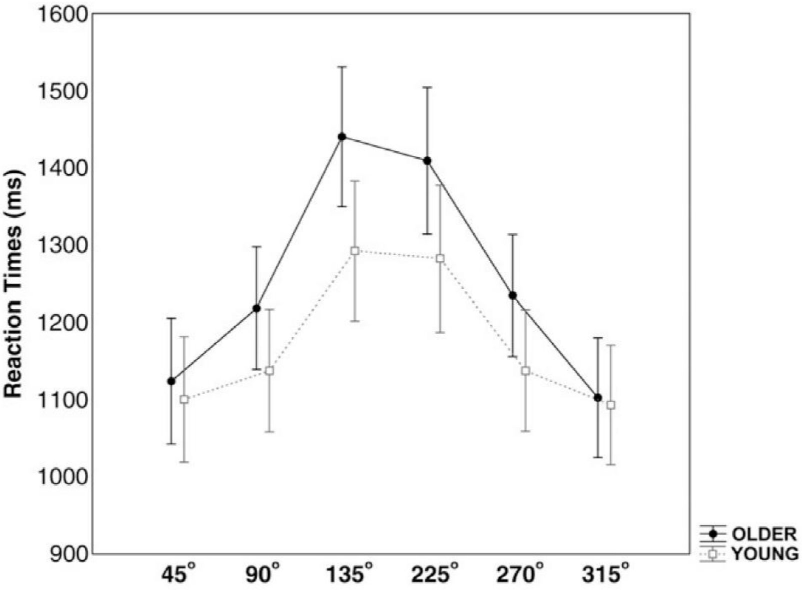


Figure 8. Allocentric task. Mean RTs at the different stimulus angular departures (45°;90°;135°;225°;270°;315°) for the two groups (elderly–young). Error bars depict the standard error of the mean. From De Simone et al. (2013).

3.3.2 MOLA effect

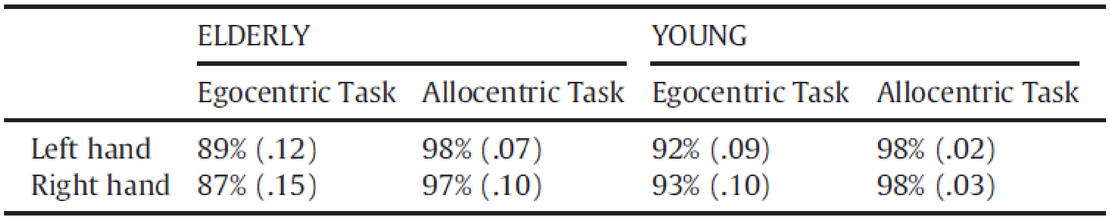
3.3.2.1 Accuracy

Significant main effects of task, F (1, 28) = 49.56, $p < .001$; $\eta^2 = .638$, with a better performance in the allocentric compared with the egocentric task, and of orientation, F (1, 28) = 4.81, $p < .05$; $\eta^2 = .146$, with MR being harder for lateral orientations than medial orientations were observed. Main effects were qualified by an interaction between these two factors, F (1, 28) = 5.23, $p < .05$; $\eta^2 = .157$. The orientation x group, F (1, 28) = 10.22, $p < .005$; $\eta^2 = .267$, and the task x orientation x group interactions, F (1, 28) = 9.27, $p < .005$; $\eta^2 = .248$, were significant. Post-hoc comparisons showed that the group of elderly participants was significantly less accurate during the egocentric task of lateral orientations compared with all other conditions (ps < .05). For both groups, there was no difference between orientations during the allocentric task (ps >

.05).The task × position interaction, F (2, 56) = 7.83, p < .001; η^2 = .218, and the three-way task × position × group interaction, F (2, 56) = 4.52, p < .05; η^2 = .139, were both significant. Post-hoc tests revealed that, relative to young participants, elderly participants' accuracy significantly differed when they adopted the egocentric task than when they adopted the allocentric task, as a function of the position of the stimulus on the screen. Here, during the egocentric task, elderly participants made significantly more errors with LP than with CP stimuli (p < .001). Performance for RP stimuli was also worse than CP stimuli but this effect was only marginally significant (p = .09). Young participants were not affected by the lateralized presentation of hands when they applied the egocentric task (ps > .05). Moreover, for both groups, participants' accuracy during the allocentric task did not differ depending on positions (ps > .05).

The factor handedness, F (1, 28) = .66, p = .42, ns, and the interaction between handedness and group, F (1, 28) = 3.42, p = .074, ns, did not reach significance (see Table 1).

Table 1. Mean accuracy reported as percentage of correct responses for the two groups in the two tasks and for the left and right responses. Standard errors of the mean are printed in brackets. From De Simone et al. (2013).



	ELDERLY		YOUNG	
	Egocentric Task	Allocentric Task	Egocentric Task	Allocentric Task
Left hand	89% (.12)	98% (.07)	92% (.09)	98% (.02)
Right hand	87% (.15)	97% (.10)	93% (.10)	98% (.03)

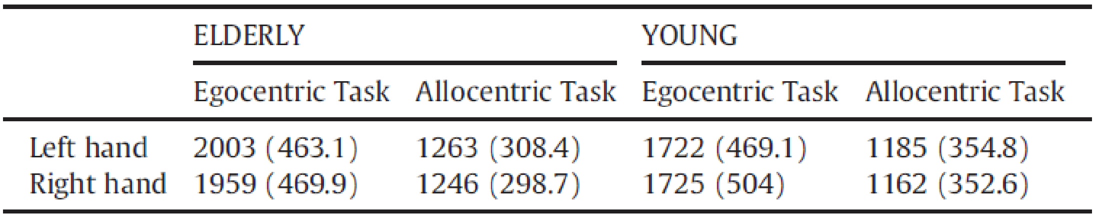
3.3.2.2 Response Times

The ANOVA showed a significant main effect of task, F (1, 28) = 104.15, p < .001; η^2 = .963, with the allocentric task being faster than the egocentric task. There was a main effect of view, F (1, 28) = 16.01, p < .001; η^2 = .363. RTs during MR of palm view hands were slower than during MR of back view hands. A main effect of position, F (2, 56) = 3.60, $p < .05$; $\eta^2 = .114$, was found significant, with RTs being slower for LP and RP stimuli compared with CP stimuli, as well as a main effect of orientation, F (1, 28) = 67.33, $p < .001$; $\eta^2 = .706$, with RTs for lateral orientations being slower than medial orientations. The task x view, F (1, 28) = 4.43, $p < .05$; $\eta^2 = .136$, view x orientation interaction, F (1, 28) = 11.01, $p < .01$; $\eta^2 = .282$, and the three-way task × view × orientation interaction, F (1, 28) = 11.69, $p < .01$; $\eta^2 = .294$, were found significant. Post-hoc analysis revealed that, during the egocentric task, RTs for lateral orientations were slower than RTs for medial orientations both for back view ($p < .001$) and palm view hands ($p < .001$). Moreover, for lateral orientations, palm view hands took longer compared to back view hands ($p < .001$), while there was no difference between RTs for back and palm view hands when showed with medial orientations ($p > .05$). View and orientation had no effect when participants performed the allocentric task (ps > .05). The position × group interaction, F (2, 56) = 4.66, $p < .05$; $\eta^2 = .142$, was accounted for by the slower performance of elderly participants with LP and RP stimuli compared with CP stimuli (ps < .05). The significant handedness × position interaction, F (2, 56) = 5.02, $p < .05$; $\eta^2 = .151$, revealed that left hand stimuli presented to the right visual field took longer than right hand stimuli presented to the center and to the right visual field (ps < .05). The ANOVA also showed a significant three-way task × position × orientation interaction, F (2, 56) = 3.50, $p < .05$; $\eta^2 = .111$, which was driven by the factors' task and orientation: the different positions of the stimuli on the screen (i.e., LP, CP, RP) did not differ from each other depending on the type of task or orientation (ps > .05).

RTs were modulated by task and orientation, F (1, 28) = 35.66, $p < .001$; $\eta^2 = .560$. Lateral orientations were significantly slower than medial orientations when participants performed the egocentric task ($p < .001$) but not when they performed the allocentric task ($p > .05$). The orientation × group interaction, F (1, 28) = 5.78, $p < .05$; $\eta^2 = .171$, and the task × orientation × group interaction, F (1, 28) = 4.22, $p < .05$; $\eta^2 = .131$, were found significant. For both groups, during the egocentric task, lateral orientations took longer than medial orientations ($ps < .005$), while in the allocentric task, RTs for medial orientations were not significantly different from RTs for lateral orientations ($ps > .05$). Only for the egocentric task (see Figure 9) was MR of laterally-oriented stimuli showed slower for elderly than young participants ($p < .05$), while MR of medially-oriented stimuli showed no difference between the two groups ($p > .05$).

Finally, the factor handedness, F (1, 28) = 3.42, p = .074, ns, and the handedness × group interaction, F (1, 28) = .91, p = .34, ns, failed to reach significance (see Table 2).

Table 2. Mean reaction times (RTs) (milliseconds) for the two groups in the two tasks and for the left and right responses. Standard errors of the mean are printed in brackets. From De Simone et al. (2013).



	ELDERLY		YOUNG	
	Egocentric Task	Allocentric Task	Egocentric Task	Allocentric Task
Left hand	2003 (463.1)	1263 (308.4)	1722 (469.1)	1185 (354.8)
Right hand	1959 (469.9)	1246 (298.7)	1725 (504)	1162 (352.6)

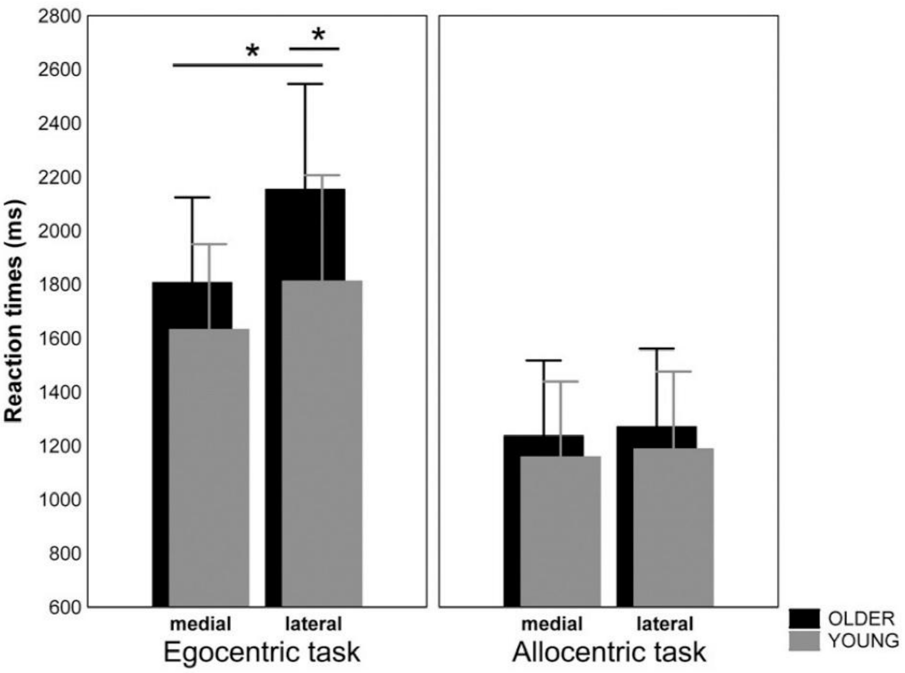


Figure 9. Mean RTs at the different orientations (lateral–medial) of the stimuli for the two groups (elderly–young) and the two tasks (egocentric–allocentric). Error bars depict the standard error of the mean. From De Simone et al. (2013).

3.3.3 Linear regression

3.3.3.1 Slopes

For the egocentric task there were significant main effects of view, F (1, 28) = 6.03, p < .05; η^2 = .177, and orientation, F (1, 28) = 8.85, p < .05; η^2 = .240. The orientation × group interaction was found significant, F (1, 28) = 4.07, p b .05; η^2 = .126. During the egocentric task the group of elderly participants showed steeper slopes for lateral orientations compared to their performance on me-dial orientations (p < .005) and to both medial and lateral orientations performed by the young participants (ps < .05). The ANOVA on the allocentric task revealed significant main effects of group, F (1, 27) = 5.89, p < .05; η^2 = .179, with the group of elderly participants showing steeper slopes than young participants, and of orientation, F (1, 27) = 15.91, p b .001; η^2 = .371, with steeper slopes for lateral orientations compared to medial orientations. The significant interaction between position, orientation, and group, F (2, 54) = 5.62, $p < .05$; $\eta^2 = .172$, was significant. The older group had steeper slopes for stimuli showed to the right with lateral orientations compared to their performance with medially oriented stimuli showed to the right ($p < .05$), and to the young participants' performance with medially oriented stimuli presented to the left, to the center and to the right of the screen (ps < .05).

3.3.3.2 Intercepts

There were significant main effects of task, F (1, 28) = 87.11, $p < .001$; $\eta^2 = .756$, and view, F (1, 28) = 25.3, $p < .001$; $\eta^2 = .474$, and a significant task × view interaction, F (1, 28) = 21.23, $p < .001$; $\eta^2 = .431$. Later intercepts were found during the egocentric task for palm view hands with respect to back view hands in the allocentric and in the egocentric task (ps < .001). Intercepts during the allocentric task for back view and palm view did not differ ($p = 1.0$). Finally, a three-way task × handedness × position interaction, F (2, 56) = 3.95, $p < .05$; $\eta^2 = .123$, was found significant, thus highlighting the influence of the lateralized presentation on the hand laterality judgment. During the egocentric task, in the left visual field the intercepts for the left hand stimuli were smaller than for the right hand stimuli ($p < .05$) and, on the right visual field, the intercepts for the right hand stimuli were smaller than the left hand stimuli ($p < .05$). No differences were found between the left hand stimuli intercepts and the right hand stimuli intercepts when showed centrally (ps > .05). There was no such a relationship with the presentation side between left and right stimuli in the allocentric task (ps > .05).

3.4 Discussion

In the present study participants were requested to perform two laterality tasks.

They had to judge either the handedness of a visual hand (egocentric task) or the location of a marker to be either on the left or right side of the same visual hand (allocentric task). I exploited the different involvement of egocentric and allocentric mental spatial transformations in the hand laterality task and in the visual laterality task in order to assess mental imagery in healthy aging. The egocentric task was characterized by the classic RTs asymmetry between left and right hand stimuli. In this task, the group of elderly participants showed slower RTs for each angle of rotation (except for 45°) between left and right hand stimuli (see Figure 5). The differences between RTs for left and right hand stimuli were coherent with the MOLA effect because left hand stimuli with 45°, 90°, and 135° of angular departures, and right hand stimuli with 225°, 270°, and 315° of angular departures were faster to be judged than right hand stimuli with 45°, 90°, and 135° of angular departures and left hand stimuli with 225°, 270°, and 315° of angular departures. This result was confirmed by the statistical analysis carried out taking into account the factor orientation. Indeed, while lateral orientations were slower than medial orientations for both groups, elderly participants were found to be significantly slower in judging the laterality of hands shown with lateral orientations (i.e., with awkward hand postures). Importantly, the specific impairment of the elderly participants for lateral orientations was present also when considering their accuracy. Here, relative to the young participants, they were significantly less accurate in judging hand laterality when the stimulus was shown with lateral orientations than medial orientations. Finally, I analyzed the speed of laterality judgments as expressed by the slope of the best fitting RTs lines. Coherently with what has been discussed above, in the egocentric task, the group of elderly participants showed steeper slopes for lateral orientations compared to medial and lateral orientations performed by the group of young participants.

Performance in the egocentric task was characterized by longer RTs, steeper slopes and later intercepts particularly when the hand stimulus was shown in palm view (see also ter Horst et al., 2010). The RT distribution for stimuli shown in palm view was markedly different from that of back view stimuli (see Figure 6). While left and right hand stimuli shown in back view were different only at 135° and 225° of angular departures, for palm view stimuli the differences between left and right hands were significant for all angles of rotation. However, the analysis of the MOLA effect showed that the task took longer as the hand stimulus was pointing away from the observer's body midline (i.e., lateral orientations) for both back and palm view stimuli.

I also found that the RTs distribution between left and right hands was sensitive to the lateralized presentation employed in the present study. Particularly, when stimuli were shown to the left or to the right visual field, the RTs differences between left and right hand stimuli for some angles of rotation were inverted (see Figure 7). Moreover, the significant interaction between task, hand, and position confirmed classical findings (Parsons et al., 1998b). Both the young group and the older group showed earlier intercepts during the egocentric task for hands presented to the contralateral hemisphere (i.e., left hands presented to the left visual field and right hands presented to the right visual field). This result bears resemblance to the central (i.e., contralateral) representation of overt motor behavior and motor imagery (Crammond, 1997; Jeannerod & Decety, 1995). However, this effect seems to be independent of the mental transformation process itself, as it was found for the intercepts of the RT linear function. For this reason I speculate that, even independently from the demands of the MR task, visual perception of body parts could automatically elicit the activation of cerebrally lateralized hand sensory-motor programs. Coherently with this result, a previous study showed that the left hemisphere advantage for right hand stimuli and the right hemisphere advantage for left hand stimuli are observed also in a simple detection task. Moreover, this contralateral bias is not due to a spatial compatibility effect between visual and proprioceptive information (Aziz-Zadeh et al., 2006). Interestingly, the elderly participants were neither influenced by the ipsilateral nor by the contralateral presentation of hands. However, their ability to apply a mental transformation upon those sensory-motor representations was selectively affected for difficult and awkward effector-centered transformations. Besides, in contrast with Saimpont et al., (2009), in which a specific impairment for left hand stimuli was reported, in the present study the ability of elderly participants to perform the hand laterality judgment task was equally affected for imagined left- and right-hand mental transformations. This finding cannot be due to their responding with the non-dominant hand because in the present study they responded using only the dominant one.

In the egocentric task elderly participants performed significantly worse and slower when stimuli were presented to the left or right side of the screen rather than to the center. Importantly this effect was independent from stimulus handedness (i.e., left/right hand stimuli). This is consistent with the notion that elderly individuals experience difficulties when they have to apply difficult and longer effector-centered transformations (Personnier et al., 2010; Skoura et al., 2005, 2008). There are several reasons that allow us to rule out any influence of spatial attention in generating this effect. First, the spatial position effect was present only during the egocentric task and not during the allocentric task. Second, the kind of lateralized presentation I employed does not trigger any spatial attention bias towards left or right. Finally, it has been demonstrated that in spatial cuing tasks the shift of spatial attention is well preserved in older individuals (Greenwood et al., 1993), especially when the task does not involve cue encoding (Folk & Hoyer, 1992).

During the allocentric task, I observed a different RTs modulation with the angle of rotation for the two groups. While the group of elderly participants took longer to judge the laterality of the visual marker as the stimulus angular departure increased, young participants' RTs were affected only by two angles (i.e., 135° and 225°) of stimulus rotation (see Figure 8). This finding suggests that the allocentric task was too easy for the young participants to cause a linear increment of RTs with the angle of stimulus rotation. Indeed, the allocentric task was performed always faster and with fewer errors than the egocentric task. It is also possible that the group of young participants may have applied a different strategy than MR in order to solve this task. Even though there were no significant differences between young and elderly participants' RTs in the allocentric task, the analysis of the slopes revealed that the speed of the mental transformation was slower for elderly participants. This result is in line with the classical finding that the speed of the mental transformation is disproportionally affected by aging (Dror & Kosslyn, 1994; Sliwinski & Hall, 1998). Differently from the egocentric task, RTs in the allocentric task were not modulated by stimulus orientation (i.e., medial vs. lateral orientations), thus demonstrating the fundamental difference between the egocentric and the allocentric mental transformation in the present tasks: the egocentric task was subject to biomechanical constraints (i.e., the MOLA effect) while the allocentric task was affected only by the angle of stimulus rotation. However, I also found that the medial and lateral orientations of the visual stimulus influenced the speed of the transformational process (i.e., the slopes) also during the allocentric task. It is possible that, as already discussed for averaged RTs data, the young group was not applying mental rotation strategies in this task, therefore modifying the linearity of the RTs distribution. Another possible explanation is that the allocentric transformation would have encompassed sensory-motor processes carrying-over the egocentric transformation from one experimental block to another.

Finally, I found that elderly individuals were selectively more impaired when they performed the egocentric task than when they performed the allocentric task. This effect was present even when the same stimuli and the same response were required in the two tasks. In particular, elderly participants were significantly less accurate and slower than young participants in judging the laterality of hands shown with awkward hand postures (i.e., lateral orientations). This interaction suggests that the older participants in the present study were selectively impaired at applying complex egocentric mental transformations. These results cannot be explained with a general age-related decline in speed processing (Birren, 1974; McDowd & Craik, 1988; Salthouse, 1996). Rather, they suggest that aging selectively affects sensory-motor brain mechanisms.

It has been shown that older adults are more susceptible than young adults to an increase in memory load rather than an increase in the display load (Fisk & Rogers, 1991), and that they show deficits of visuospatial working memory (Jenkins et al., 2000) . However, the impairment showed by elderly participants cannot exhaustively be interpreted as a working memory deficit. The elderly participants in the present study slowed down and performed less accurately with lateral, but not with medial hand orientations. There was no difference in the RTs and accuracy between the younger group and the older group in MR of medial hand orientations. Given that the amplitude of the angular departures for medial and lateral orientations is exactly the same, it is logical to assume that the working memory load is kept constant between the two factor levels. What differs between medial and lateral hand orientations is the relative involvement of multisensory and sensory-motor mechanisms respectively.

Dissociations such as the one I reported reveal that mental changes in aging are not always generalized. Indeed the present study clearly shows that aged healthy individuals meet considerable difficulties judging hand laterality, especially when the egocentric frame to be updated requires biomechanically complex transformations. This notion is supported by a specific deficit in performing mental transformations to laterally-oriented hands, as measured by the slope of the RTs linear function. On the other hand, as revealed by the analysis of the intercepts, the hemispheric sensitivity for body parts in facilitating motor responses seems to be well preserved among healthy elderly individuals. Finally, the disproportionate MOLA effect on accuracy and RTs reported here directly suggests that aging is associated with a specific degradation of sensory-motor cerebral mechanisms that are critical for the ability to imagine and to program body movements.

4. The multisensory integration account

In this chapter I will present an alternative interpretation of the hand laterality task that is based on the results from the behavioral studies of Viswanathan et al. (2012), and from its successive elaboration (Grafton and Viswanathan, 2014). The multisensory integration account (henceforth multisensory account) holds that hand laterality is recognized trough multisensory integration between the visual information of the seen hand stimulus, and the proprioceptive information of the observer's felt hand.

4.1 Introduction

The MOLA effect indicates that RTs for left hand stimuli and right hand stimuli are mirror-reversed. Specifically, left hand stimuli are judged faster when rotated in CW orientation, and right hand stimuli are judged faster when rotated in a CCW orientation (see Figure 6). This implies that participants do not compare one of their hands at random, and that they do not systematically compare one of their hands (e.g., the dominant hand) to the stimulus. In these cases, at different angles, RTs would be either the same for left and right hand stimuli or should be generally faster for one of the hands (e.g., the dominant hand) respectively. The fact that the MOLA describes a precise tuning of hand laterality with the stimulus angular departure would suggest a correct-hand-effect, whereby the observer always compares the hand that correctly corresponds to the stimulus. Central to the multisensory account is the notion that during the hand laterality task participants experience illusory feelings of movement of their hand. Viswanathan et al. (2013) considered these illusory feelings of movement the key aspect for understanding the MOLA effect. In their view, the illusory feeling of movement is an obligatory after-effect of intersensory recalibration (binding of visual features and proprioceptive information) responsible for hand laterality recognition, and the MOLA effect would correspond to the behavioral correlate of this after-effect. Viswanathan et al. (2012) have pointed out that the motor imagery account fails to explain hand laterality recognition because it implies a conundrum. In fact, the motor imagery account postulates that hand laterality is firstly recognized by implicit visual analysis after which hand movement simulations are used as confirmatory strategy (match-then-rotate strategy). However, if hand laterality can be correctly recognized by perceptual analysis - Viswanathan et al. asked - why then should one have illusory feelings of movements at all? I suggest rephrasing the question in the following way: Why should one have the need to simulate the hand movement if hand laterality has been already recognized?

The motor imagery account sees the correct-hand-effect as evidence that participants have insights into knowing already the laterality of the seen hand, and consequently simulate the movement of their hand in order to confirm this hypothesis. These simulations would correspond to mental rotation of the visual representation of the hand on which they had insight. Therefore, mental rotation would take longer depending on the orientation of the stimulus. In contrast, the multisensory account interprets the correct-hand-effect as an after-effect of successful binding between the seen hand stimulus and the corresponding felt hand of the observer. Afterwards, binding would initiate a sensorimotor recalibration to resolve the conflict between the orientation of the felt hand with the seen hand. Responses are delayed until these conflicts are resolved. In this view, the modulation of RTs as function of the stimulus angular departure would not depend on mental rotation. Moreover, the multisensory account states that, contrary to the motor imagery account, hand images would not be treated holistically but analyzed with a feature-based visual approach.

4.1.1 Viswanathan et al.'s experiment 1

The multisensory account states that hand laterality is recognized through crossmodal, visual and proprioceptive analysis of features, and that the illusory feeling of movement is an after-effect of multisensory binding that can be measured with the asymmetries of RTs between left and right hand stimuli (i.e., the MOLA effect).

Hand laterality is defined by the combination of two visual features: The shapes of the hands (i.e., Shape1 and Shape2), and their views (i.e., back and palm). The right hand has the same shape of the left hand when they are seen from different views: The right hand from the back has the same shape of the left hand seen from the palm, while the right hand from the palm has the same shape of the left hand seen from the back (see Figure 10). In this experiment the authors manipulated the availability of the hand visual features in an attentional gating task. “Since features pairing require an heteromodal integrator to receive different sensory inputs from different modalities, limiting the access of the integrator to the hand visual features (shape and view) should influence the accuracy of the binding decision” (Viswanathan et al., 2012).

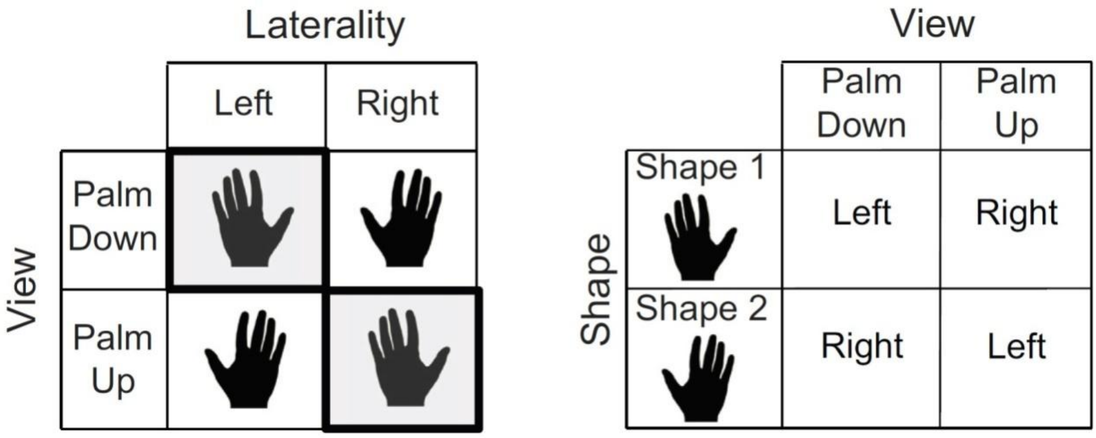


Figure 10. The black silhouettes used in Viswanathan et al.'s (2012) study. Hand laterality is defined by the combination of two features: Shape and View. Note that the shape of the left hand seen from the palm has the same shape of the right hand seen from the back, and that the shape of the left hand seen from the back has the same shape of the right hand seen from the palm.

Black silhouettes were used to represent the hand shapes, and two colored dots were used to indicate the stimulus view (i.e., a red dot indicated a back view and a green dot indicated a palm view). There were two independent conditions that specified the order of presentation of the visual features: a shape-first condition and a view-first condition. In each condition there were two types of trials: Cued and Uncued. On the cued trials of the view-first condition, a colored dot first (red or green) appeared on the monitor (the advance cue) indicating the view of the hand stimulus (back or palm). After a brief interstimulus interval an hand shape (the test stimulus) was presented in one of three angular departure (-120°; 0°; +120°). On the cued trials in the shape-first condition, a rotated hand shape was presented (the advance cue) before the colored dot was displayed (the test stimulus). On the uncued trials of both conditions, the advance cue was neutral (a grey dot) and it conveyed no information regarding the view. After a brief interstimulus interval, the test stimulus was shown and it depicted both the shape and the colored dot indicating the view. On each trials of both conditions, participants had to combine the information about the shape and the view in order to judge the laterality of the stimulus whether features were presented serially (cued trials), or simultaneously (uncued trials). Participants pressed a response key with their left hand to indicate a left hand stimulus, and pressed a right key with their right hand to indicate a right hand stimulus. Participants' hands were out of sight and rested in a palm-down position. The authors expected that in the uncued trials participants would attend to the information about the shape and the view of the hand stimulus in the same order as in the cued trials.

The authors hypothesized that in the view-first condition intersensory conflicts related to the view should be resolved before the seen hand and the felt hand are paired on the shape dimension. This would generate a correct-hand-effect. In the shape-first condition, the presented shape would be bounded with the corresponding felt hand. However, the anticipation of the binding process, hands that have the same shape but different view from the participant felt hand (that is resting in a palm-down position) should produce a wrong-hand-effect. That is, RTs of left and right hands in palm view should not be mirror-reversed.

4.1.1.1 Results of experiment 1

In the view-first condition RTs for left and right hand stimuli were mirror-reversed. RTs in the shape-first condition did not show the same mirror-reversal: RTs for palm stimuli of left and right hands had the same asymmetry as RTs for left and right hands in back view (see Figure 11). This result highlighted a wrong-hand-effect for palm views. In their view, modification of the MOLA depending on the feature that was perceived first clearly demonstrated a feature-based analysis of hand representation.

Viswanathan et al. (2012) argued that when shape information is perceived first, the presented shape is bound with the corresponding felt hand that is resting palm-down on the thigh. This means that if shape A is presented (the shape with the thumb on its right, see Fig. 10), it will be bound with the participant's left hand; if shape B is presented (the shape with the thumb on its left), it will be bound with the participant's right hand. However, because of this premature binding, when the successive information of stimulus view is presented as palm view, then the presented shape will always correspond to the other hand than the one that was bound initially with shape. For this reason, in the shape-first condition RTs for palm view stimuli were not mirror-reversed but had the same asymmetry of the opposite stimulus laterality. This caused an illusory feeling of movement in the wrong hand when the stimulus was in palm view.

Viswanathan et al. (2012) also excluded the possibility that the wrong-hand-effect would result in incorrect responses: “When the binding enters awareness, participants can evaluate whether the view of the stimulus corresponds to a palm-down or a palm-up view and can respond accordingly with either the bound hand or the opposite hand”.

4.1.2 Viswanathan et al.'s experiment 2

In this experiment the authors manipulated attention to the proprioceptive information of either the left or the right hand. The task employed was a view judgment task (back/palm view judgments). An advance cue (the word "left" or the word "right") specified the laterality of the test stimulus and also the hand with which participants had to respond. After 500ms a test stimulus corresponding to an hand shape was presented in five possible angular departures (-120°; -60°: 0°: +60°: +120°). Participants judged whether the combination of hand laterality (the advance cue) and hand shape (the test stimulus) corresponded to an hand seen from the back or from the palm.

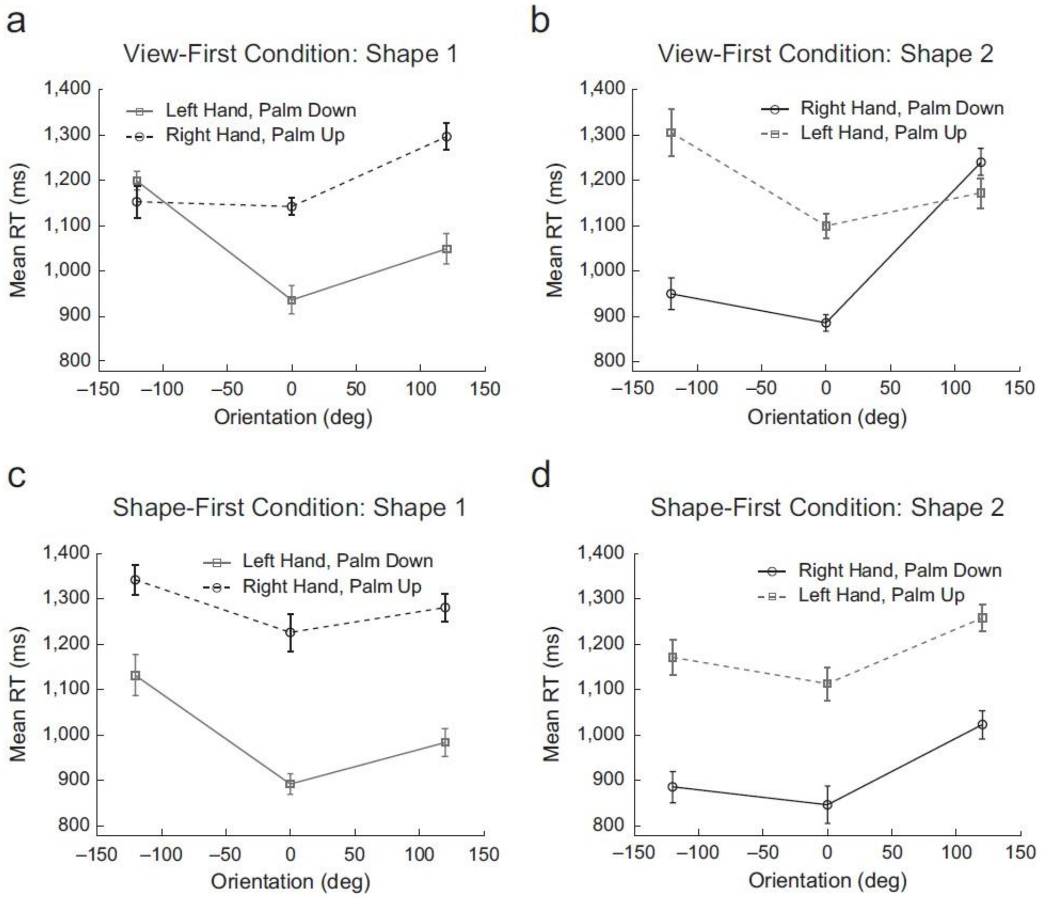


Figure 11. Results from experiment 1. RTs for laterality judgments on uncued trials in the view-first (a,b) and shape-first condition (c,d). In the view-first condition RTs for left hand right hand stimuli are mirror-reversed. In the shape-first condition RTs for left and right hand stimuli are mirror-reversed only for hands shown in back view. Error bars depict within subjects errors of the mean. From Viswanathan et al. (2012).

The authors hypothesized that the advance preparation of the responding hand would induce attention to the hand proprioceptive representation with suppression of the sensory information from the other, non-responding hand. The multisensory account predicts that successful binding and the illusory feeling of movement should be present only when the shapes are congruent with the palm-down response hand. Stimuli corresponding with the palm-up view of the response hand should not lead to successful binding even though they are congruent with the palm-down view of the other, non-responding hand. If palm-up stimuli cannot be bound to the proprioceptive representation of the observer's own hand then there will be no illusory feeling of movement, and consequently no RTs asymmetries for these stimuli. Thus, it was expected that RTs for left and right hands would have been mirror-reversed only for back view stimuli.

4.1.2.1 Results of experiment 2

As expected RTs for left and right hand stimuli were mirror-reversed only for stimuli in back view. For palm view stimuli RTs were not mirror-reversed (see Figure 12). In the authors view, the lack of RTs asymmetries for palm view stimuli implied that the illusory feeling of movement is an after-effect of successful binding. For palm-up stimuli there could be no binding because observers' attention was focused on the proprioceptive information of the hand that was in an actual palm-down position, and that therefore represented a different hand shape than the stimulus. Information from the other hand would be also suppressed because attention was centered on the responding hand.

The authors discussed these results also as indicating that mental rotation was not necessary to identify hand laterality because in that case the asymmetries on RTs should have been found for both back and palm view stimuli.

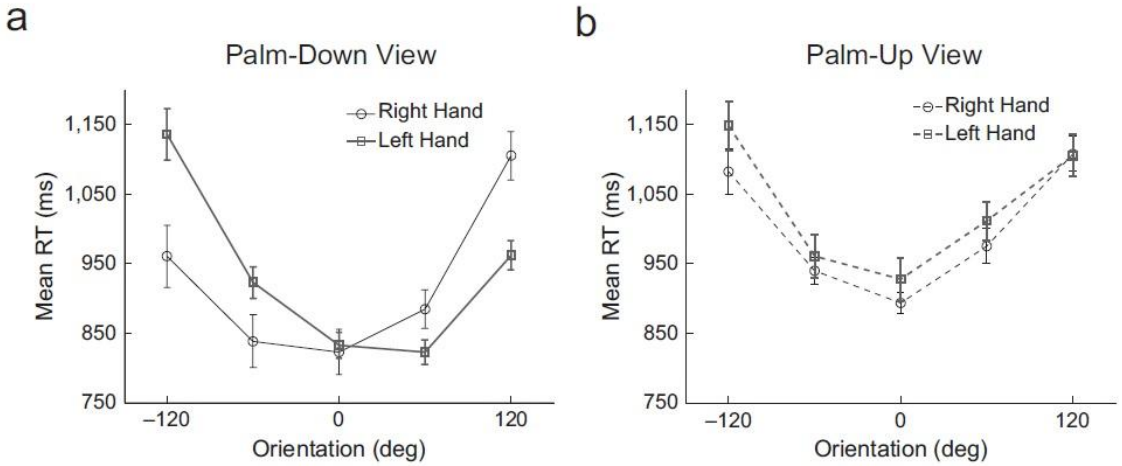


Figure 12. Results from experiment 2. The graph in (a) shows mean response times (RTs) for stimuli in the palm-down view as a function of stimulus orientation and hand. The graph in (b) shows mean RTs for stimuli in the palm-up view as a function of stimulus orientation and hand. Error bars depict within subjects errors of the mean. From Viswanathan et al. (2012).

5. The attentional hypothesis

Both the motor imagery and the multisensory integration accounts explain performance in the hand laterality task and the MOLA as the result of the *correct-hand-effect*. Thus on each trial, participants pair the correct hand that corresponds with the stimulus, either by simulating its movement or by binding its proprioceptive feature with the stimulus visual features. This idea derives from interpreting the specific mirror-reversed configuration of RTs: If RTs are systematically faster for medially-oriented than laterally oriented-hands, then the observer should "know" which hand is displayed prima facie. If the observer tried to pair one hand at random or always one hand consistently (e.g., the dominant hand), then RTs would look differently. Following this reasoning, pairing one hand at random would generate approximately equal averaged RTs for left and right hands, while pairing always the dominant hand would make RTs for right hand stimuli faster. It is this interpretation of the RTs function that stimulates the idea of the *correct-hand-effect*. The motor imagery account explains this facilitation by invoking the parallelism between actual and imagined actions: Hand-arm movements towards the body midline are easier to be executed than movements directed away from it, and so are imagined movements similarly to hand mental rotation. In its original formulation the multisensory account does not explain why laterality judgments of medially-oriented hands are easier than judgments of laterally-oriented hands (Viswanathan et al., 2012). The MOLA effect would correspond to an after-effect of multisensory binding, but a direct explanation of why this effect facilitates medial orientations and not lateral orientations is lacking.

Why should multisensory binding be faster for some combinations of hand laterality and stimulus orientation? In a more recent article, Grafton & Viswanathan, (2014) admitted the possibility that "the sensitivity of the laterality task to extreme body postures could be based on biomechanically constrained boundary conditions placed on an internal model of the body schema rather than on limitations to the range of possible simulated motor commands". As correctly pointed out by Viswanathan et al. (2012), and Grafton & Viswanathan (2014), the motor imagery account poses a paradox: Why should one imagine the movement of her/his hand If the stimulus is identified before motor simulation takes place? These authors propose that the behavioral features of the hand laterality task are not due to motor simulation but are the result of multisensory hand binding and the following illusory feeling of movement. According to this view, upon stimulus presentation there is a simultaneous cross-modal comparison between the seen hand and the proprioceptive representation of the observer's corresponding own hand. This comparison is independent of stimulus orientation (orientation-invariant), and it results in a binding of the visual representation of the seen hand with the proprioceptive representation of the “matching” responding hand, or vice versa. Importantly, the outcome of this cross-modal comparison cannot be used as a signal (i.e., match/mismatch) for perceptual decision making (Grafton & Viswanathan, 2014). Then, binding produces an intermodal discrepancy between the bound felt and seen hand due to their different orientation. This triggers a sensorimotor recalibration to align the two representations into the same orientation (an after-effect that can produce a feeling of movement). The response would be delayed until this intermodal conflict is resolved. In this way RTs should depend both on the orientation of the stimulus (given by recalibration) and on its laterality (given by the correct-hand-effect). Since the response delay is related to recalibration of body position and not to the perceptual decision making, then in the authors' view, this does not imply a conundrum (Grafton & Viswanathan, 2014). They speculate that this recalibration is necessary for the motor system to have a consistent representation of body position in order to generate a motor command (i.e., the response). Specifically, the recalibration would be obtained by relating the two different sensory reference frames (visual and proprioceptive) with respect to each other.

In trying to solve the paradox introduced by the match-then-rotate notion implied in the motor imagery account, the multisensory account generates another conundrum: If binding of visual and proprioceptive features cannot be used for perceptual decision, and if the aim of the successive sensorimotor recalibration is only to generate a consistent representation of body position in order to give a motor response (Grafton & Viswanathan, 2014), then what are these multisensory and sensorimotor processes good for? It is also not clear in which way the illusory feeling of movement accompanying the sensorimotor recalibration can determine the configuration of RTs and, if so, how the illusion of movement can be related to stimulus identification.

The multisensory integration account fails to explain hand laterality recognition because it interprets the mirror-reversed configuration of RTs (i.e., the MOLA) as an index of the correct-hand-effect. In this chapter I will present experimental and theoretical evidence demonstrating that the source of the MOLA effect resides in attentional modulation given by the spatial codes of the hand stimulus. The results of the experiments that will be presented in the following sections suggest that the role of proprioception in the hand laterality task should be reconsidered. For example, it is difficult for the multisensory account to address results obtained studying patients with congenital amelia (Vannuscorps et al., 2012; Vannuscorps & Caramazza, 2015; see section 2.3.1). If patients born without arms and without phantom sensations can perform the hand laterality task with a comparable MOLA effect as healthy individuals, then the asymmetry of RTs cannot be neither linked to visual and proprioceptive integrative mechanisms nor to action simulation.

5.1 Spatial compatibility for misoriented objects

The mirror-reversal of RTs for left and right hand stimuli can be observed in Figure 6. A graphical exemplification of the RTs asymmetries that configure the MOLA effect can be found in Figure 13. Two main differences in RTs determine this effect. Firstly, there are differences in RTs between hand stimuli with the same laterality but different orientations: RTs for left hand stimuli are faster when they are rotated in CW orientations than in CCW orientations, and RTs for right hand stimuli are faster when they are rotated in CCW orientations than in CW orientations (see Figure 13a). Furthermore, RTs for hands with different literalities but with the same orientations are different: RTs of left hand stimuli in CW orientations are faster than RTs of right hand stimuli in CW orientations, and RTs of right hand stimuli in CCW orientations are faster than RTs of left hands in CCW orientations (see Figure 13b). It is important to notice that the particular configuration of RTs expressed by these two interactions is clearly independent from the shape and from the back-palm view of the stimuli. Therefore, what seems to be important for generating these effects is the relationship between the laterality of the response (i.e., the laterality of the stimulus) with the direction of stimulus rotation in CW or CCW orientations.

Similar interactions were found in earlier studies on mental rotation. For example, in the left/right direction of facing task, where participants are presented with plane-rotated figures of asymmetric objects (for which a left and a right version can be obtained with reflection around the vertical axis) and are asked to judge the direction of facing of that object. Jolicoeur (1985, 1988) found that RTs of left/right facing stimuli were asymmetric relative to 180° of stimulus rotation. Also here, two main differences in RTs were found. Firstly, left-facing stimuli were judged faster when presented in CW than in CCW orientation, and right-facing stimuli were judged faster when presented in CCW than in CW orientations (significant differences for rotations of 120° from the upright). Moreover, left stimuli in CW orientations were judged faster than right stimuli in CW orientations (at 60° this difference was not significant; cf. Jolicoeur, 1985), and right stimuli in CCW orientations were judged faster than left stimuli in CCW orientations (see Figure 14).

This was interpreted as a form of compatibility between the direction of mental rotation and the direction of facing of the stimulus. When both were congruent RTs were faster (Jolicoeur, 1988). For instance, if the stimulus was rotated in CW direction (i.e., +60° and +120°), a left facing object should have been mentally rotated in the same direction it was facing (i.e., from the +120° or +60° angle to the left, towards the upright), thus producing faster RTs. However, If the stimulus was rotated in CW direction (i.e., +60° and +120°), but it was facing to the right, then the stimulus should have been mentally rotated in the opposite direction towards which it was facing (i.e., from the +120° or +60° angle to the left, towards the upright), thus producing longer RTs.

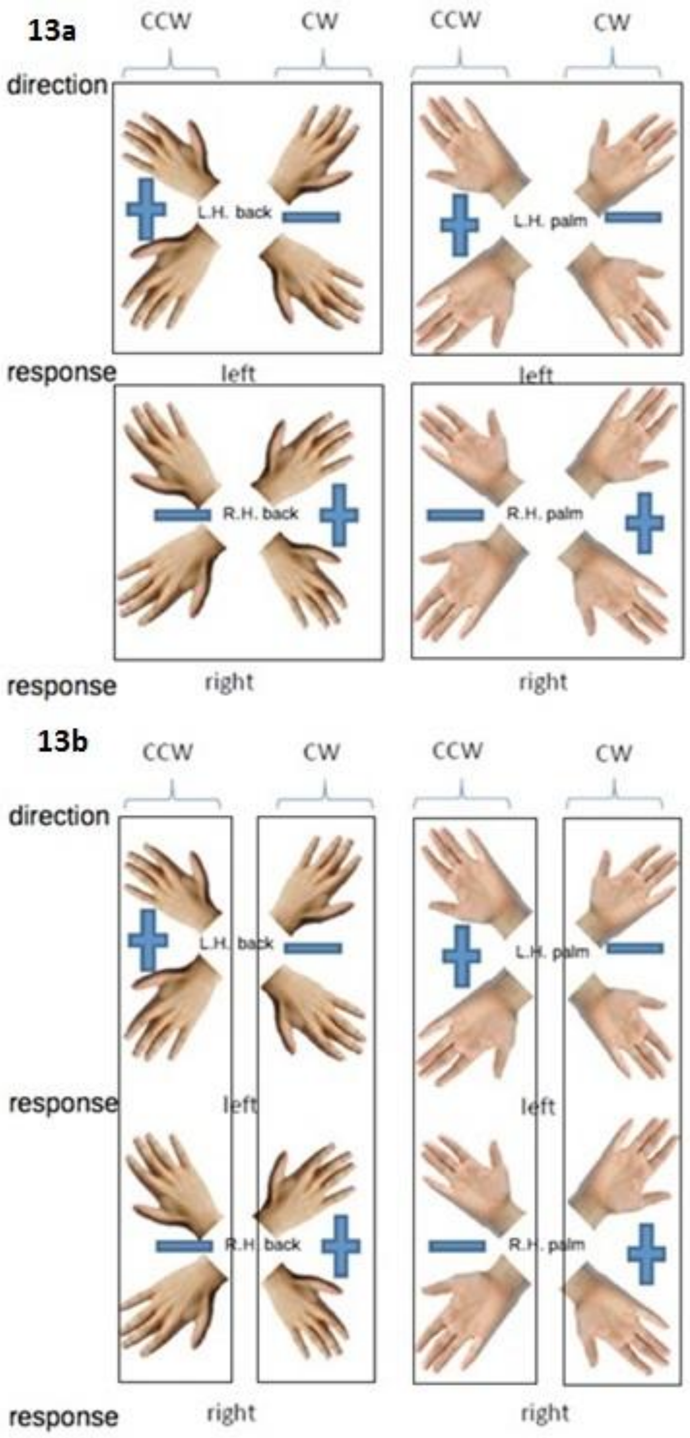


Figure13. Synoptic description of the differences in RTs in the hand laterality task for left and right hand stimuli (i.e., left and right responses) shown in back and palm view when displayed in CW and CCW orientations. The blue symbols represent faster RTs (- symbol) or longer RTs (+ symbol). 12a: Differences between hands with same laterality and different orientations (squares).12b: Differences between hands with same orientations and different laterality (rectangles).

In Jolicoeur's study (1988) the stimuli used were selected from the set of Snodgrass and Vanderwart (1980) that mostly includes figures of different asymmetrical objects with a clear left-right direction of facing. In figure 15 a graphical exemplification of the asymmetry of RTs for left and right facing stimuli, and an exemplar stimulus (i.e., the drawing of a cat) are shown. Similar asymmetries on RTs for left and right responses and CW/CCW orientation can also be found in other mental rotation studies (Carpenter & Eisenberg, 1978; Koriat & Norman, 1985). In another experiment that also employed the direction of facing task (Jolicoeur et al., 1998), it was shown that if the stimulus was displayed as actually rotating with a perceived rotatory motion towards the CW or CCW direction, then RTs were faster for stimuli shown in CCW (i.e., -120°) or in CW orientations (i.e., 120°) respectively for the CW and the CCW motion rotations. Interestingly, it has been shown that head tilt to the left or to the right influences the RTs distribution for left/right judgments in a direction of facing task, but not in a naming task (McMullen & Jolicoeur, 1990). Left head tilt was associated with faster judgments for stimuli rotated in CW than in CCW direction. Right head tilt was associated with faster judgments for stimuli rotated in CCW than in CW direction (see Figure 16). Since in the above discussed studies on mental rotation and in the hand laterality task RTs are analyzed only for correct responses, it follows that the laterality of the stimulus inevitably corresponds always to the laterality of the response. Observing Figure 6 and Figure 13 it is clear that observers judge left hand stimuli presented in CW orientations by pressing a left key (or uttering the word “left”) faster than judging right hand stimuli presented in CW orientations by pressing a right key (or uttering the word “right”). This interaction is reversed when they judge right hand stimuli presented in CCW orientations by pressing a right key (or uttering the word “right”) faster than when they judge left hand stimuli presented in CCW orientations by pressing a left key (or uttering the word “left”). At the same time, left responses are faster for left stimuli presented in

CW than left responses for left stimuli presented in CCW, while right responses are faster for right stimuli presented in CCW than right responses for right stimuli presented in CW. In other words, the asymmetrical differences between RTs for left hand stimuli in CW and in CCW orientations are mirror reflections of the asymmetrical differences between RTs for right hand stimuli in CW and CCW orientations. The same observations can be made about the cat of Figure 15. These data are in line with the idea that judgments of plane rotated stimuli are sensitive to spatial stimulus-response compatibility effects. The attentional hypothesis that will be describe in the following sections interprets these effects as the result of compatibility between the orientation of the stimulus and the side of motor response (or the laterality of vocal left/right responses).

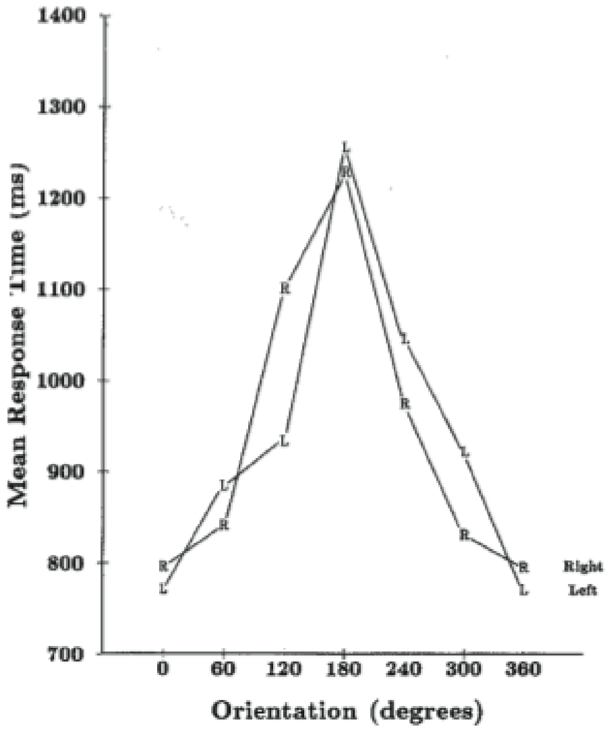


Figure 14. Mean response times in milliseconds for left and right responses at each orientation in the left-right direction of facing task of Jolicoeur (1988).

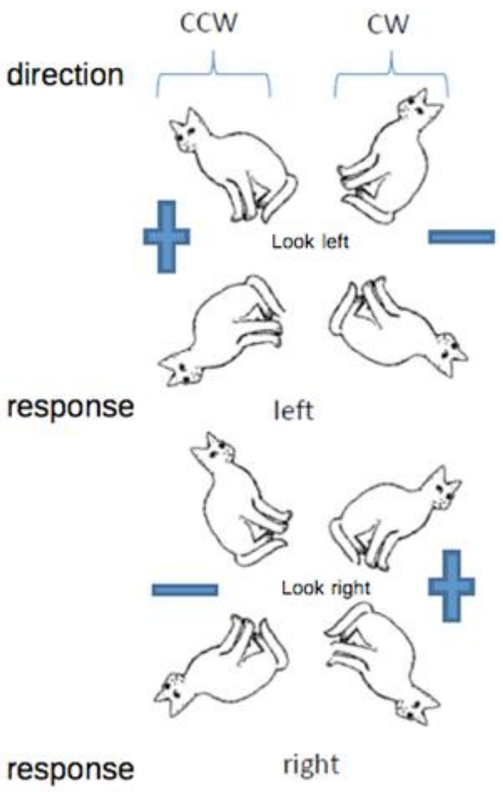


Figure 15. Synoptic description of the differences in RTs in the direction of facing task for left-facing and right-facing asymmetrical objects (i.e., left and right responses) when displayed in CW and CCW orientations. The blue symbols represent faster RTs (- symbol) and longer RTs (+ symbol).

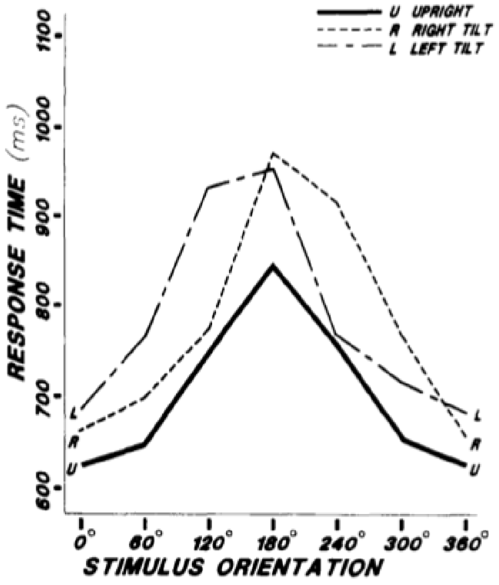


Figure 16. Mean response times in a left-right direction of facing task for each stimulus orientation and head-tilt position. From McMullen and Jolicoeur (1990).

5.1.1 Spatial stimulus-response compatibility

Spatial stimulus-response compatibility effects refer to the phenomenon present in many choice-RT tasks where stimulus location influences the time of responses. For example, in the Simon task the relevant stimulus dimension (on which the response is based) is an attribute of the stimulus that is not spatial (e.g., the color) assigned to left and right responses. Instead, the left-right location of the stimulus (where the stimulus will be presented) is the irrelevant stimulus dimension. The Simon effect reflects faster RTs when the stimulus location corresponds to the side of the motor response than when it does not (for a review see Simon, 1990). Thus, the location of the stimulus influences RTs though it is the irrelevant stimulus dimension. On the other hand, in the stimulus-response compatibility effect proper the location of the stimulus is the relevant stimulus dimension. In this case, left responses are faster for stimuli presented to the left than to the right, and right responses are faster for stimuli presented to the right than to the left (e.g., Proctor & Reeve, 1990).

These effects are commonly attributed to the level of information processing corresponding to the response selection stage. The dimensional overlap account states that the effects of compatibility are the result of similarities between the stimulus dimension and the response dimension. When there is overlap between the two dimensions, like in the response dimension and the irrelevant stimulus dimension of the Simon task, responses are faster if they coincide and slower if they conflict (Kornblum et al., 1990). The spatial coding account holds that when stimulus location is irrelevant, a spatial code is formed together with the spatial codes of the response. Response selection is slowed-down when the stimulus code and the response code are different. Moreover, the spatial code of the response does not depend on which limb is operating the response because the Simon effect is obtained even if the left and right responding hands are crossed (e.g., Wallace, 1971). Therefore, it is not the absolute location of the response to determine the Simon effect but the spatial codes formed as left and right locations. For example, if participants perform the Simon task responding with sticks that operate the response on the opposite space from the hand that is manipulating the stick, compatibility effects are found in relation to the end of the stick (Riggio et al., 1986). Also the location of the stimuli that influence the occurrence of the Simon effect is relative rather than absolute. Indeed, the Simon effect is obtained not only when stimuli are presented to the left and right hemispace, but also when they are presented in one hemispace with relative left and right locations (Umiltà & Nicoletti, 1985; 1987). The attentional account holds that the spatial codes that generate the compatibility effects like in the Simon task depend on the location at which attention is deployed. In the study of Nicoletti and Umiltà (1989) observers responded with left or right key presses to a rectangle or square target presented in one of six horizontally arranged boxes (see Figure 17). Participants fixated their gaze on a cross presented at the left or right end of the display. A black square was presented between two of the six boxes, and after 500ms the target was displayed within one of the two boxes adjacent to the previously presented black square. The obtained Simon effect did not depend on where in the display the target was presented (i.e., to the left or right within the display). The effect occurred relatively to the location where attention was directed, namely in relation to the black square presented as target cue (see also Nicoletti & Umiltà, 1994).

Considering the pattern of RTs consistently obtained among studies that used the hand laterality task, we can notice that if stimulus-response compatibility mechanisms are involved then the effect of spatial compatibility is reversed. Indeed, faster RTs are observed when the direction of rotation of the hand stimulus is opposite to the side of response. The mirror-reversal of RTs does indeed describe faster RTs for left responses when the stimulus is pointing towards the right (CW orientation), as well as faster RTs for right responses when the stimulus is pointing toward the left (CCW orientaiton). This effect is exactly the inversion of what would be expected if stimulus-response compatibility mechanisms like the Simon effect would play a role. In the Simon task, it is the correspondence mapping between stimulus and response spatial codes that give rise to the effect. In the hand laterality task it is the reversed mapping that counts, thus it is the mapping of non-correspondence between stimulus and response spatial codes that is associated with the MOLA effect.

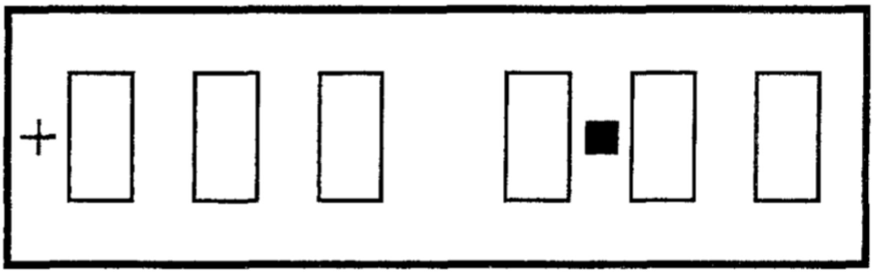


Figure 17. Display used by Nicoletti and Umiltà (1989).

Previous studies have shown that the spatial code of the irrelevant stimulus dimension is formed rapidly and automatically, and then decays over time (e.g., Hommel, 1994; Simon et al., 1976). Indeed, if the time interval between the formation of the irrelevant spatial stimulus code and the relevant non-spatial stimulus code is increased this produces a smaller, or even no Simon effect (e.g., Hommel, 1993). In some circumstances the Simon effect can be reversed, resulting in faster RTs for incompatible than compatible stimulus-response mappings (De Jong et al., 1994; Rubichi et al., 1997). Rubichi et al. (1997) had participants performing a visual discrimination task while fixating on a cross in the center of the monitor, with two lateral target placeholders on the left and on the right of fixation. One of four possible letters appeared for 100ms at the beginning of each trial below the fixation cross. One of the four letters signaled a catch trial on which no response should have been executed. The target (a square or a rectangle) was presented for 100ms in one of the two target placeholders after 500ms from the presentation of the letter. Half of the participant responded to rectangles with a left-side key press and to squares with a right-side key press. The other half had the reverse response mapping. Responses were also analyzed by dividing the RTs in five bins representing the five ranks (i.e., quantiles) of the raw data. This type of analysis consistently returns a continuous decrease of the Simon effect from the fastest to the slowest bin. It is an useful way to study the time course of spatial compatibility effects (see De Jong et al., 1994). Results of this first experiment showed a reversed Simon effect for all RTs bins except the first, fastest bin. Left responses were faster when the target appeared in the right placeholder than in the left placeholder, and right responses were faster when the target appeared in the left placeholder than in the right placeholder. The authors attributed this “negative Simon effect” to shifts of spatial attention that were made in the direction of the response. Therefore, in their view, what mattered was not the location of the stimulus in relation to the side of response but the direction of the shift of spatial attention relative to the side of response. Indeed, in this experiment after the target was presented participants were very likely to shift their attention back to the fixation cross. This shift of attention occurred overlapping in time with the selection of the left-right response. For instance, when the target appeared in the right placeholder left responses were faster because attention was moving from the right to the left, on the fixation cross. In the second and third experiment of this study the authors created conditions for which attention would not shift to the central cross before response selection. In the second experiment the discrimination of the target was made easier with consequently faster RTs. With this modification a standard Simon effect was obtained: The easier recognition of the target made participants shift their attention to fixation after the left-right response was selected. In the third experiment, the target remained visible for 400ms rather than the

100ms of the first experiment. Also in this case a regular Simon effect was obtained. The longer exposure to the target made participants' attention to remain on the target and to shift towards fixation only after the response was selected. In the fourth and critical experiment, the letters appeared either to the center below the fixation cross, or to the left of the left placeholder, or to the right of the right placeholder. At variance with the other experiments, the letter signaling a possible catch trial was presented after target presentation. The Simon effect was expected to occur in relation to the position of the letter relative to the target and not in relation to the position of the letter relative to fixation. In other words, the Simon effect should have been influenced by the last shift of attention before response execution, namely the shift of attention from the target to the letter. This is exactly what the authors found. When considering only trials with the central letter, that is the condition in which attention first shifted to the target and then to the opposite direction (i.e., to the central fixation), a reversed Simon effect was found significant for all bins. The study of Rubichi et al. (1997) demonstrates that a reversed Simon effect can be obtained in a discrimination task when stimulus processing is demanding. If stimulus processing was made easier, and RTs were faster, then the standard Simon effect was restored. In the first experiment the reversed Simon effect was obtained with RTs averaging 564ms for corresponding trials, and 542ms for non corresponding trials. In the second experiment the standard Simon effect was present with faster RTs, that averaged 400ms for corresponding trials, and 418ms for non corresponding trials. This seems to fit nicely with the notion that spatial attention is first directed to the stimulus at its onset, and then is automatically disengaged from it moving in the opposite direction (Posner, 1980; Posner & Cohen, 1980; 1984). The reversed Simon effect in the first experiment and the standard Simon effect in the second and third experiment depended on the different timing of disengagement of spatial attention from the target. In the first experiment attention was moved from the target to fixation before response selection. In the second and third experiment attention was disengaged from the stimulus after response selection.

A reversed Simon effect was found also in study of Mapelli et al. (2003). They studied the interaction between the SNARC (i.e., the spatial-numerical association of response codes) and the Simon effect. The SNARC effect corresponds to the finding that in a parity judgment task small numbers are judged faster with left responses, and large numbers are judged faster with right responses (Dehaene et al., 1993). The Simon and the SNARC effect are similar because they both involve the facilitation or slowing of RTs that is due to a task irrelevant feature: The position of the stimulus in the Simon task, and the magnitude of the number in the SNARC. Participants fixated on a central cross that was presented for about 400ms followed by a blank screen for 500ms. Afterwards, a number could be presented either to the left or to the right of fixation and participants judged number parity with a left-right key press. The authors were interested to look for an interaction between the Simon and the SNARC effect. An interaction would have suggested that the two effects rely on a common processing stage. Of interest here are the results obtained for the Simon effect. Indeed, applying the same bin analysis I have described above, in their first experiment Mapelli et al. (2003) found a standard Simon effect for the first three bins, thus only for faster responses. In the second experiment, stimuli were presented with more eccentricity and with a smaller font. In this case RTs were longer than in the first experiment because the task was more difficult. The authors found a significant standard Simon effect for the first two bins and a reversed Simon effect for the other bins that represented longer RTs. Also in this case, the reversed Simon effect emerged with longer responses and increased stimulus processing demand.

Another study found an inversion of the RTs pattern for left-right responses in a task that involved mental imagery (Bachtold et al., 1998). Two tasks were performed. In the first task a number was presented centrally and participants imagined as if the number was indicating the centimeter on a ruler. They had to indicate if the number corresponded to a distance longer or shorter than 6 centimeters. In the second task a number was presented centrally and participants imagined as if the number indicated the hours of the day on a analog clock. Participants had to judge if the number represented an hour earlier than 6 o'clock or later than 6 o'clock. In the first task, RTs were faster for left responses than right responses when numbers were shorter than 6. When the number was longer than 6, right responses were faster than left responses.

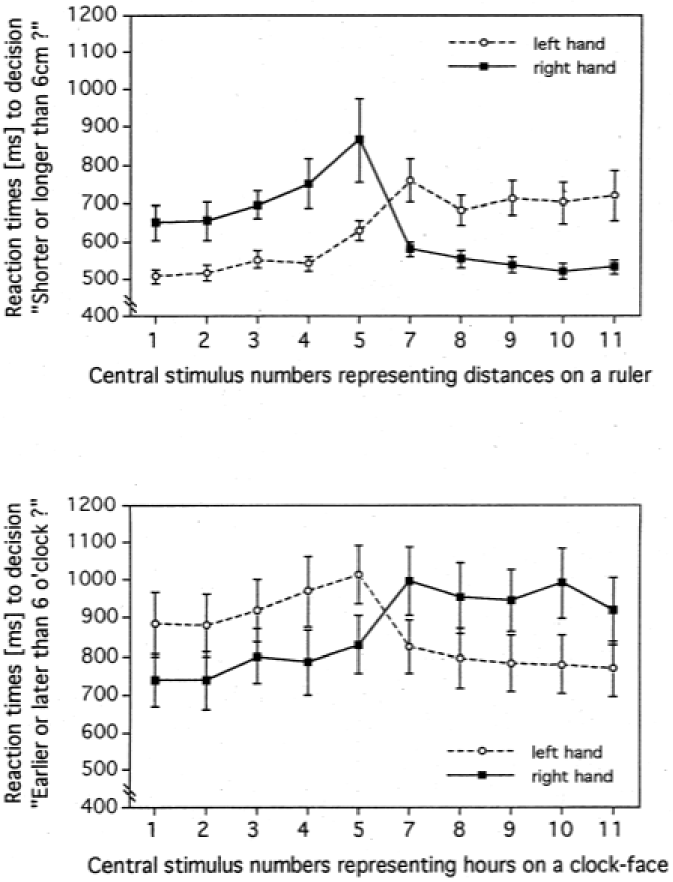


Figure18. Mean response time for left and right responses in the “ruler task” (top) and in the “clock task” (bottom). Error bars represent the standard errors of the mean.

In the second task the opposite pattern of results was revealed (see Figure 18). The inversion of the effect in the second task depends was related the spatial representation of numbers on the clock. On analog clocks, small numbers are displayed on the right side of the clock while larger numbers are displayed on the left side of the clock. It is plausible that either a shift of attention in the scanning of the mental image towards the number spatial position, or the activation of left-right spatial codes of the imagined stimulus was responsible of the RTs reversal in this study. The notion that stimulus-response compatibility effects are obtained in tasks that reflects the exploration of visual information stored in working memory is supported also by another study that investigated the latency of left-right responses in a visual imagery task (Tlauka & McKenna, 1998). In this study Simon-like spatial compatibility effects were observed for stimuli that were not directly perceived but that were recalled from memory.

Interestingly, viewers' aesthetic preferences about the position of visual objects reveal a close similarity with the mirror-reversal of RTs found in the hand laterality task and in the direction of facing task. Palmer et al. (2008) asked observers to chose (drag and drop of pictures in a rectangular space) the position within an image frame for left-facing and right-facing objects that would be the most aesthetically pleasing. Results revealed an “inward bias” with right-facing objects more frequently “dropped” on the left side of the frame, and right-facing objects more frequently “dropped” on the right side of the frame (see Figure 19). It is conceivable to think that this result depends on the allocation of attention in the direction of facing of the object. For instance, right-facing objects attract attention to their right side, and therefore are perceived aesthetically better if the portion of empty space is present on that side.

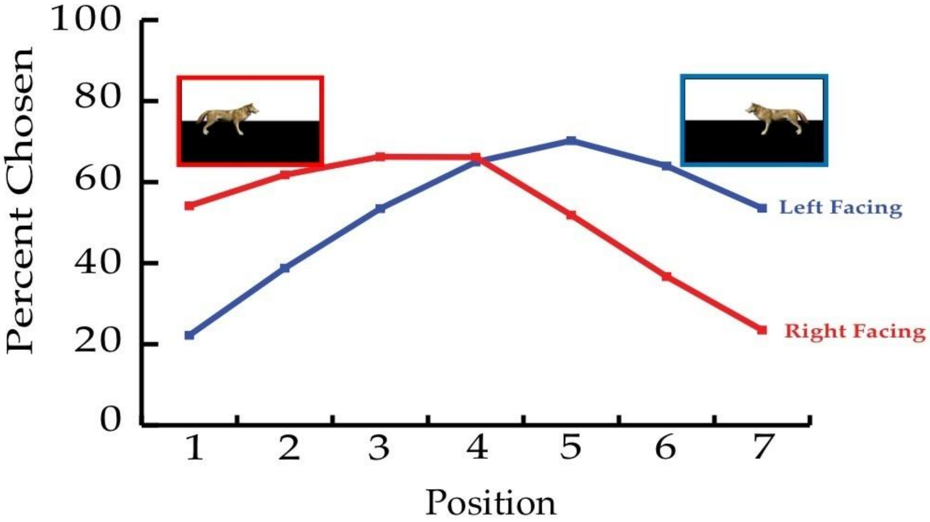


Figure 19. The average percentage of time a left-facing and a right-facing object is chosen to be positioned in the rectangular frame, plotted as a function of the position of the object center from the frame's left (1), to its right (7). From Palmer et al. (2008).

5.1.2 "Conceptual" spatial compatibility

Traditional approaches studied human information processing considering the perceptual domain as separate from the domain of actions. In this view, the flow of sensorial processing is sufficient to extract and make sense of information about the visual world. Modern cognitive science endorses an integrated comprehension of the complex stream of sensorimotor events that relates to the conscious representation of the external world. In this view mental representations of percepts and actions are stored and processed together (e.g., Hommel et al., 2001). This is true also for imagined events, where perceptual information is reactivated from stable visual representations (e.g., Bachtold et al., 1998; Tlauka & McKenna, 1998). In line with this notion, the conceptual relationship between the stimulus and the response also influences the integration of task-related visual and motor features. For example, spatial compatibility effects are present even when left-right responses are produced vocally (Proctor and Vu, 2002; Wühr, 2006), or when the spatial stimulus dimension is not defined by physical location but by location words (e.g., McCarthy and Donchin, 1981), or by arrows (Weeks and Proctor, 1990). There is also ample evidence that sensorimotor integration supports spatial, temporal and numerical estimation (De Simone, 2013). In the SNARC effect (Dehaene et al., 1990, 1993) judgments about numbers parity with lateral responses yields to faster left responses for small number and faster right responses for big numbers. Similarly in the temporal domain, short and long time intervals are judged faster with left and right responses respectively (e.g., Vallesi et al., 2008). Other studies have also demonstrated that the typical size of a visually perceived object influence response latencies. For example, judgments about living-nonliving things are faster with right than left responses for big visual objects (e.g., an elephant or a house), and faster with left than right responses for small visual objects (e.g., a bee or a key), even though stimuli were presented as pictures of the same size (e.g., Sellaro et al., 2014).

5.1.3 Spatial compatibility by pictures of tools

Compatibility effects have been documented for judgments of manipulable objects. In a seminal paper, Tucker and Ellis (1998) exploited spatial stimulus-response compatibility to study the automatic processing of tools during visual perception. Series of objects pictures were presented either upright or upside-down, and participants were required to determine their orientation. Half of the objects depicted in the pictures had their handle that was positioned to the left, while the other half had the handle positioned to the right. The idea was that tools perception would automatically prime actions associated with their use. When responses were assigned to manual left and right key-press (experiment 1) there were faster responses for spatially compatible association between the side of the object's handle and the side of response. However, when responding with the left and right index finger of the right hand (experiment 2) the spatial compatibility remained significant only for the left response-left handle pairing. This was taken as evidence of an action priming effect independent from spatial compatibility effects like the Simon effect. Indeed, the Simon effect can emerge also when lateral responses are given with the fingers of one hand rather than with left and right manual responses, suggesting that is the relative response location that is essential (Shulman and McConkie, 1973; Umiltà & Nicoletti, 1990). Thus, the facilitation of lateral responses was thought to be related to the action the object afforded because when only the right hand was used to respond the spatial compatibility found in experiment 1 was not present. Following the study of Tucker and Ellis (1998) other investigations have replicated the action priming effect using left-right key presses (Iani et al., 2011; Tipper et al., 2006). These data were interpreted as the result of an automatic activation of action plans upon visual perception of objects (e.g., Grèzes & Decety, 2002; Tucker & Ellis, 1998). In this view objects' affordances are able to prime related actions without an actual intention from the observer to use or grasp the tool.

Action priming effects have been found also for responses that mimic the action afforded by the object. Reaching and grasping responses show spatial compatibility effects that parallel the actual use of the observed tools (Bub & Masson, 2006; Tucker & Ellis, 2004). There is ample evidence that tools perception facilitates compatible responses that are executed either with a power grip or a precision grip (e.g., Ellis & Tucker, 2000; Grèzes et al., 2003; Tucker & Ellis, 2004; Vainio et al., 2008). Others have found that responses are sensitive to an object's affordances only when they are similar to the actual use of the tool (i.e., the type of grip) than when they consist in button presses (Bub & Masson, 2010; Pavese & Buxbaum, 2002).

Notwithstanding, a recent study failed to replicate the original action priming effect of Tucker and Ellis (Yu et al., 2014). Only when participants were explicitly instructed to imagine pick up the objects the action priming effect emerged. These authors failed to replicate the action priming effect even when responses were performed on buttons placed close to the stimuli, like in the study of Wilf et al. (2013). Moreover, an inverse compatibility effect was observed in most of their experiments when no instructions were given, with faster RTs for the non-corresponding pairing between the object's handle side and the side of motor response (Yu et al., 2014). Other action priming studies have found an inverse compatibility effect. For example in the study of Anderson et al. (2002), the facilitation of manual responses was found to be linked to the stimulus relevant feature on which observers' attention was directed during the task. Asymmetrical objects were presented as slightly rotated (by 18°) either in CW or in CCW orientation and the task consisted in judging their orientation (i.e., CW or CCW orientations). When presented with an image of a pair of scissors, those who found that the relevant feature that defined object's orientation was the scissors handle showed an action priming compatibility effect with faster responses on the side corresponding with the side of the handle. However, those participants who focused on the pointed ends of the scissors showed the opposite pattern of response latencies. Moreover, when abstract asymmetrical shapes were used as stimuli the compatibility found was relative to the half of the asymmetrical object that was bigger. This would suggest that it is not the particular action afforded by the object to generate the compatibility effect. The study of Cho and Proctor (2011) goes in the same direction. Here spatial compatibility effects were demonstrated using images of teapots oriented to the left or to the right. The compatibility effect was significant for both color judgments and orientation judgments. Surprisingly, the reported effect was influenced by the spatial relation between the side of response and the location of spout, rather than the location of the handle. Moreover, the effect was larger when responses were given with the fingers of the dominant hand than with left-right manual responses. When either the handle or the spout were removed this caused the compatibility effect to be dependent on the remaining object part. That is, when the handle was present without the spout spatial stimulus-response compatibility was observed in relation to the handle. When the teapot image included only the spout, responses were faster relatively to the location of this teapot's part. The study of Matheson et al. (2014) also suggests the important role of attention in generating action priming effects because spatial compatibility was present for both pictures of manipulable objects and pictures of animals. While with tools RTs were faster for spatial responses that were congruent with the spatial position of the object handle, with animals RTs were faster for responses that were congruent with the spatial position of the animal head.

Other researchers have supported the idea that object perception automatically triggers action potentiation. When a tea mug was displayed as rotating with its handle continuously and predictably changing position, a clear compatibility effect emerged, with faster left responses when the handle was moving towards the left side of the mug, and with faster right responses when the handle was moving towards the right side of the mug (Fischer & Dahl, 2007). Pellicano et al. (2010) used images of a torch in an orientation judgment task like in Tucker and Ellis' study, and in a task where the color of the torch had to be judged. The “functional state” of the object was also manipulated so that there were two types of stimuli: A torch switched on and a torch switched off. In the color judgment task, a reversed compatibility effect was observed: faster RTs were obtained for the incompatible mapping between the side of the handle and the side of motor response. Instead, the orientation judgment task yielded a standard action priming effect. This effect was significant only when the functional state of the object was perceivable, namely when the torch was switched on. Results were discussed in the light of the action priming concept. It should be noted however that stimuli were not equated in size, and this could have favored the compatibility effect in the orientation judgment because the torch switched on was bigger than the torch switched off.

Moreover, the reversed compatibility effect in the color task cannot be explained by action priming because the facilitation of RTs was in the direction of the light and not in the direction of the handle.

Riggio et al. (2008) tried to disentangle action priming from Simon-like spatial compatibility effects with an orientation (upright vs. upside-down) judgment task similar to the original study of Tucker and Ellis. In the first experiment an object was presented either above or below a fixation cross and remained visible until a response was given (onset condition). In another condition pairs of objects were displayed one above, and one below fixation. After 500ms one of the stimuli disappeared and orientation judgments were given about this object (offset condition). Results showed an action priming effect in both conditions, even in the condition in which the object was not present in the display. In the second experiment the authors wished to rule out the hypothesis that stimulus offset captured attention to the location of the handle, therefore explaining the compatibility effect of the first experiment without referring to the pragmatic aspects of the object. So they studied in two different conditions orientation judgments for the disappearing object, like in the offset condition of the first experiment, and also for the object of the pair that remained visible. The rationale was that for judgments of the visible object there was no offset that could attract attention towards it, so any compatibility effect could not be explained by a shift of attention. Since a compatibility effect was significant also in this experiment, the authors concluded that the action priming effect of the first experiment was not due to the offset of the stimulus attracting attention to the handle of the object. In the third experiment stimuli were displayed to the left and right of fixation and, as in the second experiment, orientation judgments were made for either off set stimuli or for the stimuli that remained visible (permanence condition). In this way they tried to find out if the offset of one of the two stimuli attracted attention and generated a Simon effect. This experiment resulted in a significant Simon effect in the offset condition and in a reversed Simon effect in the permanence condition. The Simon effect always occurred in relation to the offset of the stimulus. A small action priming effect was also significant in relation to the target, even when its location was different than the offset event. The authors concluded that the Simon effect and the action priming effect are not completely independent processes. In their view spatial attention can play differential roles in generating the Simon and the action priming effects.

Symes et al. (2007) have shown that the perception of a disoriented dowel influences left-right responses in a spatial compatible way especially if the object is oriented in depth as if affording a grasping action. Pictures of dowels were successively displayed in one of two orientations (-45° left-down orientation, and +45° right-down orientation) and subjects judged the visual pattern that composed the surface of the object similarly to a color judgment task. As expected, objects oriented +45° right-down orientation were associated with faster right responses, and objects oriented in -45° left-down orientation were associated with faster left responses. This was expected because these orientations depicted one part of the object closer either to the left hand (-45° left-down orientation), or to the right hand (+45° right-down orientation). When a simple rectangle with no 3D structure was used as stimulus no such a compatibility effect emerged. Moreover, if the dowels were shown slightly rotated in depth by 45° of rotation and interleaved with the dowels rotated in the picture plane, then the compatibility effect was observed exclusively for the former dowels. This was due to the fact that the depth-rotated objects were asymmetrical and pointed directly towards the participants left or right hand. In a final experiment the authors tried to differentiate potential action priming effects from attentional processing. They compared the judgment about type of object's surface with a detection task. In this latter task a target dot appeared on one end of the cylinder and responses were given on a central spacebar. The comparison should have revealed if the spatial compatibility observed in the judgment task is attributable to enhanced attentional processing of the extreme end of the dowel. If so, detection times were expected to be faster for targets presented on the end part of the object because attention should have been already focused on the object's part that points towards the participant's hand. Since the detection task resulted in no significant interaction between target location and object orientation the authors concluded that the compatibility effect for the dowel was not related to attentional mechanisms but that it was directly linked to the affordance of the object. The same group of researchers found evidence suggesting that the Simon effect and the action priming effect are two partially independent phenomena (Symes et al., 2005). In this study participants made judgments about the type of object (i.e., kitchen's object vs. garage's object) that could be presented to the right or to the left visual space, and that could be displayed with a leftward or with a rightward orientation of the handle. Results showed a significant Simon effect together with a significant action priming effect (i.e., an orientation effect). The Simon effect corresponded to an interaction between location and laterality of response while the action priming effect was determined by an interaction between object's orientation and laterality of response. However the second-order interaction between location, stimulus orientation and response was not significant. This was taken as evidence of the additive contribution of the two effects on RTs. There was also an interaction between stimulus position and orientation of the handle so that leftward objects were judged faster when presented to the left space, and rightward objects were judged faster when presented to the right space. In a second experiment, responses were given with the feet, and most of the results of the first experiment were replicated, except for the interaction between stimulus location and orientation. It was concluded that the action afforded by the object's orientation was coded in an abstract fashion. In the final experiment responses were associated with the object's color (i.e., green or red). In this case the Simon effect was significant while the orientation effect was not. However a cross-experiment analysis revealed that there were no significant differences for this effect between the three experiments. The authors argued that when low-level visual features are the stimulus relevant dimension the motor representation is not formed in combination with object's orientation. Nevertheless, it may be also that there was no sufficient time to code the orientation of the object because the response to color was very fast.

Phillips and Ward (2002) used pictures of a frying pan displayed with the handle pointing to the left or to the right, away from or towards the observer. These pictures were used to prime left-right responses that were given in relation to a target that appeared at different SOAs (0, 400, 800, 1200ms) from the onset of the prime. They found responses compatible with the orientation of the handle to be faster at longer SOAs. This result was obtained also when observers responded with their hands crossed or with feet. It was the spatial correspondence of the response with the location of the handle and not the specific effector used to respond that was important. It was concluded that object's affordance generate a spatial code that is abstract and that potentiate a variety of lateralized responses.

Vainio et al. (2007) also tried to distinguish the source of the object priming effect but used different classes of manipulable objects. In the first experiment there was a fixation point presented for 1000ms. This was replaced by the presentation of a prime object oriented to the left or to the right. After 300ms or 600ms a target color appeared at the location of the central fixation point presented previously. Left and right manual responses were given depending on color. Only at the short SOA there was a significant compatibility effect with facilitation of lateral responses in correspondence of the object handle. The same experiment was run with responses given with the index and middle finger of the right hand: The action priming effect was present only at the longer SOA (experiment 4). In the second experiment, the fixation point stayed visible throughout the trial. In this case there was no facilitation of lateral responses at any SOA. In the third experiment a central cross surrounded by four square target placeholders (top left, top right, bottom left, bottom right) was presented for 1200ms. A prime object oriented to the left or to the right was presented for 300ms superimposed on the boxes. When the object was presented leftward oriented, it was shown with the handle falling on the bottom left box, and with the top of the object falling on the top right box. The opposite was true for rightward orientated objects. Basically, the objects were shown diagonally through the visual field with the handle always pointing towards the observer. Afterwards, the prime object disappeared and after 100ms or 200ms it was followed by the target onset in one of the target placeholders. The target discrimination was between an “X” and an “O” letter. In this way, the object was used to prime an attentional shift towards one of the boxes. Fixation was not monitored and that the fixation point disappeared after the presentation of the prime trough the trial. Results showed a Simon-like effect with targets displayed to the left (top and bottom) discriminated faster with left responses and targets displayed to the right (top and bottom) discriminated faster with right responses. An interaction between object orientation and target location was significant: When the prime object was oriented to the left, target discrimination was faster when it appeared in the bottom left box and in the top right box than in the other two boxes. When the prime object was oriented to the right, target discrimination was faster when it appeared in the bottom right box and in the top left box than in the other two boxes. The authors concluded that the object did not attract attention to its handle but to the entire surface of the object. This would speak against an attentional processing account where processing of the handle is the source of the action priming effect. They concluded that “the orientation of a viewed object is capable of priming responses in the absence of an attention shift”. In this view, shift of attention are unnecessary for an action priming effect to occur. What would explain compatibility effects with the object handle is “an object-based orienting of attention to the entire object, which in turn prepares simultaneously actions that are compatible with the object's affordances such as orientation”.

Vainio et al. (2011) used an image of a mug that could be shown for 30ms and 70ms, or after 170ms and 370ms (in different blocks). A picture of a mug was used to prime lateral responses that were given relative to a target arrow displayed after 50ms from the mug's offset. They found inverse compatibility effects when prime objects were presented for 30ms or 70ms, and a standard compatibility effect when they were displayed for 370ms. The authors proposed that affordances can activate the associated motor representation gradually. When the stimulus stays on the screen the activation builds up and produces a standard compatibility effect. When the prime is removed this triggers inhibition of the motor representation because the prime object is no longer relevant, and this causes the reversed compatibility effect. This explanation was derived from similarities found between their task and the results of the masked-priming paradigm (for a review see Eimer & Schlaghecken, 2003). In the masked-prime task a double pointing arrow is shown as prime (<< or >> or <>), followed by a mask for 100ms and the target arrow (<< or >>) for 100ms. Relative to the neutral prime stimulus (<>) lateral responses about the target are faster when the prime and the target differ while they are slower when the prime and the target point in the same direction. This “negative compatibility effect” is present only when the prime stimulus is presented subliminally: A suprathreshold prime produces a positive compatibility effect. Moreover, with feet responses this effect is not present. Using lateralized readiness potentials (LRPs) it has been shown that the prime stimulus activates the corresponding hand for response execution. However, when the target stimulus is compatible with the prime this response is inhibited, while it is facilitated when the target and the prime are incompatible (Eimer & Schlaghecken, 1998). If prime and target were presented with a SOA of 0ms a positive compatibility effect emerged, while at 250ms of SOA a negative compatibility effect was present. Aron et al. (2003) have shown that with the 0ms SOA significant activations were found in the contralateral primary motor cortex relative to the target. At 150ms SOA significant activations were found in the posterior parietal cortex and subcortical structures such as the caudate, and the thalamus. Therefore the inhibition process of motor activity in the masked-priming task (endogenous inhibition) seems to be independent of prefrontal mechanisms usually responsible for exogenous inhibition of responses as in go/nogo or stop-signal tasks.

Two main interpretations of the action priming effect with tools have been proposed. On the one hand, the spatial compatibility between the tool's handle and the laterality of response is seen as a pure attentional phenomenon. For example, similarly to the study of Anderson et al. (2002), Symes and collaborators (2007) found increased compatibility effects for asymmetrical objects (i.e., the dowel rotated in depth). This suggests that in absence of other task-relevant dimensions, the asymmetry of the stimulus induces an attentional bias towards an object's part that is responsible for the facilitation of lateralized responses independently of the effector used. This notion is in line with the idea that attentional allocation and motor planning are tightly linked (e.g., Craighero et al., 1997; Rizzolatti et al., 1987; Schneider & Deubel, 2002). On the other hand, the action priming effect by pictures of tools would be related to the potential actions the object affords (Tucker & Ellis, 1998). Therefore, the action priming effect would be dissociable from spatial stimulus-response compatibility. The studies of Vainio et al. (2007), and Riggio et al. (2008) go in this direction. Nevertheless, it seems more plausible that attentional mechanisms are involved in the “perception of affordances” rather than being a dissociable phenomenon. The finding that action priming effects are present also when feet responses are used suggest that object affordances are coded in an abstract code that interacts with response codes not linked to a specific effector.

An important consideration should be made about the direction of the compatibility effect. As already mentioned, Yu et al. (2014) could not replicate the original effect of Tucker and Ellis (1998). These authors found a reversed compatibility effect between side of response and the orientation of the object handle. We have seen that observers' attentional modulation towards different object's parts can explain standard and reversed compatibility effects (Anderson et al., 2002; Cho & Proctor, 2011). A similar explanation can be applied also for the study of Pellicaro et al. (2010) where the physical aspect of the stimuli rather than the “functional state” of the object could explain the compatibility effects that were found. Another aspect that influences the occurrence of standard and reversed effects is the time of presentation of the stimuli, and the timing of response selection relative to the onset-offset of the stimuli. In the study by Riggio et al. (2008) a reversed compatibility effect was obtained when one of two stimuli (placed to the left or right of fixation) disappeared after 500ms from presentation, and the to-be-judged object remained visible. In the study by Vainio et al. (2011) a picture of a mug was presented briefly as a prime and responses were relative to a target arrow presented soon after the prime (50ms). The reversed compatibility effect was obtained at very short SOA between prime and target (i.e., 30ms and 70ms) while for the longer SOA (i.e., 370) it was the standard compatibility effect that was significant. These results are in line with the notion that the reversed and the standard compatibility effects are influenced by the temporal window in which response selection overlaps with the allocation of spatial attention in space's locations (e.g., Rubichi et al., 1997). These temporal dynamics depends on the timing of presentation of the stimuli as well as on the specific task demands. For example, Koch (2009) performed an experiment very similar to that of Vainio et al. (2011). In this study a standard compatibility effect emerged when the briefly exposed prime object had to be recognized afterward as oriented to the left or right. Responses regarded a high or low tone presented after the prime. When the prime had not to be recognized for its orientation, either no compatibility effect was found or the effect was reversed by 5ms.

5.2 Experiment 1: Spatial stimulus-response compatibility for misoriented hand pictures

In this experiment I tested the hypothesis that the orientation of a hand stimulus can influence RTs for left-right responses even if orientation is not relevant to the task. After stimulus onset, visual processing of the hand fingers is accompanied by eye movement and/or shift of spatial attention in the direction of stimulus rotation (see experiment 2 in the next section). This eventually generates another shift of attention in the opposite direction (e.g., Posner & Cohen, 1984; Rafal et al., 1989) that facilitate responses in the corresponding side of space. The time between stimulus abrupt onset and the processing of the stimulus informative features would predict faster or longer RTs for spatially corresponding responses. Short intervals between stimulus onset and the processing of its relevant features should generate facilitation of responses for the ipsilateral stimulus rotation-laterality of response pairing (CW rotations paired with right responses; CCW rotations paired with left responses). Longer intervals, usually associated with difficult recognition, should facilitate responses for the contralateral stimulus rotation-laterality of response pairing (CW rotations paired with left responses; CCW rotations paired with right responses). This latter case corresponds with the situation in play when performing the hand laterality task. Therefore, perception of rotated visual objects like hand images should be associated with stimulus-response integration processes subject to the temporal dynamics of spatial attention. In order to test this hypothesis, in the following experiment left and right responses about rotated pictures of hands were given for a non-spatial relevant stimulus dimension that was defined by the color of the hand shape. I hypothesized that the orientation of stimulus rotation influences RTs for left-right responses depending on the timing between stimulus onset and the presentation of the shape's color relevant dimension.

5.2.1 Methods

5.2.1.1 Participants

Eighteen right-handed participants (ESHI = 94.3, SD = 5.8; Oldfield, 1971) took part in the study (10 female, 8male; mean age = 21.6, SD = 2.6).

5.2.1.2 Stimuli and task procedure

Stimuli were realistic pictures of left and right hands. Each image was the result of a rotation and/or reflection of two basic hand pictures (3.5° x 6° visual angle) of a right hand seen from the back and of the same hand seen from the palm. Participants sat in front of a PC screen (15″ and 70 Hz refresh rate) at a distance of 75 cm away. Trials begun with the presentation of the central fixation cross (0.2° visual angle) for 2500ms followed by the presentation of the hand stimulus. Each hand stimulus was presented on a white background in six different angular departures (-120°, -60°, 0°, 180°, +60°, +120°). After either 250ms or 1000ms (SOA) the border of the hand shape turned into the target color red or blue. The size of the colored border did not alter the stimulus physical dimension because it was included inside the hand picture. The stimulus target remained visible until a response was collected after which another trial started. Stimuli were randomly presented and the assignment of the target colors to left and right responses was counterbalanced across participants. They responded with the index finger of the right hand for right responses, and with the index finger of the left hand for left responses. They were instructed to constantly pay attention to the hand stimulus and to avoid response anticipation. Participants were requested to respond as fast and also as accurate as possible. The “alt” and the “right arrow” keys were used to give left and right responses respectively. The response keyboard was placed under the table and it could not be seen while performing the task. Participants executed four blocks of 96 trials each, for a total of 384 trials.

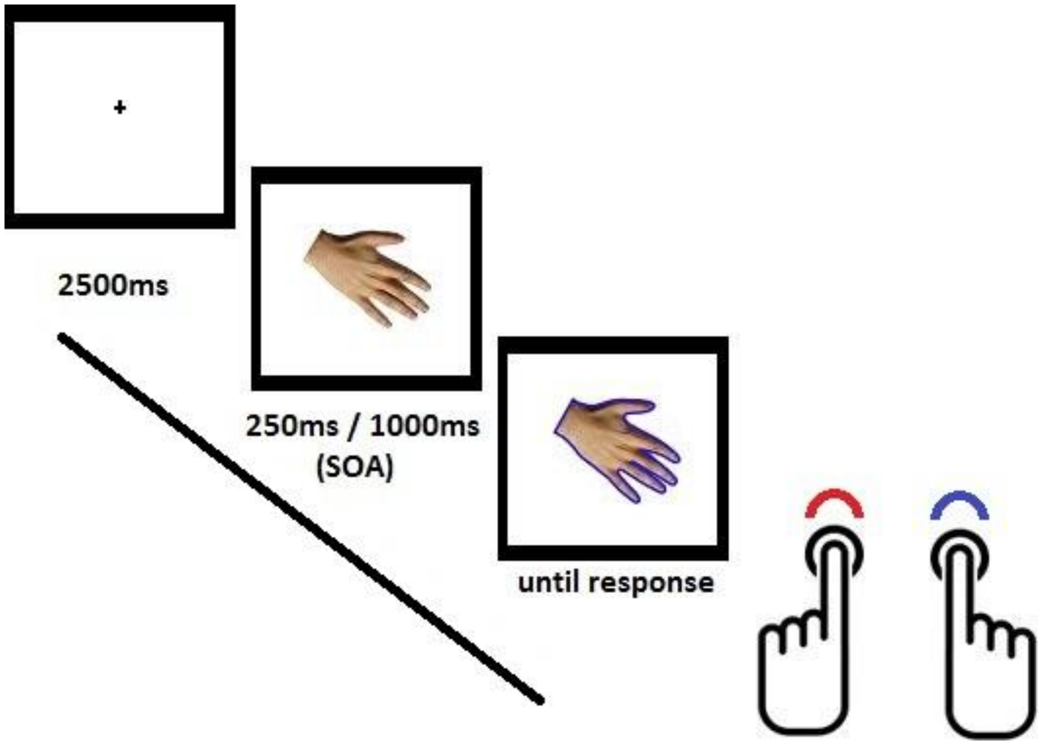


Figure 20. Experiment 1's task procedure

5.2.1 Results

RTs greater than three standard deviations above the mean were discarded from data. RTs were computed as the average time of response on correct trials from target onset. For each participant, Z scores were computed from RTs. Accuracy was calculated as the proportion of errors before removing RTs outliers. A 2 (SOA: 250ms, 500ms) x 2 (response: left, right) x 6 (angle: -120°, -60°, 0°, 180°, +60°, +120°) repeated measures analysis of variance (ANOVA) was performed on Z scores and on accuracy data.

For Z scores, there was a main effect of angle, *F* (5, 85) = 2.27, *p* < .05 (see Figure 21): Responses were faster for stimuli presented with CW orientations (i.e., +60°, +120°) relative to the CCW orientations (i.e., -60°, -120°). This was mainly true on trials with short SOA (250ms), than long SOA (1000ms), *F* (5, 85) = 2.31, *p* < .05 (see Figure 22).The ANOVA confirmed a three-way interaction of SOA, response, and angle, *F* (5, 85) = 5.43, *p* < .001 (see Figure 23). As predicted, the angle of stimulus presentation interacted with the laterality of response depending on the time between stimulus onset and the presentation of the relevant stimulus dimension. When the SOA was short (250ms), there were faster RTs for left responses than right responses when stimuli were rotated in -120°, and faster right responses than left responses for stimuli rotated in +120°. At the longer SOA (1000ms) the opposite pattern of results emerged: There were faster RTs for left responses than right responses for stimuli rotated in +60°, and +120°, and faster RTs for right responses than left responses for stimuli rotated in -60°, -120°.

The analysis on proportion of errors showed that participant made significantly more errors with right responses, *F* (1, 17) = 5.91, *p* < .05.

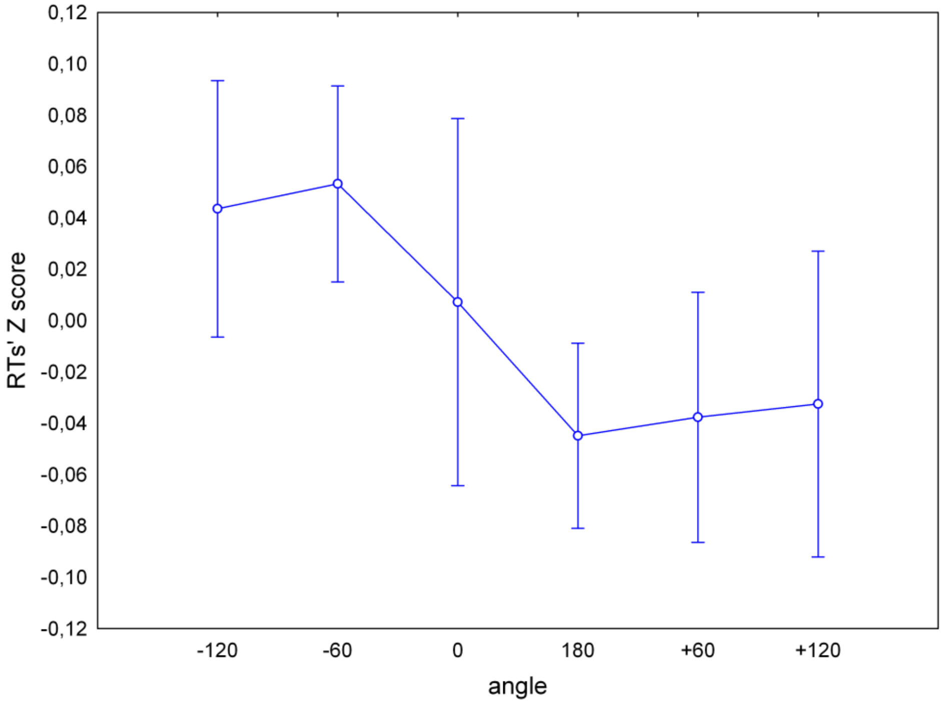


Figure 21. Mean Z scores as a function of stimulus orientation. Error bars represent the standard error of the mean.

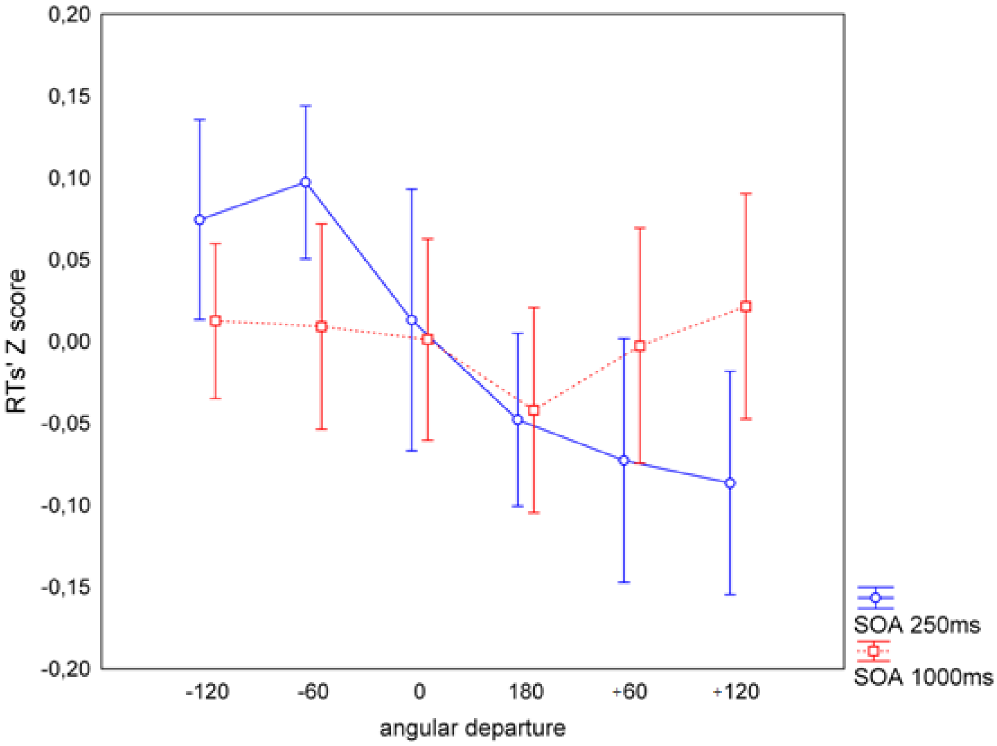


Figure 22. Mean Z scores for trials with 250ms and 500ms of SOA as a function of stimulus orientation. Error bars represent the standard error of the mean.

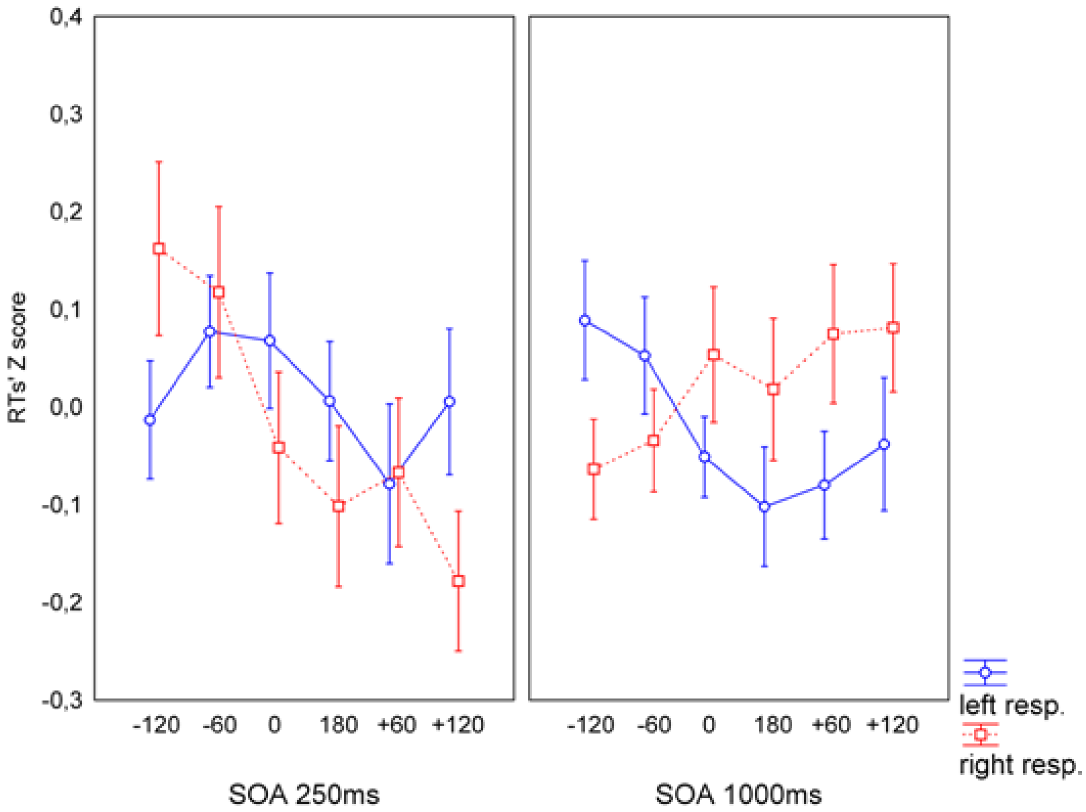


Figure 23. Mean Z scores for left and right responses on trials with 250ms and 500ms of SOA as a function of stimulus orientation. Error bars represent the standard error of the mean.

5.2.1 Discussion

The aim of experiment 1 was to test if the orientation of a misoriented hand picture can influence the time of lateral responses even when orientation is not the relevant stimulus dimension. The results indicate that the orientation of the stimulus triggered a shift of attention towards its direction of rotation. This facilitated spatially-compatible lateral responses at the short SOA (250ms) for those orientations of the stimulus that pointed towards the observer (i.e., -120° and +120°). It is possible that within this relatively short presentation of the target, attention was attracted more by shapes that were oriented towards the observer's responding hands, namely when stimuli were rotated in +120°, and -120°. This result is in line with the experiments in which pictures of tools are employed and responses are faster in the conditions where the object handle points towards the participant's hand of response (e.g., Symes, 2007). However, when the SOA was longer (1000ms) lateral responses were faster when the direction of stimulus rotation pointed in the opposite direction of the response. This was expected because of the exogenous re-orienting of attention from the previously attended location, similarly to the well documented attentional phenomenon of inhibition of return (e.g., Posner & Cohen, 1980; 1984; Rafal et al., 1989).

There are obvious differences between the present experiment and the hand laterality task. Nevertheless, what was important to show here is that the orientation of the hand stimulus automatically attracts attention towards its direction of rotation, so that corresponding lateral responses are faster than non-corresponding responses. More importantly, an exogenous shift of attention in the opposite direction at the longer SOA explains the faster RTs for non-corresponding lateral responses. In the hand laterality task, this re-orienting of attention should overlap temporally with stimulus recognition and the selection of the left-right response. Similarly to the long SOA condition of the present experiment, in the hand laterality task lateral responses are faster when hand laterality (and so the lateral response) is opposite to the direction of stimulus rotation.

The main effect of angle showed that RTs were faster for stimuli presented in CW than in CCW orientation. This result bears resemblance to the advantage found in visual search tasks for targets presented in the right visual field (e.g., Efron & Yund, 1996; Graziano & Sigman 2008), an effect that seems not to be driven by participants' handedness (Yund et al., 1990).

The standard compatibility effect at short SOA and the reversed compatibility effect at the longer SOA of the present experiment can potentially solve the discrepancy present in the literature that examined the spatial compatibility of tools. As I have discussed in the previous sections, there is no clear interpretation of why images of tools generate facilitation of spatially corresponding responses in some cases, while in others they generate reverse compatibility effects. It is plausible that the timing between the presentation of the stimulus and the presentation of the relevant stimulus dimension has an important role in generating faster or slower RTs for corresponding and non-corresponding stimulus-response pairings. Moreover, in the present study target's color was presented in the form of a border that surrounded the whole stimulus and that did not alter its size. This aspect should be considered particularly because usually experiments with tools' images presented the relevant stimulus dimension in the form of a separate object, such as an arrow or a colored dot. By presenting the target color "attached" to the border of the object shape it would be more difficult for the observer to focus on other visual features than the shape and its orientation.

5.3 Experiment 2:
An eye-tracking study on "the thumb effect"

In order to characterize the spatial extent of visual processing during perception of rotated hand pictures, an eye-tracking study was performed. The aim of this study was to define what sections of the hand stimulus, independently of its orientation, were processed when observers judged hand laterality. To the best of my knowledge, despite the conspicuous number of studies that have employed the hand laterality task, this is the first investigation of eye movement during left-right judgments of hand laterality. However, a previous study (Nielsen et al., 2008) compared eye movement patterns in humans and monkeys during discrimination of three shapes (a hand, a bottle, and a drain pipe). While humans were able to use the same feature independently of shapes orientation, monkeys focused on individual features differently for each shape's orientation. For the hand shape, humans' data showed that the most informative feature independent of orientation corresponded with a region adjacent to the middle finger. Nevertheless, their task involved discrimination between different objects and therefore it does not tell us much about the object's parts that are informative for left and right hands identification.

5.3.1 Methods

Realistic pictures of hands were used as stimuli (see Figure 4). Stimuli could represent a left or a right hand seen from the back or from the palm. Each stimulus was displayed in one of four possible orientations (-120°, -60°, +60°, +120°). Stimuli' size were as follow: For the -120° and + 120° rotations stimuli subtended 8.9° x 7° of visual angle; For the -60° and + 60° rotations stimuli subtended 8.5° x 7.9° of visual angle. There were a total of 16 different stimuli. Participants (n=12) performed a unique block of 96 trials. They sat in front of a PC screen (15″ and 70 Hz refresh rate) at a distance of 80 cm away. Each trial started with the presentation of a white slide for 2500ms followed by the presentation of a hand stimulus for 3000ms. They judged stimulus laterality by uttering the word "sinistra" (i.e., left) or "destra" (i.e., right) soon after the presentation of the stimulus. However, there was no time constraint on responses. Eye movements were recorded with a Tobii x50 equipment (frame rate = 50 Hz) with binocular gaze tracking. Fixations were defined as the maintenance of eye position in a fixation radius of 30 pixels for a minimum of 100ms.

5.3.2 Results

Three areas of interest (AOIs) were defined for each stimulus. These AOIs were centered on the thumb (henceforth thumb's AOI), the other four fingers (henceforth fingers' AOI), and the remaining area of the hand (henceforth wrist's AOI). For each participant, the average total number of fixations (see Figure 24), and the average sum of the individual fixations durations (see Figure 25) were computed for each AOI. The average number of fixations made on the wrist's AOI (M = 40.8, SEM = 6.2) were fewer than the fixations made on the thumb's AOI (M = 150.5, SEM = 17), and on the fingers' AOI (M = 157.3, SEM = 11.1), F (2, 22) = 25.1, $p < .0001$. The average fixation duration on the thumb's AOI was longer (M = 263 ms, SEM = 24.2) than for the fingers' AOI (M = 237.1ms, SEM = 18.4) and the wrist's AOI (M = 237.4ms, SEM = 16.4), F (2, 22) = 3.65, $p < .05$. The eye tracking data indicated that the thumb was the most informative stimulus feature in helping observers determining hand laterality: This was the feature that was associated with longer looking times. The number of fixations did not differ between the thumb's AOI and the fingers' AOI. However, the AOI defined on the thumb was smaller than the AOI centered on the remaining fingers. Therefore, even if for the thumb's AOI the number of fixations were as numerous as for the other fingers' AOI, this could be explained by the larger surface of the fingers' AOI. These results strongly suggest that visual processing of the thumb is crucial in providing the necessary information to distinguish the left from the right hand. Importantly, this experiment demonstrates that perception of rotated hand images is associated with visual processing in the direction of rotation of the stimulus along its fingers, independently from the stimulus angle of presentation.

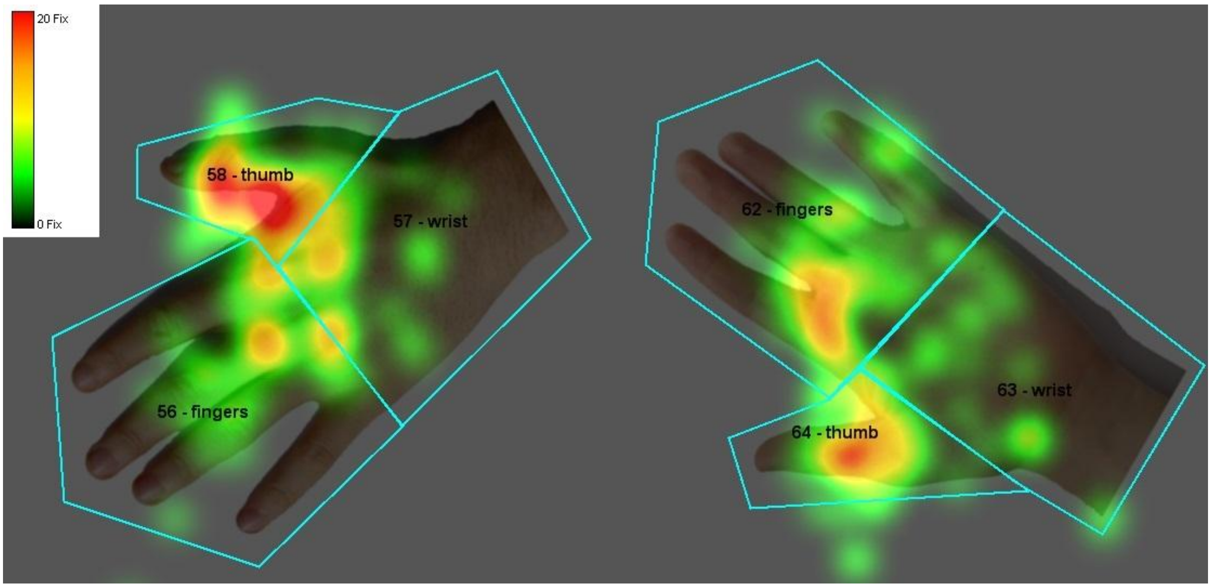


Figure 24. Heat map: Sum of the number of fixations of the experimental group for each image AOI. Fixations are within 30 pixels radius for 100ms minimum duration. The two exemplars hand stimuli shown correspond to a left hand in back view with -120° rotation (left image), and a left hand in palm view with -60° rotation (right image).

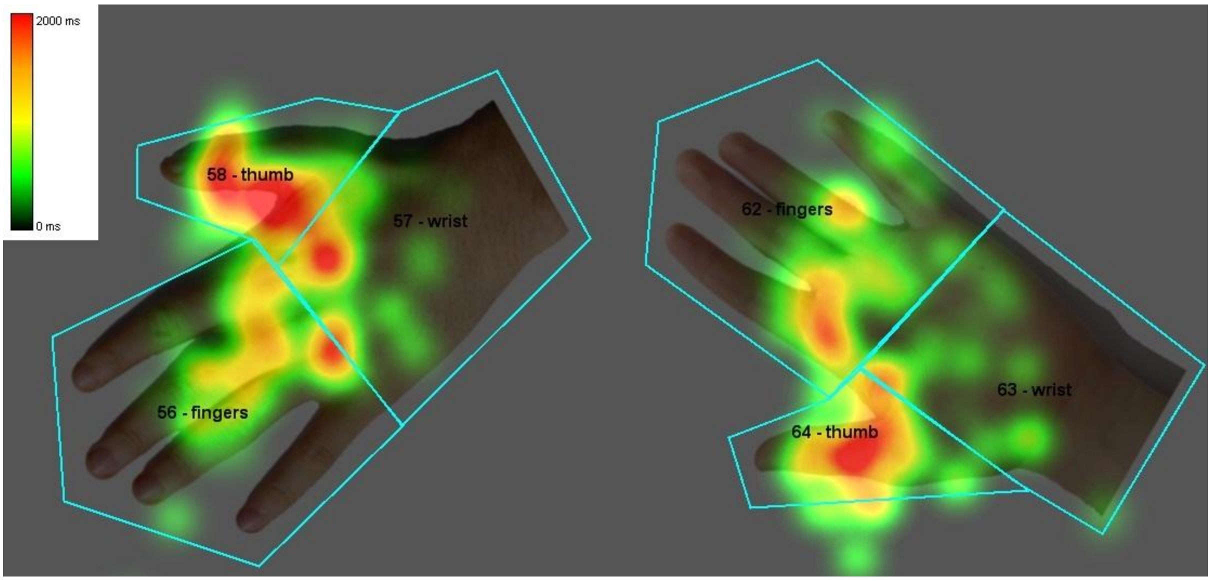


Figure 25. Heat map: Sum of the total fixations' lengths for all recordings of the experimental group expressed in milliseconds. The two exemplars hand stimuli shown correspond to a left hand in back view with -120° rotation (left image), and a left hand in palm view with -60° rotation (right image).

5.4 Experiment 3: View judgment of rear-view mirror shapes

In the classic hand laterality task the mirror-reversal of RTs can emerge for stimuli displayed from both the view of the hand's back and from the view of the hand's palm (e.g., De Simone et al., 2013, see Figure 6; cf. ter Horst et al., 2010). In their experiment 2, Viswanathan et al. (2012) showed that the mirror-reversal of RTs between left and right hands was absent for palm view stimuli in a view judgment task (see Figure 12). This seemed to be strong evidence that the RTs asymmetry reflected successful binding only for stimuli in back view. Indeed, the successful binding for back view stimuli was supposedly determined by the congruence of the seen hand shape with the observer's responding hand shape. Given that the palm view stimuli had a different shape than the hand used to respond (held in a palm-down position) this apparently produced no binding for these stimuli. The present experiment reproduces Viswanathan et al. second study with three main variations. Firstly, the stimuli used depicted an object rather than a body part. If it is possible to obtain the RTs mirror-reversal with another chiral object than a body part, then this would strongly suggest that the MOLA does not reflect a special case of motor imagery, nor it would reflect multisensory integration between vision and proprioception. For this purpose I created two new chiral stimuli. Interestingly, there are not so many chiral objects in the world that can be defined as inherently left or right, namely as “the left object” or “the right object”. Obviously one can create all sorts of visual objects, even abstract objects, and can give them the propriety of chirality with the good disposition of visual features. However, these objects will hardly be associated with a specific laterality like hand images are. Gloves and shoes are chiral objects too, but these are still related to a visual representation of the body and therefore are not suitable for the aim of the present study. There is another class of objects that satisfy the requirement for this experiment. Rear-view mirrors are chiral objects and can be identified as being “the left rear-view” or “the right rear-view”. In the following experiment I employed shapes of rear-view mirrors as stimuli and performed a view judgment task following Viswanathan et al.' (2012) procedure. Two pairs of rear-view mirror shapes were created. One pair had either the informative feature on its right when the object was a left rear-view mirror seen from the front (i.e., from the mirror), or had the informative feature on its left when the object was a right rear-view mirror seen from the front. The other pair either presented the informative feature on its left when the object was a left rear-view mirror seen from the front, or presented the informative feature on its right when the object was a right rear-view mirror seen from the front. These stimuli represented two hypothetic types of rear-view mirrors for motorcycles (see Figure 26 and 27). The former pair was named H type, and the latter pair was named R type. H type shapes are similar to hand shapes in that they either present the informative feature on the right (shape1) when the object is left and it is seen from the front, or they present the informative feature on the left (shape2) when the object is right and it is seen from the front. The same is true for hands' shapes. Indeed left hands seen from the back view have the thumb on the right, and right hands seen from the back view have the thumb on the left. R type shapes showed the opposite configuration: They either have the informative feature on the left (shape1) when the object is left and is seen from the glass, or they have the informative feature on the right (shape2) when the object is right and is seen from the glass. For H type shapes the informative stimulus feature corresponds with the bottom part of the object that is deflected either to the right (shape1) or to the left (shape2). This is the object's part that would be used to connect the rear-view mirror to the rest of the motorcycle. For R type, the informative feature is the circular part that contains the mirror that can be either deflected to the left (shape1) or to the right (shape2). There are no other features that can allow discrimination between the two exemplars of each rear-view type.

Vocal responses were used instead of left and right manual key presses. This allowed to avoid any confound with the responding hand. The attentional hypothesis predicts for vocal responses the same results obtained with lateral button presses. Differently from Viswanathan et al., the attentional hypothesis sees the RTs mirror-reversal as independent from the effectors used to respond. Finally, participants performed the task with their hands either in a palm-down posture or in a palm-up posture. This was done to clarify if the state of the observer hands has an impact on the cognitive operations involved in this task. One may indeed hypothesize that the state of the observer's hands affects visual judgments of the observed object if the cognitive operations carried out during perception shares some features with planning reaching and grasping movements towards it. Moreover, this manipulation was needed to compare the results of the present experiment with the results from another view judgment task with hand stimuli where hand posture was also manipulated. This latter experiment will be described in the following sections.

As I have shown in the previous experiment, misoriented images of hands can elicit stimulus-response compatibility effects due to stimulus orientation and laterality of response. This result indicates that perception of misoriented hand shapes is accompanied by visual processing that is systematically shifted in the direction of stimulus rotation. In the present experiment I have tested an alternative interpretation of Viswanathan et al.' results (2012; experiment 2) drawing on the stimulus-response compatibility effect found with button presses. In the present experiment participants judged if shapes of a rear-view mirror would be seen with a view from the "glass" (i.e., seeing the rear-view from the mirror) or with a view from the "plastic" (i.e., seeing the back of the rear-view) were these shapes representing either a left rear-view or a right rear-view mirror. I hypothesized that Viswanathan et al.'s result can be explained by the interactions between the spatial codes of the stimulus and its direction of rotation. The stimulus' spatial codes correspond to the laterality of the stimulus (left-right), and to the laterality of the informative stimulus' feature in object-centered coordinates (i.e., the left-right location of the thumb relative to the other fingers). This hypothesis foresees that the RTs mirror-reversal emerges when the laterality of the stimulus and the laterality of the informative stimulus feature are different as for H type rear-view shapes judged from the "glass" and R type shapes judges from the "plastic".

I expected to found the RTs mirror-reversal in the view judgment task with the type H shapes when participants made judgments of "glass" but not when they made judgments of "plastic". The difference between the spatial codes of the stimulus should modulate spatial attention generating the mirror-reversal of RTs. For H shapes in glass view RTs were expected to be faster when the orientation of the stimulus is in the opposite direction of stimulus laterality: Left stimuli should be judged faster when rotated in CW orientation (i.e., to the right), and right stimuli should be judged faster when rotated in CCW orientation (i.e., to the left). With the type H shapes the same results obtained with the hand shapes in the original study was expected. Indeed, when judging the glass view of the H shapes the laterality of the stimulus is always different from the laterality of the informative stimulus feature: When the stimulus is left the informative feature is on the right of the object, and when the stimulus is right the informative feature is on the left of the object. Judgments of plastic view for H shapes should not produce significant RTs asymmetries.

For R shapes the patter of results was expected to change, with RTs asymmetries for judgments of plastic view but not for judgment of glass view. Judgments of plastic view of R shapes involve different stimulus laterality and position of the informative stimulus feature: When the stimulus is left the informative feature is on the right of the object, while when the object is right the informative feature is on the left of the object.

For these stimuli, RTs were expected to be faster for left objects rotated in CCW orientations than CW orientations, and faster RTs for right objects in CW orientations than CCW orientations. The effect of the laterality of the stimulus and the direction of rotation on RTs should be inverted relative to the H shapes in glass view. Indeed, for R shapes in plastic view the comparison with the canonical version of the rear-view mirror involves a rotation in the picture plane as well as a rotation in the horizontal plane. Thus, left stimuli were expected to be judged faster when shown in CCW orientation and right stimuli were expected to be judged faster when shown in CW orientation. For R shapes in glass view no RTs asymmetries were expected because in this case the laterality of the stimulus corresponds with the position of the informative stimulus feature.

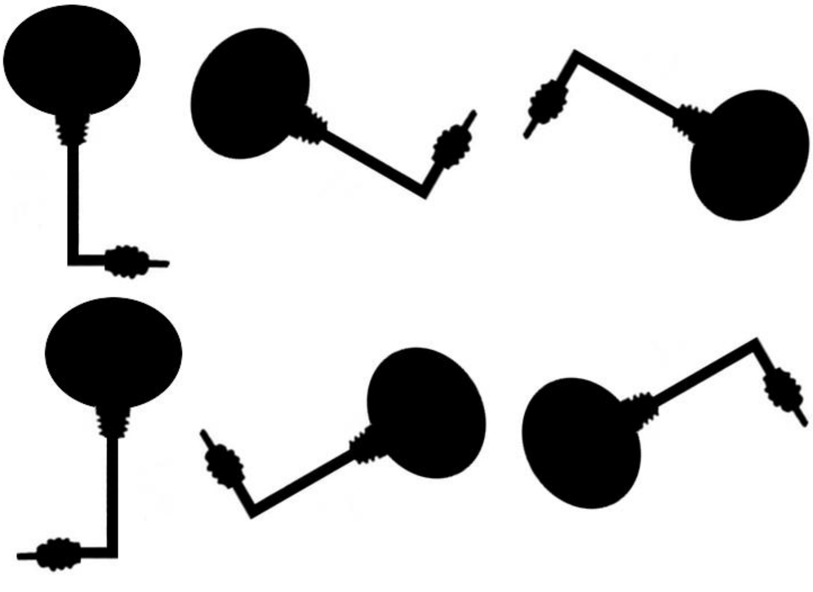


Figure 26. Examples of H type shapes. From top left to top right: Shape1: 0°, Shape1: -60°, Shape1: +120°. From bottom left to bottom right: Shape2: 0°, Shape2: +60°, Shape2: -120°.

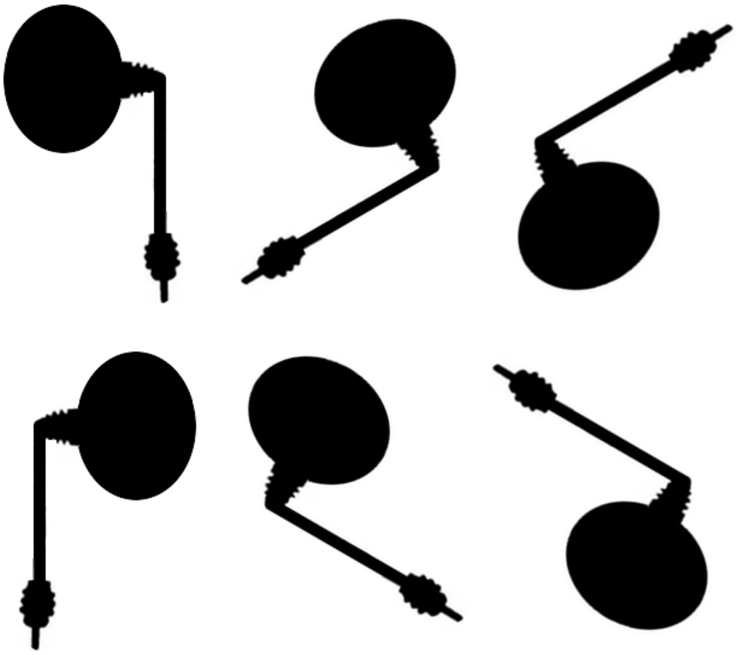


Figure 27. Examples of R type shapes. From top left to top right: Shape1: 0°, Shape1: +60°, Shape1: -120°. From bottom left to bottom right: Shape2: 0°, Shape2: -60°, Shape2: +120°.

5.4.1 Type H shapes

5.4.1.1 Methods

5.4.1.1.1 Participants

Ten right-handed (ESHI = 93.9, SD = 3.3; Oldfield, 1971) participants took part in the study (mean age = 21.7, SD = 2.9).

5.4.1.1.2 Stimuli and task procedure

Stimuli consisted of black silhouettes representing the rear-view mirrors of a motorcycle. Each shape was derived from rotation and/or reflection of a basic silhouette (4° x 5.4° visual angle). Participants sat in front of a PC screen (15″ and 70 Hz refresh rate) at a distance of 75 cm away. Trials begun with a fixation dot (0.3° visual angle). After 500ms the cue word “sinistro” (i.e., left), or the word “destro” (i.e., right) was displayed under the fixation dot for 1000ms. After cue offset, the fixation dot remained visible on the monitor for 1500ms. After this interval the shape stimulus was shown until a response was collected. If no response was recorded the stimulus remained visible for 2500ms after which the next trial stared. Each shape stimulus was randomly presented on a white background in five different angular departures (-120°, -60°, 0°, +60°, +120°). There were a total of 6 blocks, each composed by 80 trials. Three blocks were performed with the hands resting on the tight in a palm-down posture, and three blocks with the hands resting on the tight in a palm-up posture. Half of the participants performed the three blocks with the palm-down position first, and the other half started performing the task with the palm-up position. They could not see their hands during the task. The task consisted in determining the view (from the glass or from the plastic) in which the stimulus would be displayed when the stimulus shape corresponded to a right rear-view mirror or when it corresponded to a left rear-view mirror, as indicated by the cue word shown at the beginning of each trial. They were instructed to respond by saying “vetro” (i.e., glass), or “plastica” (i.e., plastic). Responses were collected by means of a microphone with vocal RTs recorded at the nearest millisecond. Before the experiment started, participants were shown all possible shapes. They were asked to represent themselves sited on a motorcycle and to imagine seeing the rear-view mirrors of the motorcycle from that perspective. If Shape1 was shown and it was cued by the word “left”, then the rear-view mirror would have been seen with its glass facing in the direction of the subject (correct response “glass”). If Shape2 was shown and it was cued by the word “right” then the rear-view mirror would have been with its glass facing in the direction of the subject (correct response “glass”). Instead, when Shape1 was shown after the word right, and Shape2 was shown after the word left, the rear-view mirror would have been seen with its plastic part facing in the direction of the subject (correct response “plastic”). All participants performed a block of practice trials (n=15) before the experiment started. Speed and accuracy requirements were emphasized.

5.4.1.2 Results: Type H shapes

RTs greater than three standard deviations above the mean were excluded from analysis. Two repeated measures ANOVAs with 2 (view: glass, plastic) x 2 (shape: Shape1, Shape2) x 5 (angle: -120°, -60°, 0°, +60°, +120°) within-subjects factors were performed on each hand posture condition. Since the analyses of the palm-down and palm-up posture conditions returned the same results, I combined these data in a unique data set. The analysis on accuracy data did not reveal any significant effect.

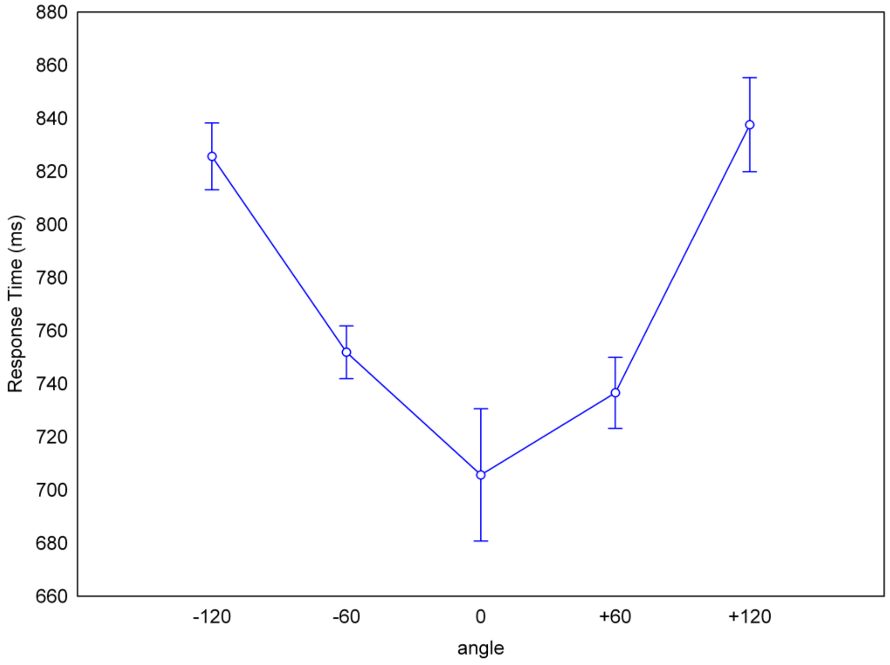


Figure 28. Mean RTs as a function of H type shapes orientation. Error bars represent the within-subject standard error of the mean.

There were main effects of view, *F* (1, 9) = 520.95, *p* < .0001, and angle, *F* (4, 36) = 38.61, *p* < .0001. RTs increased as the angle of stimulus presentation increased (see Figure 28), with stimuli in plastic view taking longer to be judged than glass view stimuli. The interaction of shape and angle was also significant *F* (4, 36) = 9.58, *p* < .0001, (see Figure 29). The interaction of view and angle, *F* (4, 36) = 3.62, *p* < .05, and the three-way interaction of view, shape, and angle were significant *F* (4, 36) = 3.17, *p* < .05, (see Figure 30). There was a mirror-reversal for stimuli in glass view and no effect for plastic view stimuli. Indeed the interaction between shape and angle was significant only for glass view stimuli, *F* (4, 36) = 12.49, *p* < .0001, but not for plastic view stimuli, *F* (4, 36) = 1.35, *p* > .2. For judgments of glass view RTs were faster for left stimuli (i.e., shape1) rotated in CW orientation and slower for left stimuli rotated in CCW orientation. Moreover, RTs were faster for right stimuli (i.e., shape2) rotated in CW orientation and slower for right stimuli rotated in CCW orientation.

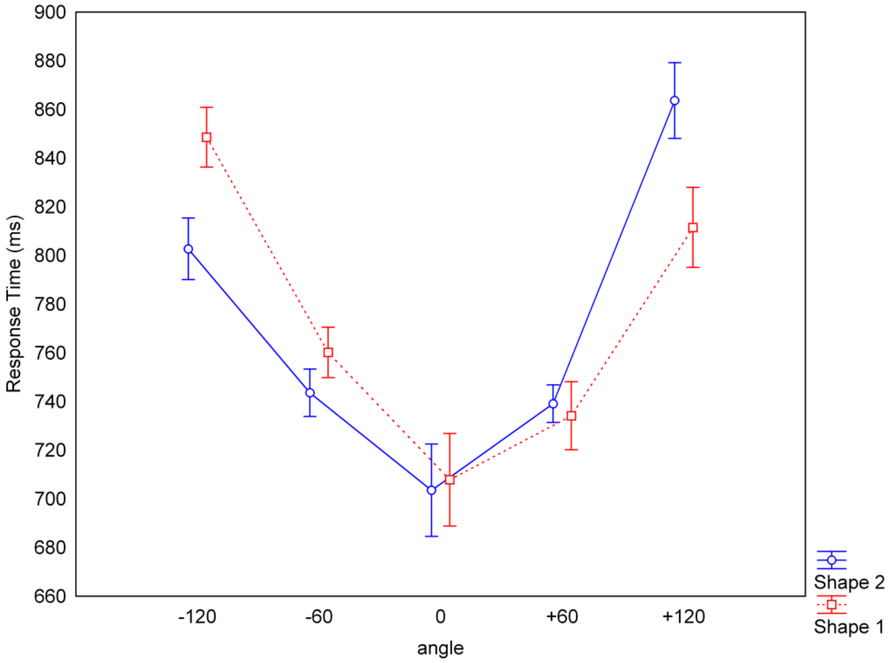


Figure 29. Mean RTs of H type shape1 and shape2 as a function of stimulus orientation. Error bars represent the within-subject standard error of the mean.

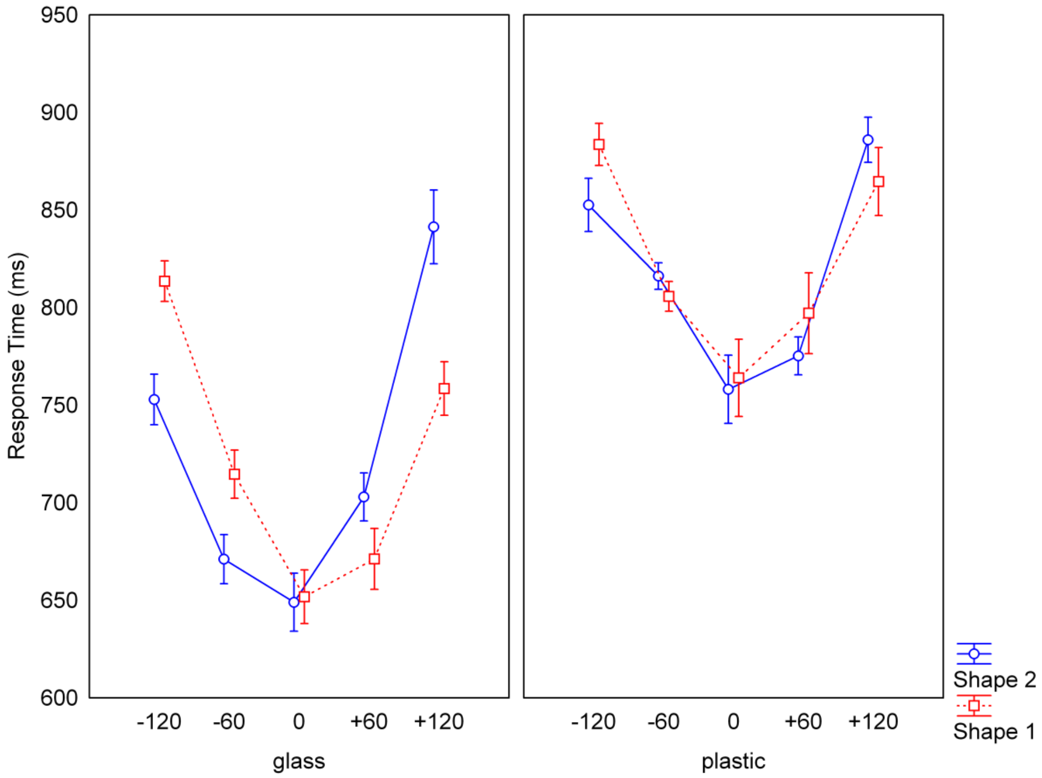


Figure 30. Mean RTs of H type shape1 and shape2 for the glass and the plastic view as a function of stimulus orientation. Error bars represent the within-subject standard error of the mean.

5.4.2Type R shapes

5.4.2.1Methods

5.4.2.1.1Participants

Ten right-handed (ESHI = 95.2, SD = 3.8; Oldfield, 1971) naive participants took part in the study (mean age = 23.1, SD = 4.1).

5.4.2.1.2 Stimuli and task procedure

The same experimental procedure of the previous experiment was employed. The two experiments differed only in the type of stimuli used.

5.4.2.2 Results: Type R shapes

RTs greater than three standard deviations above the mean were excluded from analysis. Two repeated measures ANOVAs with 2 (view: glass, plastic) x 2 (shape: Shape1, Shape2) x 5 (angle: -120°, -60°, 0°, +60°, +120°) within-subjects factors were performed on each hand posture condition. Since the analyses of the palm-down and palm-up posture conditions returned the same results, I combined again these data in a unique data set. The analysis on accuracy data did not reveal any significant effect also for R shapes.

The main effects of angle, F (4, 36) = 30.63, $p < .0001$, and of view, F (4, 36) = 32.6, $p < .0005$, were significant. There were longer RTs for plastic view stimuli than glass view stimuli, and RTs were longer as the angle of stimulus presentation was further from the upright (see Figure 31). The interaction of shape and angle, F (4, 36) = 3.99, $p < .05$, and the three-way interaction (see Figure 32) of view, shape and angle, F (4, 36) = 4.66, $p < .005$, were both significant. These results (see Figure 33) indicated that the interaction of shape and angle was significant for plastic view stimuli, F (4, 36) = 6.45, $p < .005$, but not for glass view stimuli, F (4, 36) = 1.47, $p > .2$. For judgments of plastic view RTs were faster for left stimuli (i.e., shape2) rotated in CCW orientation and slower for left stimuli rotated in CW orientation. RTs were also faster for right stimuli (i.e., shape1) rotated in CW orientation and slower for right stimuli rotated in CCW orientation.

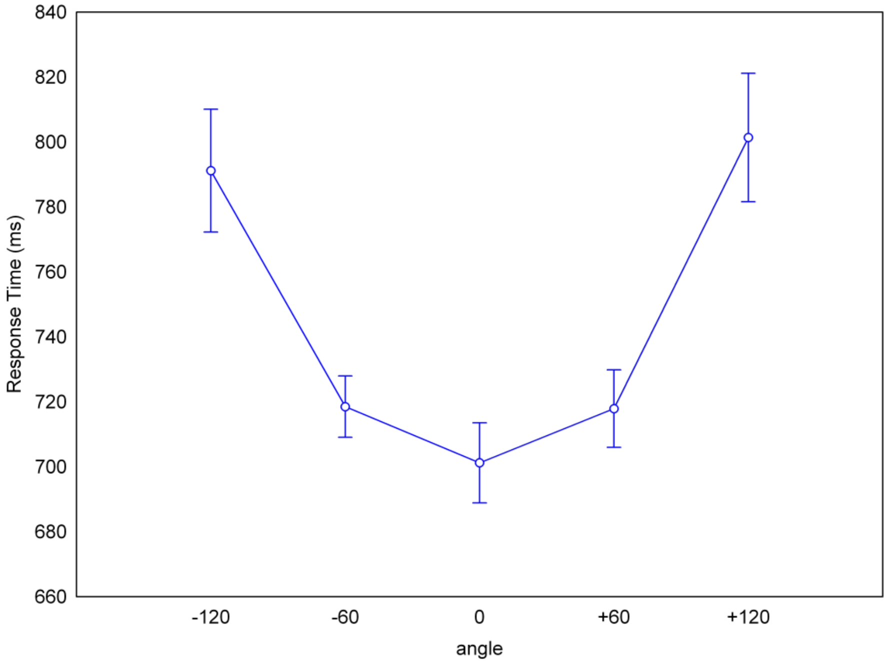


Figure 31. Mean RTs as a function of R type shapes orientation. Error bars represent the standard error of the mean. Error bars represent the within-subject standard error of the mean.

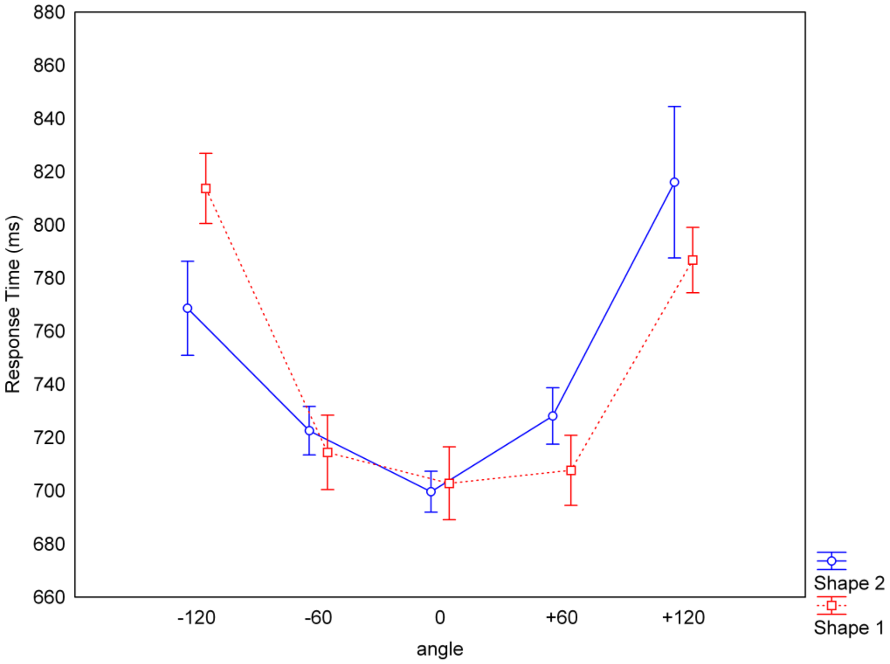


Figure 32. Mean RTs of R type shape1 and shape2 as a function of stimulus orientation. Error bars represent the within-subject standard error of the mean.

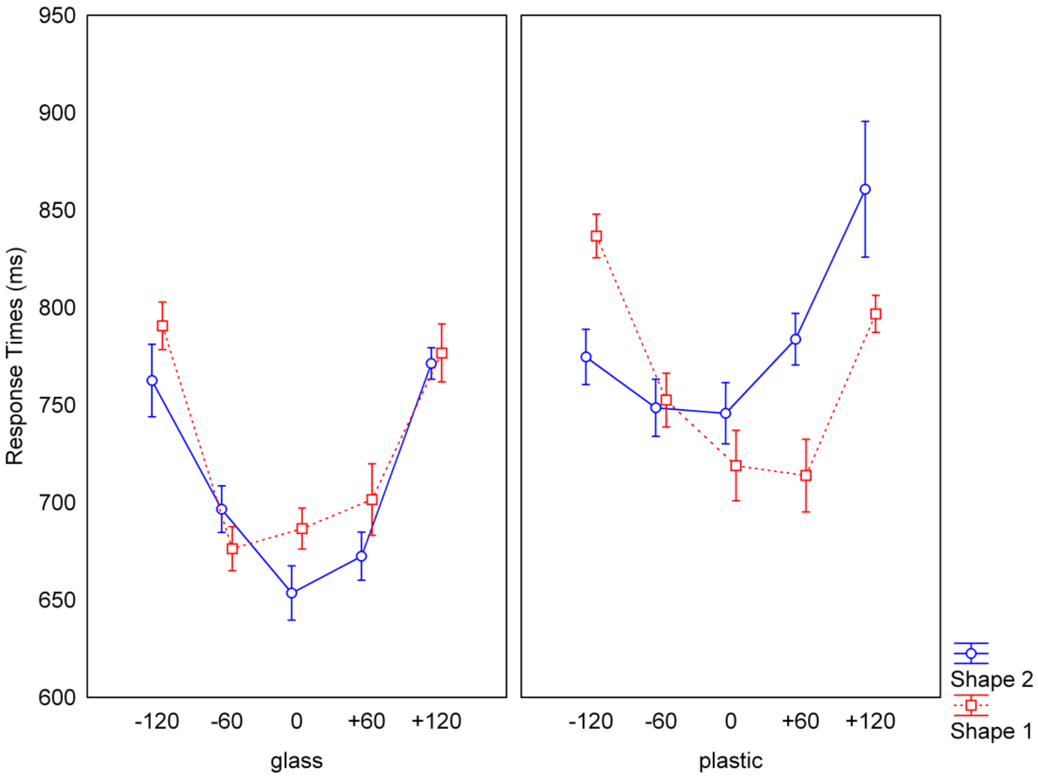


Figure 33. Mean RTs of R type shape1 and shape2 for the glass and the plastic view as a function of stimulus orientation. Error bars represent the within-subject standard error of the mean.

5.4.3 Discussion

The aim of the above described experiments was to test the hypothesis that the results of Viswanathan et al. (2012) depend on compatibility effects generated between the spatial codes of the stimulus. All predictions made based on this new interpretation were confirmed. Table 3 summarizes the results of experiment 3 and 4. The configuration of stimulus laterality and location of the informative stimulus feature for the H shapes was the same as for hand images. In the glass view, H shape's left stimuli had the informative feature on their right, while H shape's right stimuli had the informative feature on their left. In plastic view, H shape's left stimuli had the informative feature on their left, while H shape's right stimuli had the informative feature on their right. The results of the view judgment task with H shapes confirmed the same pattern of results of the original study with hand stimuli. Indeed, when H shapes were judged to be in glass view, a significant interaction between shape and orientation was found. On the other hand, plastic judgment of H shapes were not influenced by the combination of shape and angle. This result is in line with the attentional hypothesis. However, if the effect depended entirely on the interaction between the stimulus spatial codes and not on the type of judgment required in the task (i.e., glass vs. plastic judgment), then the same effect should have been found exclusively for plastic judgments when the relationship between stimulus laterality and location of the informative feature was inverted. The R type shapes served to test this alternative explanation. R type shapes presented the configuration of stimulus laterality and the location of the informative feature as inverted relative to the H type shapes. For R type shapes in glass view, left stimuli had the informative feature on their left, and right stimuli had the informative feature on their right. For R type shapes in plastic view, left stimuli had the informative feature on their right, and right stimuli had the informative feature on their left. Results from the view judgment task with R type shapes confirmed the predictions made by the attentional hypothesis: The interaction between shape and angle was significant only for stimuli in plastic view.

These results pose a serious problem for the multisensory account's claim that the asymmetry of RTs is explained by crossmodal integration and the resulting after-effect of an illusory feeling of movement. In the present experiments RTs were mirror-reversed for view judgments of stimuli that did not share any characteristic with hand images, if not for the configuration of the stimuli' spatial codes. Moreover, RTs were not affected by the observers' hand posture during the task. This suggests that the cognitive operations carried out during the task did not rely on proprioception nor they possibly shared features with action planning processes. For these reasons it is difficult to conceive how the multisensory account can explain the present RTs asymmetries for object's shapes.

An interesting issue that follows these results regards the underlying cognitive processes related to the modulation of RTs as function of the stimulus angular departure. Two possible mechanisms could be at work. One possibility is that mental rotation would transform the shape's image into congruence with a standard, canonical representation of the object. As suggested by the main effects of angle in both tasks with H and R shapes, presenting stimuli further from the upright requires more time to perform the task. If one accepts this interpretation, then mental rotation is also influenced by the compatibility between the spatial codes of the stimulus, because the same modulation of RTs changes not only as function of the angle but also relative to the type of shape that is judged (i.e., the RTs asymmetry for different shapes). Therefore mental rotation is influenced by the dynamics of spatial attention with faster RTs when attention moves in the same direction of mental rotation. The modulation of spatial attention given by the discrepant laterality of the stimulus and the laterality of the informative stimulus feature generates effects of facilitation and inhibition for different orientations. For H shapes, judgments of glass view were faster when the left stimulus (i.e., shape1) was rotated to the right (i.e., CW orientation) and when the right stimulus (i.e., shape2) was rotated to the left (i.e., CCW orientation), but were slower when the left stimulus was rotated to the left (i.e., CW orientation) and the right stimulus was rotated to the right (i.e., CW orientation). For R shapes, judgments of plastic view were faster when the left stimulus (i.e., shape2) was rotated to the left (i.e., CCW orientation) and when the right stimulus (i.e., shape1) was rotated to the right (i.e., CW orientation), but were slower when the left stimulus was rotated to the right (i.e., CW orientation) and when the right stimulus was rotated to the left (i.e., CW orientation). It is important to notice the different effect on RTs for H shapes in glass view and R shapes in plastic view. Indeed for the H shapes in glass view RTs are faster when the direction of rotation is opposite to the laterality of the stimulus. For R shapes in plastic view RTs are faster when the direction of rotation is the same as the laterality of the stimulus. These differences are related to the different visual transformation (i.e., mental rotation) adopted for glass and plastic view judgments. For glass judgments the transformation of the stimulus performed in order to match it with the canonical representation of the object involves a rotation on the picture plane. For plastic judgments the transformation of the stimulus is performed on the picture plane and also on the horizontal plane. This interpretation draws on the assumption that stimuli rotated in CW orientation are mentally rotated towards the upright with a CCW mental rotation, and stimuli rotated in CCW orientation are mentally rotated towards the upright with a CW mental rotation. In this view RTs are mirror-reversed because shifts of spatial attention due to the intrinsic spatial codes of the stimulus happen to be in the same direction of mental rotation (faster RTs) or in the opposite direction (longer RTs). For example, the involvement of spatial attention in mental imagery is supported by an fMRI study where brain activations in response to visual imagery overlapped with a control condition in which attention was directed to the left or right space (Slotnick et al., 2005). Another possibility is that the effect of the angular departure depends strongly on stimulus-response integration. In this view RTs are slower when the stimulus is hardly integrated with the response given its orientation. Therefore the effect of stimulus angular departure on RTs would be generated by more demanding integration at the response selection stage. It is clear from the present data that RTs slow-down dramatically after rotations of 120°, while the effects of 60° rotations are smaller. This could be explained by stimulus-response integration being harder when the spatial coordinates of the stimulus relevant feature do not match the egocentric coordinates of the observer. Indeed, when the stimulus is rotated by 120° in either direction, the features of the object have spatial coordinates that in the egocentric reference frame are inverted relative to the coordinates of the same features in the object-centered reference frame. For example, if the informative stimulus feature is on the right of the object it will be also on the right of the observer when the object is upright. However, the same feature will be still on the right of the object when it is rotated by 120°, but it will be also on the left of the observer when presented in that orientation, thus inverting the relationship between allocentric and egocentric reference frames.

5.4 Experiment 4:
View judgment of hand shapes

Human hands are chiral objects: The two hands cannot be superimposed on each other. Chiral objects are things that can be distinguished from their mirror images. The word chiral comes from the Greek *χειρ* (*kheir*): "hand". Imagine the printed letters “b” and “d”. For these 2D letters it is possible to superimpose one letter on the other by rotating and translating it in the 3D space. The same cannot be done with all 3D objects present in the world. If the 3D object is chiral this transformation would be impossible.

Hand images have two visual features: the shape and the view. There are two possible shapes and two possible views (see Figure 10). Shapes can be defined by the position of the thumb relative to the other fingers. Therefore shape1 is the shape with the thumb on the right of the hand, and shape2 is the shape with the thumb on the left of the hand. The two views indicate if the hand is seen from the back or from the palm. The combination of these two visual features (shape and view) defines the identity of the chiral object: If it is a left hand or a right hand. Being chiral, the left hand and the right hand seen from different views have the same shape. The left hand seen from the palm has the same shape of the right hand seen from the back; the left hand seen from the back has the same shape of the right hand seen from the palm.

In the present experiment, participants performed the same view judgment task of Viswanathan et al. (2012; experiment 2) while having the hands resting on their thighs, either in a palm-down position as in their study, or in a palm-up position. Like in the previous experiments, in the present study vocal RTs were collected instead of key presses. If successful binding and the asymmetry of RTs are related to focusing attention selectively to the responding hand (Viswanathan et al., 2012), then vocal responses should change the pattern of RTs in the view judgment by producing no RTs mirror-reversal. The multisensory account states that participants' hand position during the task gives rise to successful binding only when the shape of the responding hand (the hand cued at the beginning of each trial) is congruent with the shape of the seen hand. If the mirror-reversal of RTs is determined by successful binding between the seen and the felt hand, then the incongruence between the observer's hand shape and the seen hand shape should cause the binding process to fail. It follows that with the palm-up posture there should be no mirror-reversal of RTs for back view stimuli because the two shapes are not congruent. The attentional hypothesis predicts instead that the RTs’ asymmetry for back view stimuli should remain unchanged even if the shape of the cued felt hand is incongruent with the shape of the seen hand. It has been shown that when hand’s view and shape are irrelevant to the task, and color is the relevant stimulus dimension, there is a preferred attentional capture of shape1 and shape2 that makes shape1 automatically associated with faster left responses, and shape2 with faster right responses (Ottoboni et al., 2005). In my opinion, the specific hand shapes that facilitate lateral responses (independently of the view) in the study of Ottoboni et al. (2015) reflect an over learned visual association. Since born, we are used to observe (and to feel) our hands more often from the back than from the palm perspective. For this reason, shape1 (with the thumb on its right) is implicitly associated with the left hand,

and shape 2 (with the thumb on its left) is implicitly associated with the right hand. This visual association between hand's shape and laterality is so strong, that even altering the observer's hands posture between prone and supine (i.e., between the palm-down and the palm-up posture) should not change it. Therefore the attentional hypothesis predicts that for stimuli in back view visual processing of hand shapes should remain subject to the spatial-compatibility rules observed in the previous experiment with rear-view mirrors even if hand posture is changed. This is because the over-learned association of shape and laterality makes it worthless to rely also on somatosensory information arising from the observer's hands. For back view stimuli, when the laterality of the stimulus is left and the informative feature is on the right RTs should be faster for CW orientations than CCW orientations. When the laterality of the stimulus is right and the informative feature is on the left RTs should be faster for CCW orientations than CW orientations. This pattern of results was expected for both the palm-down and the palm-up actual posture.

The multisensory account predicts that when participants judge the stimulus view while having the hands in a palm-up position, successful binding should occur for shapes that match the observer's actual hand position. Therefore, with the palm-up posture there should be a mirror-reversal of RTs for palm view stimuli. The attentional hypothesis also predicts that if the observer's actual hand position is palm-up, this will generate a mirror-reversal of RTs for stimuli in palm view. Unlike the condition in which participants hold their hands in the palm-down posture, in the palm-up posture condition participants can exploit the congruence between the felt position of their thumbs and the position of the thumb in the shape stimulus. This situation generates a dimensional overlap between the position of the thumb in the stimulus and the felt position of the observer's thumb. In this case there should be attentional modulation even if the laterality of the stimulus and the position of the informative feature (i.e., the thumb) have the same spatial code. As shown in the previous view judgment experiments with rear-view mirrors, the RTs mirror-reversal emerged when stimulus laterality and the laterality of the informative stimulus feature were different. When the two spatial codes were the same no effect emerged. For stimuli in palm view, the laterality of the stimulus and the laterality of the informative feature are always the same. Thus, there should be no mirror-reversal of RTs. Nevertheless, the dimensional overlap between visual and proprioceptive information in the palm-up posture condition should attract attention to the participant felt position of the thumb. When the stimulus is left and shape2 is presented the observer will shift attention towards the felt position of the thumb of the left hand that is on the left side relative to the other hand fingers. This should make RTs for judgments of stimuli rotated towards the opposite-right space faster (CW orientations), than for stimuli rotated towards the same-left space (CCW orientations). When the stimulus is right and shape1 is presented the observer will shift attention towards the felt position of the thumb of the right hand that is on the right side relative to the other hand fingers. This should make RTs for judgments of stimuli rotated towards the opposite-left space faster (CW orientations), than for stimuli rotated towards the same-right space (CCW orientations).

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5.4.1 Methods

5.4.1.1 Participants

Twelve right-handed (ESHI = 94.6, SD = 4.1; Oldfield, 1971) participants took part in the study (mean age = 22.2, SD = 2.7).

5.4.1.2 Stimuli and task procedure

Stimuli consisted of black silhouettes representing a human hand shape. Each hand shape was derived from rotation and/or reflection of a basic silhouette (4° x 5.4° visual angle). Participants sat in front of a PC screen (15″ and 70 Hz refresh rate) at a distance of 75 cm away. Trials begun with a fixation dot (0.3° visual angle). After 500ms the cue word "sinistra" (i.e., left), or the word "destra" (i.e., right) was displayed under the fixation dot for 1000ms. After cue offset the fixation dot remained visible on the monitor for 1500ms. After this interval the shape stimulus was shown until a response was collected or for a maximum duration of 2500ms. Each shape stimulus was randomly presented on a white background in five different angular departures (-120°, -60°, 0°, +60°, +120°). There were a total of 6 blocks, each composed by 80 trials. Three blocks were performed with the hands resting on the tight in a palm-down posture, and the other three blocks with the hands resting on the tight in a palm-up posture. Half of the participants performed the three blocks with the palm-down position first, and the other half started performing the task with the palm-up position. They could not see their hands during the task. The task consisted in determining the view (back or palm) in which the stimulus hand shape would be displayed when the shape corresponded to a right hand or to a left hand, as indicated by the cue word. They responded by saying "dorso" (i.e., back) or "palmo" (i.e., palm). Responses were collected by means of a microphone with vocal RTs recorded at the nearest millisecond. Participants were required to respond as fast and as accurate as possible. Before the experiment started they performed 15 practice trials.

5.4.2 Results

5.4.2.1 Response Time

RTs greater than three standard deviations above the mean were discarded from data. For each participant and each combination of view, shape, and angle, RTs were computed as the average time of response on correct trials from stimulus onset. Accuracy was calculated as the proportion of errors before removing RTs outliers. Two repeated measures ANOVAs with 2 (view: back, palm) x 2 (shape: shape1, shape2) x 5 (angle: -120°, -60°, 0°, +60°, +120°) within-subjects factors were performed on each hand posture condition (hands in palm-down vs. hands in palm-up position).

In the palm-down posture condition there was a main effect of angle, F (4, 44) = 25.47, $p < .0001$, with longer RTs for stimuli rotated further from upright (see Figure 34). The main effect of view almost reached significance, F (1, 11) = 4.75, $p = .052$, suggesting that judgments of palm view may have taken longer than back view. The significant interaction of view and shape, F (1, 11) = 40.44, $p < .001$, indicated that shape 2 in back view (i.e., the right hand), and shape 1 in palm view (i.e., the right hand) were judged faster than shape 1 in back view (i.e., the left hand), and shape 2 in palm view (i.e., the left hand). The shape x angle interaction, F (4, 44) = 5.46, $p < .005$ (see Figure 35) indicated faster RTs for shape 1 than shape 2 when shown with CW orientations (+60°, +120°), and faster RTs for shape 2 than shape 1 when shown with CCW orientations (-120°, -60°). The three-way interaction between view, shape, and angle was significant, F (4, 44) = 4.9, $p < .005$ (see Figure 36). This interaction highlighted the significant RTs' mirror-reversal for stimuli in back view. For these back view stimuli the interaction between shape and angle was significant, F (4, 40) = 9.71, $p < .0001$, with faster RTs for left stimuli (shape1) rotated in CW orientation and right stimuli (shape2) rotated in CCW orientation, but with slower RTs for left stimuli rotated in

CCW orientation and right stimuli rotated in CW orientation. As expected, RTs for palm stimuli did not show the interaction of shape and angle indicative of the RTs' mirror-reversal, *F* (4, 40) = .16, *p* > .9.

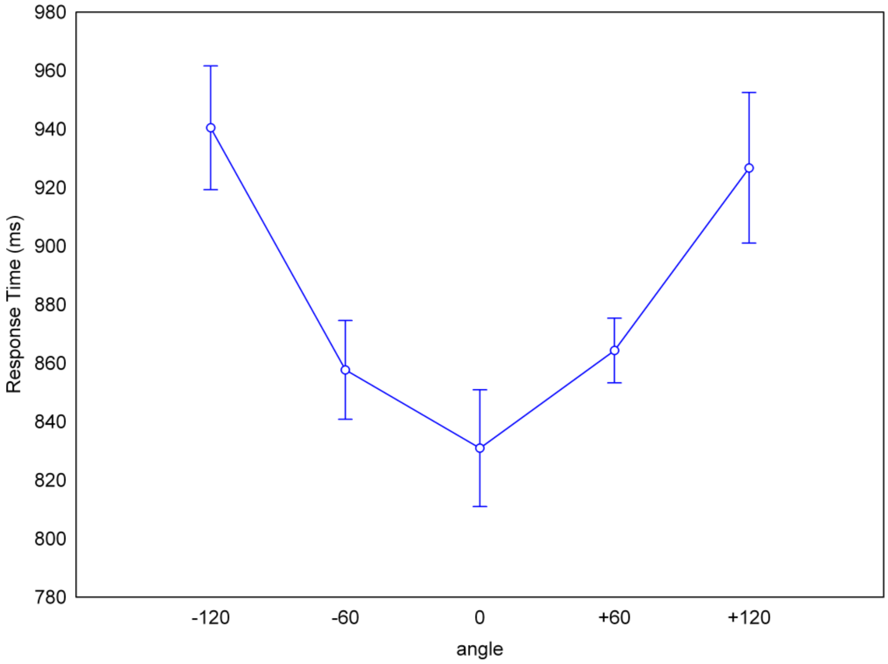

Figure 34. Mean RTs as a function of H type shapes orientation in the *palm-down posture condition*. Error bars represent the within-subject standard error of the mean.

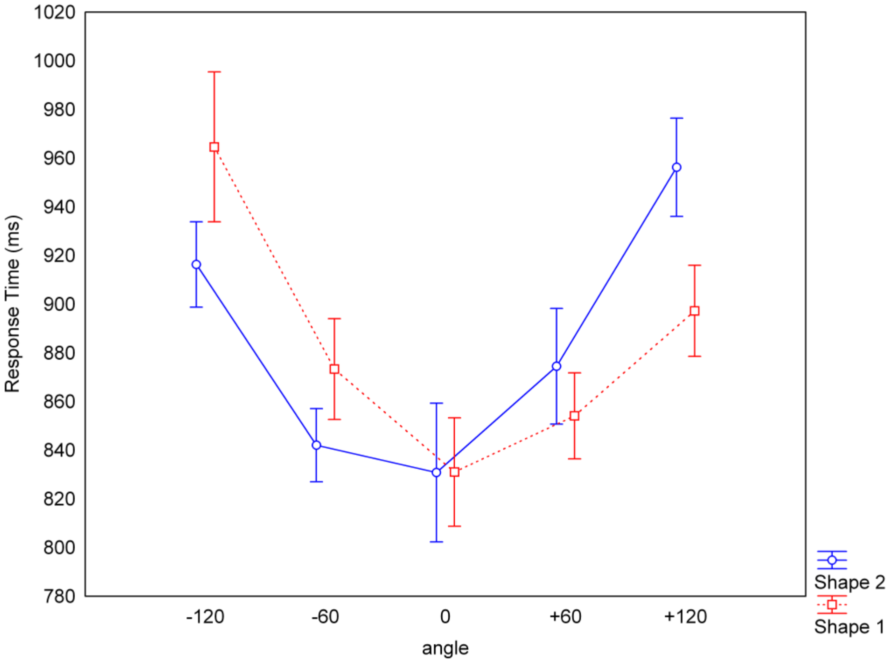

Figure 35. Mean RTs for shape1 and shape2 as a function of stimulus orientation in the *palm-down posture condition*. Error bars represent the within-subject standard error of the mean.

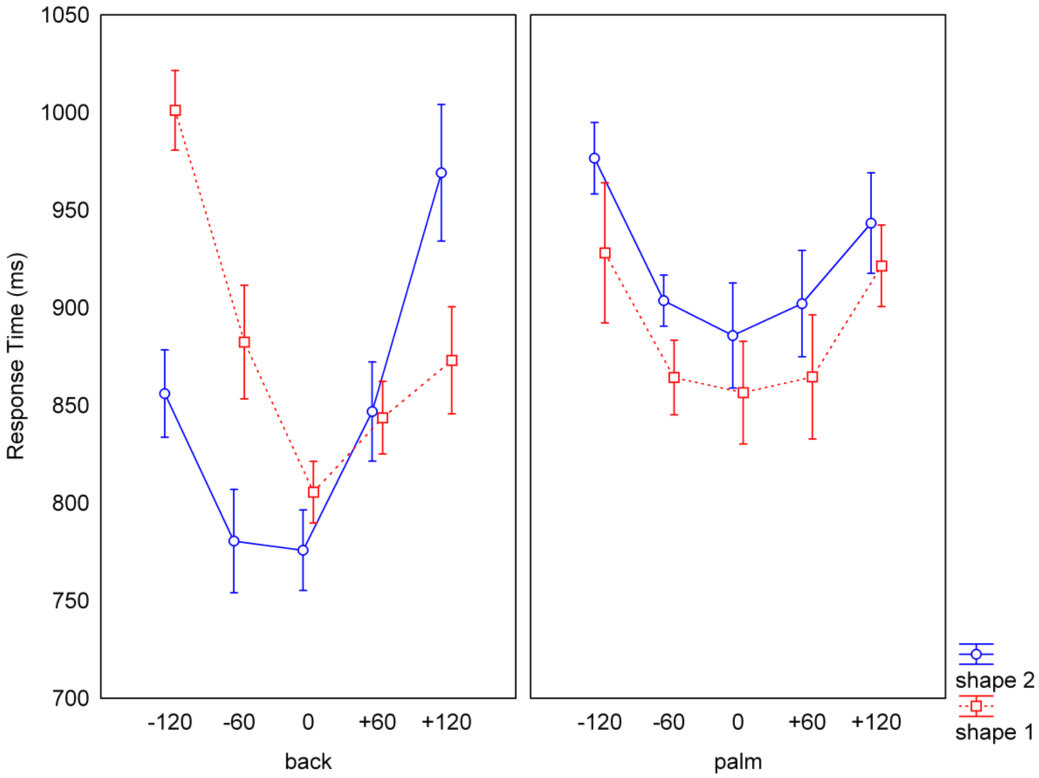

Figure 36. Mean RTs for shape stimuli (shape1, shape2) for back and palm trials as a function of stimulus orientation in the *palm-down posture condition*. Error bars represent the within-subject standard error of the mean.

In the palm-up posture condition the main effect of angle (see Figure 37), *F* (4, 44) = 23.95, *p* < .0001, and the interactions of view and shape, *F* (1, 11) = 14.75, *p* < .005 were significant. These effects exactly paralleled the results in the palm-down posture condition: RTs increased as stimulus angle increased, and were faster for judgments of right hands (i.e., shape1 in palm view, and shape 2 in back view) than left hands (i.e., shape 2 in palm view, and shape 1 in back view). The interaction of shape and angle, *F* (4, 44) = 3.93, *p* < .05, also replicated the palm-down posture condition (see Figure 38): There were faster RTs for shape 1 than shape 2 when rotated in CW (+60°, +120°), and faster RTs for shape 2 than shape 1 when rotated in CCW (-120°, -60°).

The second-order interaction of view, shape, and angle was significant, *F* (4, 44) = 16.46, *p* < .0001 (see Figure 39). As predicted by the attentional hypothesis, RTs for both back and palm view stimuli were mirror-reversed. Indeed, the interaction between shape and angle was significant for back stimuli, *F* (4, 40) = 14.29, *p* < .0001, as well as for palm stimuli, *F* (4, 40) = 4.73, *p* < .001. For both back and palm stimuli RTs were faster with left stimuli rotated in CW orientation and with right stimuli rotated in CCW orientation, and were slower for left stimuli rotated in CCW orientation and right stimuli rotated in CW orientation.

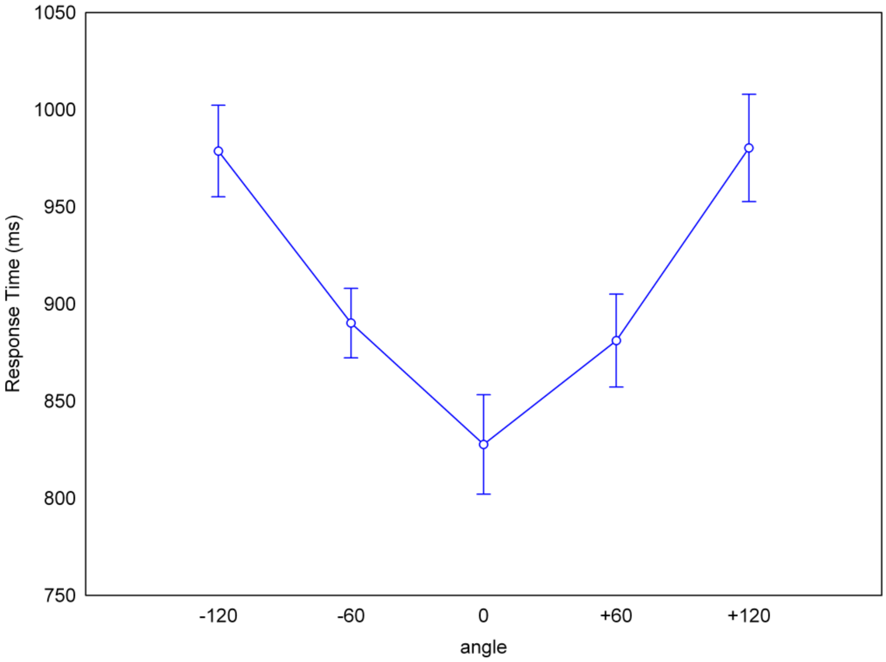

Figure 37. Mean RTs as a function of H type shapes orientation in the *palm-up posture condition*. Error bars represent the within-subject standard error of the mean.

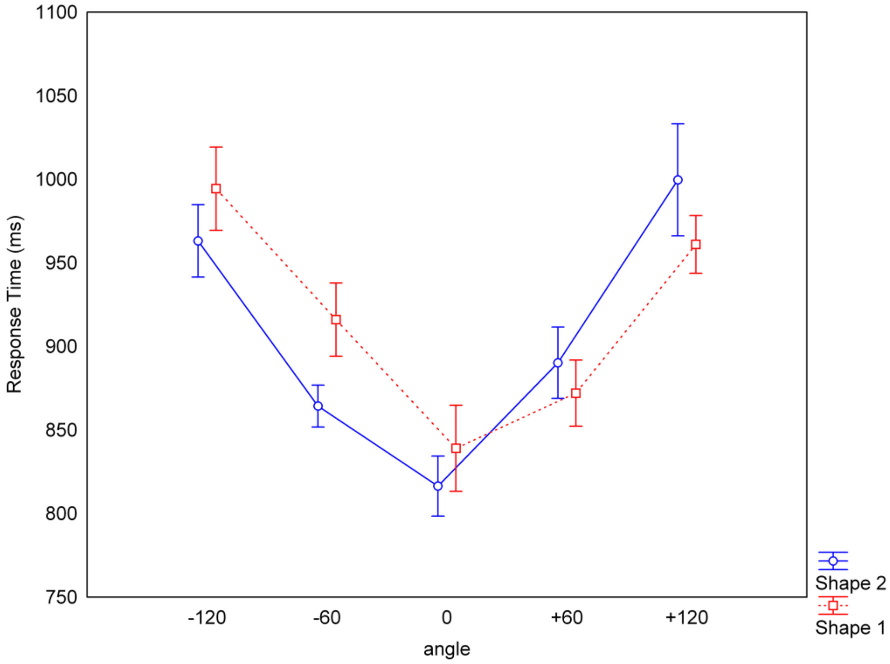

Figure 38. Mean RTs for shape1 and shape2 as a function of stimulus orientation in the *palm-up posture condition*. Error bars represent the within-subject standard error of the mean.

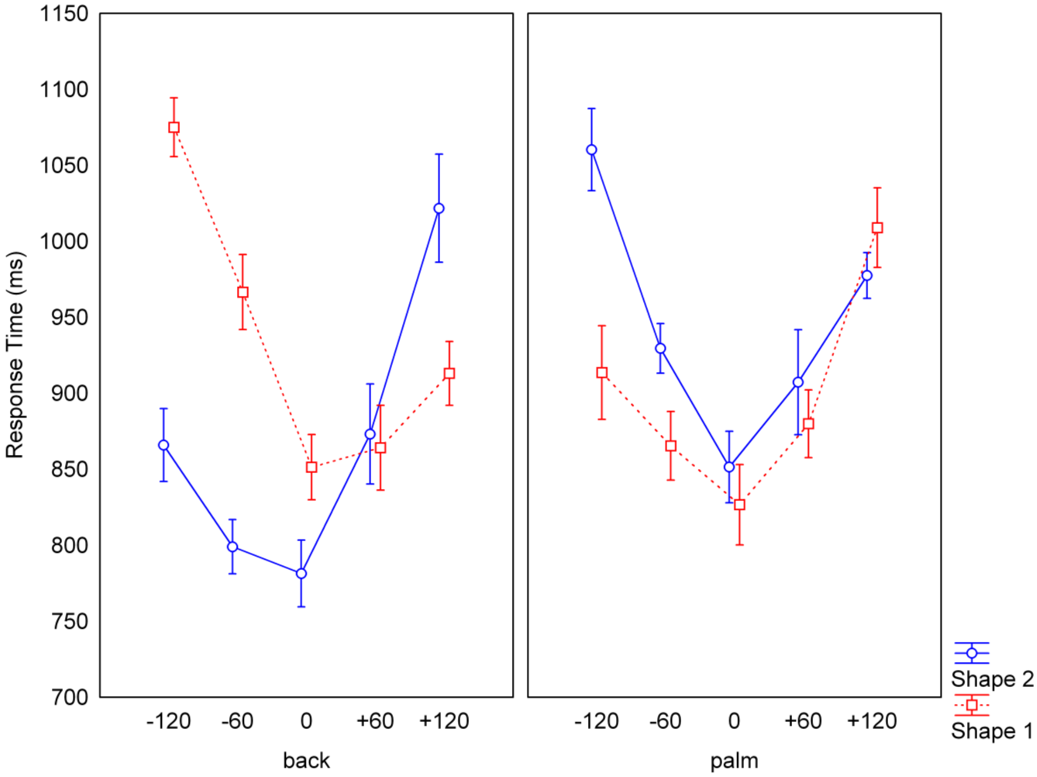

Figure 39. Mean RTs for shape stimuli (shape1, shape2) for back and palm trials as a function of stimulus orientation in the *palm-up posture condition*. Error bars represent the within-subject standard error of the mean.

5.4.2.2 Accuracy

In the palm-down posture condition the ANOVA on the proportion of errors returned the significant main effect of view, *F* (1, 11) = 5.3, *p* < .05 with more difficult judgments of stimuli in palm view than in back view. The significant three-way interaction of view, shape, and angle, *F* (4, 44) = 3.02, *p* < .05 (see Figure 40), suggest that the most difficult stimulus to be judged was the left hand in back view (shape1 from the back) presented in CCW orientations (at -120° and -60° of angle) than the right hand in the same orientations.

In the palm-up condition there was a main effect of angle, *F* (4, 44) = 2.8, *p* < .05, and a significant second order interaction on accuracy of view, shape, and angle, *F* (4, 44) = 4.01, *p* < .05 (see Figure 41). Here there were differences in accuracy also for palm view stimuli, with more errors for the left hand in palm view (shape2 from the palm) presented in CCW orientations (at -120° and -60° of angle) than the right hand in the same orientations.

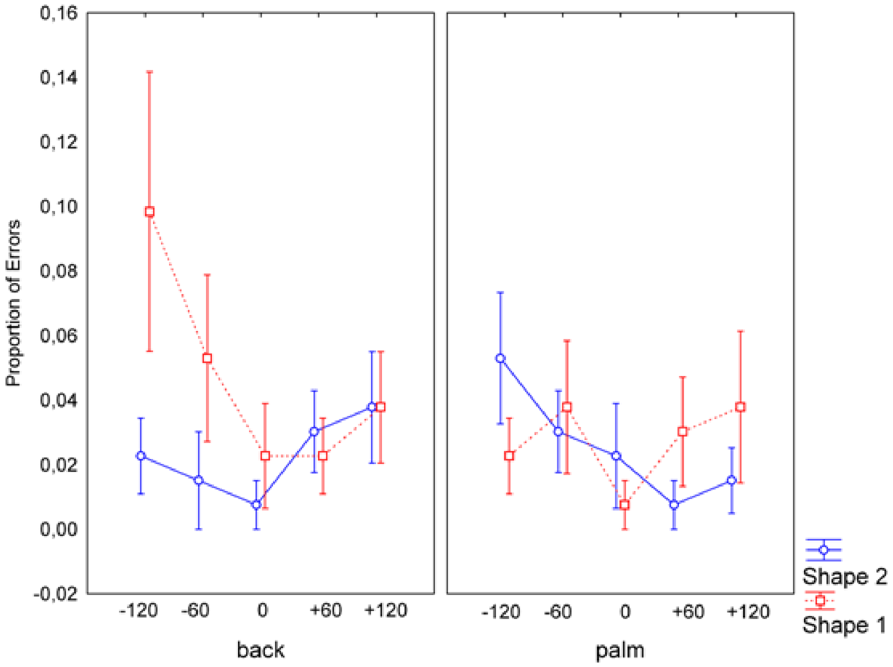

Figure 40. Mean proportion of errors for shape stimuli (shape1, shape2) for back and palm trials as a function of stimulus orientation in the *palm-down posture condition*. Error bars represent the standard error of the mean.

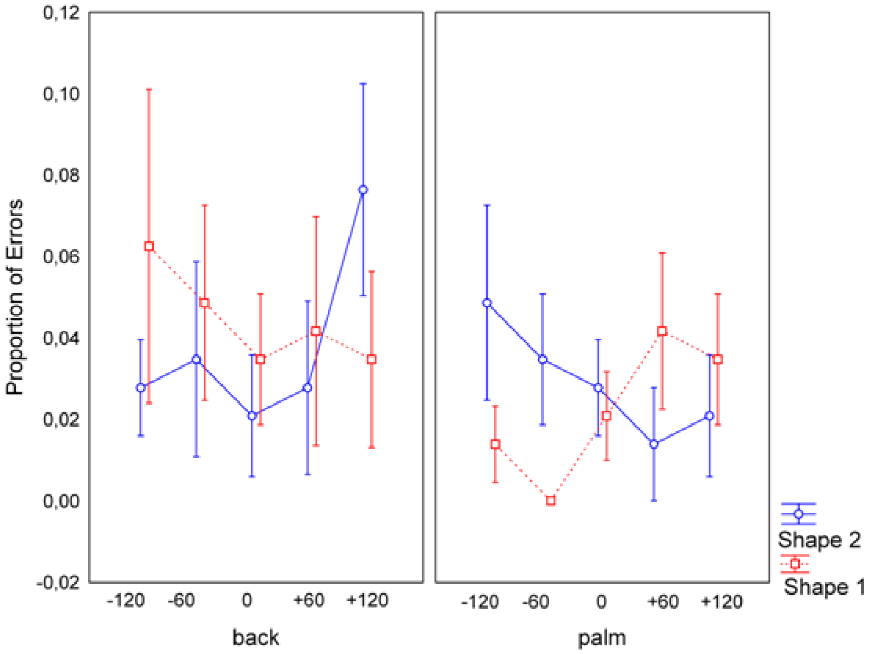

Figure 41. Mean proportion of errors for shape stimuli (shape1, shape2) for back and palm trials as a function of stimulus orientation in the *palm-up posture condition*. Error bars represent the standard error of the mean.

5.4.3 Discussion

Two main variations from the experiment 2 of the original study by Viswanathan et al. (2012) were implemented in the present experiment. Firstly, responses were given vocally. This was done to test one of the claims of the multisensory integration account that wants the RTs' mirror-reversal linked to the sensory input of the responding effectors. Indeed, these authors claimed "that the advance preparation of the response hand would induce observers to selectively attend to that hand's proprioceptive representation while suppressing inputs from the other (nonresponding) hand" (Viswanathan et al., 2012). I hypothesized that if attending to the responding hand is an important aspect of the RTs mirror-reversal, then responding vocally should have influenced the RTs distribution by removing the effect. The results of the present experiment show that it is not necessary to pay attention to one’s own hand while it is used to respond in order for the RTs mirror-reversal to emerge. Results were indeed in line with those obtained in the original study with manual responses. The only difference with the original study was the orientation effect on RTs for left and right hand stimuli at +60° of rotation. Indeed, in both the palm-down and the palm-up posture condition back view judgments for left and right hand stimuli did not differ at +60° orientations. This particular difference may be related to response modality because in the original study with button presses this difference was significant.

The other modification was relative to the participants’ hands posture during the task. In the present experiment, hands' posture was manipulated so that each participant performed the task with the hands resting in a palm-up posture, and in a different phase of the experiment with the hands resting in a palm-down posture. This procedure allowed for a better test of the multisensory integration account and the attentional hypothesis. The former account states that successful binding occurs when the shape of the stimulus is congruent with the shape of the responding hand (i.e., the cued hand), and this would be responsible for the RTs’ mirror-reversal. It follows that when participants’ hand posture is in the palm-up posture, the shapes congruent with this posture should be bound together generating the RTs mirror-reversal. So, when the stimulus is in palm view and the participant’s hands are in the palm-up posture, RTs should be mirror-reversed. Moreover, since successful binding can only occur when the presented shape stimulus and the actual hand position match, then this account also predicts that with the palm-up posture there should be no binding of visual and proprioceptive features when the stimulus is in back view.

The present results rule out the multisensory account interpretation and confirm the predictions made by the attentional hypothesis. For stimuli in back view, RTs were mirror-reversed regardless of the observer's hand posture. For these stimuli, visual processing was a sufficient source of information for determining the view of the stimulus. In this context, the contrasting spatial codes of stimulus laterality and that of the informative feature location modulated attention facilitating judgments for stimuli with orientations that were opposite to stimulus laterality (left stimuli judged faster when rotated to the right-CW orientations, and right stimuli judged faster when rotated to the left-CCW orientations). The palm-up posture condition created dimensional overlap between the location of the informative stimulus feature and the position of the observer's thumbs. In contrast with the palm-down posture condition, the dimensional overlap favored the emergence of the RTs mirror-reversal also for judgments of palm view stimuli. Indeed, the palm-up posture manipulation gave participants the possibility to rely on their hands as comparators by attending to the location of one of their thumbs. This created an advantage for orientations that were opposite to the position of the "felt thumb". For this reason the mirror-reversal was present even if the position of the stimulus' informative feature had the same spatial code of stimulus' laterality.

The attentional hypothesis made precise predictions about the conditions that determine the different modulation of RTs for medially-oriented and laterally-oriented chiral stimuli. While the present results confirmed the idea that attentional modulation is responsible for the MOLA, the multisensory account cannot explain these specific effects without relying on the conceptual construct of the body schema, thus making the multisensory interpretation become redundant.

Table 3. Results from experiment 3 and 4. For each stimulus is indicated the view, the laterality, the position of the informative feature, the mirror-reversal on RTs if present, and the faster (-) or slower (+) RTs for each orientation CW-CCW.

		view	laterality	feature	mirror reversal	CW	CCW
	H shape1	glass	left	right	yes	-	+
	H shape2	glass	right	left	Yes	+	-
	H shape1	plastic	right	right	No		
	H shape2	plastic	left	left	No		
	R shape1	glass	left	left	No		
	R shape2	glass	right	right	No		
	R shape1	plastic	right	left	Yes	-	+
	R shape2	plastic	left	right	Yes	+	-
palm down posture	hand shape1	back	left	right	Yes	-	+
palm down posture	hand shape2	back	right	left	Yes	+	-
palm down posture	hand shape1	palm	right	right	No		
palm down posture	hand shape2	palm	left	left	No		
palm up posture	hand shape1	back	left	right	Yes	-	+
palm up posture	hand shape2	back	right	left	Yes	+	-
palm up posture	hand shape1	palm	right	right	Yes	+	-
palm up posture	hand shape2	palm	left	left	Yes	-	+

6. The unilateral neglect misjudgement for left-handed chiral objects

Unilateral Neglect (UN) is a complex neuropsychological disorder whereby patients fail to detect or to respond to sensory events occurring in the side of the space contralateral to the damaged cerebral hemisphere. UN frequently follows right cerebral hemisphere infarction, and its diagnosis must exclude that symptoms can be primarily explained by elementary sensory or motor deficits. The observation of patients' selective deficits affecting specific spatial representations has provided a deeper understanding of human spatial cognition and its neural underpinnings. Some patients may show representational neglect (i.e., imagery neglect), failing to describe the contralesional side of mentally generated images (Bisiach & Luzzatti, 1978). Other patients may experience representational neglect for personal space (i.e., personal neglect), showing difficulties in exploring their contralesional hemisoma because they are less able to locate and spatially represent the space occupied by its belonging body parts. Personal neglect is usually accompanied by extrapersonal explorative deficits (Bisiach et al., 1986; Beschin & Robertson, 1997; Maguire & Ogden, 2002), even though the dissociation between personal and extrapersonal symptoms has been reported (Guariglia & Antonucci, 1992). UN patients may show also explorative deficits for stimuli in the extrapersonal space, whether they are presented in the within-reach peripersonal space (Halligan & Marshall, 1991), or in the far extrapersonal space (Vuilleumier et al., 1998). Together with the distinction between "premotor" and "perceptual" components of UN symptoms (for a review see Vallar & Mancini, 2010), and between the frame of reference within which the left-sided omissions can occur (egocentric and allocentric neglect; Marsh & Hillis, 2008), these dissociable behavioural patterns show that specific form of space representation can be affected in UN.

UN patients may also fail to identify the laterality of left-handed chiral objects. Coslett (1998) reported that patients with left UN (i.e., with explorative deficits of the left peripersonal space) judged the laterality of left hand images less reliably than right hand images. Compared with left and right brain damaged patients without UN, three UN patients identified left hands less accurately than right hands, but were still able to discriminate between two hand pictures. Coslett argued that this behavior reflects a disturbance of the body schema. The idea that good hand laterality identification reflects the functioning of an intact body schema was already present in Parsons' studies using the hand laterality task. Parsons noted that the configuration of RTs and the effect of hand posture during judgment of hand laterality matched "the current kinematic configuration of one's body" that is likely related to the body schema (1994). The body schema can be conceptualized as a multisensory, on-line, abstract representation of the body in space (Head & Holmes, 1911), essential to implement and monitor actions. The theoretical construct of the body schema reflects the continuous update of proprioceptive, vestibular, tactile, and visual information from the body together with the efference copy of executed actions. It is usually distinct from other body representations such as the body image, and the body structural description. The former concept has been invoked to describe the semantic knowledge of one's own body parts, including their names and the functional association with external objects (e.g., Coslett et al., 2002). The body structural description is a topological map of body structure based primarily on vision (e.g., Sirigu et al., 1991). Disturbance of this representation brings to the condition of autotopagnosia, in which the patient is unable to point to body parts on her/his self or others. Unfortunately, there is no consensus in the use of this terminology, at least for what concern the body image and the body schema (Berlucchi

& Aglioti, 2010). For example, Paillard (1999) and Gallagher (2005) defined the body schema as a sensorimotor map of the body space that relies prevalently on propriocetion, and the body image as a representation based mainly on visual information. The latter is activated consciously and is related to self-consciousness, while the body schema regards forms of processing prior to conscious though that are involved in controlling and making bodily movements possible. This distinction is based on observations of double dissociations between, for instance, UN patients and patients with somatic deafferentation. Some UN patients may deny the ownership of a limb (i.e., somatoparaphrenia) while at the same time they can use it to perform actions without difficulties. On the other hand, patients that have lost somatic afference from the body can perform actions only if paying attention to the vision of the involved body part and its movements (Cole & Paillard, 1995). However, if we consider the classification of Schwoebel and Coslett (2005), the body schema is implicated also in the simulation of actions and can be studied with tasks that tap the mental representation of movements such as explicit motor imagery tasks, and the hand laterality task. Patients suffering from complex regional pain syndrome were attributed disturbance of body schema because they were slower in identifying pictures corresponding to the laterality of their affected limbs (Coslett et al., 2010; Moseley, 2004; Schwoebel et al., 2001, 2002). In this view, nociceptive signals can disrupt the body schema. This would impact the ability to mentally simulate movements with the affected body part, which in turn would be expressed in difficulties in the identification of body part's laterality.

After Coslett's first report of three left UN patients (1998), researchers have associated the UN's left misjudgement to personal neglect rather than to explorative deficits of the left peripersonal space (Baas et al., 2011; Reinhart et al., 2012). Personal neglect was assessed by asking the blindfolded patient to reach with the ipsilesional hand for a number of targets that were placed on the left, and on the right side of the patient’s body (The Fluff Test: Cocchini et al., 2001). In Baas et al.'s (2011) study, the patients that showed asymmetries on the Fluff Test judged poorly both the laterality of left hands and of left-handed object pictures (i.e., motorcycle’s rear-view mirrors). The authors suggested that the left visual misjudgement reflects a general alteration of the UN patient’s contralesional space that encompasses the body and the extrapersonal space representation.

An alternative explanation of the left visual misjudgement is that UN patients have difficulties in integrating the spatial codes of the stimulus with the spatial codes of the to-be-produced response. The UN behavioural asymmetries may be determined by difficulties in producing left-lateralized responses when these are called upon discriminable stimuli presented in the peripersonal space. Indeed UN can manifest also as neglect for the location of responses (Làdavas et al., 1994). In this study the task consisted in responding to the number “1” and to the number “2” that could be displayed either in the left visual space or in the right visual space. Patients responded using the ipsilesional hand with either a left (index finger) or a right (middle finger) button press. The same task was performed with the response device rotated by 180°, so that the index and the middle finger would operate while located on the right and on the left egocentric space respectively. Given the high number of omissions on the left space, only data collected on the right visual space were analyzed. In both standard and reversed condition of response, UN patients were slower to respond with left responses, thus independently from the anatomical position of the responding effectors. When stimuli were presented either to the upper or to the lower visual space, UN patients were slower for left responses than right responses, even if the response device was rotated to invert the spatial correspondence between the stimuli and the anatomical location of the responding effectors. Behrmann et al. (1995) furthermore demonstrated that the functional association between spatial attention orientation and the integration of stimulus and response codes is altered in UN. They found that UN patients' performance in an action cuing task was slower when a contralesional (left) response was invalidly cued by an arrow pointing to the ipsilesional side (to the right). In addition, UN patients were slower at detecting invalidly cued (to the right) contralesional (left) stimuli when responses were made centrally with no left-right code of responses. This study clearly showed that the UN patients that have problems in processing left-sided stimuli experience also difficulties in performing actions on the left space. Therefore, the UN impairment in automatically orienting attention to the contralesional hemispace is accompanied by neglect for the contralesional space of response.

Other motor deficits associated with UN should be distinguished from neglect of response space. It has been shown that patients with UN may exhibit "directional hypokinesia" (Heilman et al. 1985) and "directional bradykinesia" (Mattingley et al. 1992). Directional hypokinesia is a difficulty in initiating movements from the ipsilesional to the contralestional side, while directional bradykinesia is characterized by a slowing in the time of execution of movements towards the contralesional space. These motor impairments are also manifested in eye-scanning and saccades towards the contralesional hemispace (Ishiai, 2006; Girotti et al., 1983).

Other studies have investigated the possibility that problems in stimulus-response integration might underlie performance of UN patients in tasks designed to tap on representational abilities. For example, in the study by Bartolomeo et al. (2005), a group of French patients were asked to press one of two adjacent left-right response keys coherently with the geographical position of a French city (i.e., on the right or on the left of Paris), whose name was auditorily presented. In order to do so, patients were induced to produce and explore a mental image of the map of France. As a control task patients pressed the left or the right key to “left” and “right” words. Only two out of seven UN patients demonstrated asymmetries in the representational task that could not be predicted by their asymmetries on the control task. In a subsequent study (Bourlon et al., 2008), the control task consisted in pressing the left or the right key according to whether a red marker appeared on the left or on the right side of Paris, as displayed on an empty map of France. Again, the impact of response bias was significant, with only one UN patient out of sixteen that performed with asymmetries on the representational task only. Moreover, when the representational task was performed with vocal responses one UN patient out of nineteen performed less accurately for left-sided than right-sided stimuli (Bourlon et al., 2011). Nevertheless, the use of the vocal response modality, as also in the study by Bass et al. (2012), does not exclude that the reported responses' asymmetries are influenced by deficits of stimulus-response integration. Indeed stimulus-response compatibility effects are consistently shown in the vocal response modality with location words such as "left" and "right" (Proctor and Vu, 2002; Wühr, 2006).

This evidence proves that UN interferes with response selection between the left and right hemispace while integrating visual information with the production of spatially organized responses. Thus, the interpretation of UN patients' behaviour on representational abilities may be problematic when measures are taken by asking patients to produce spatially coded responses. Indeed, the left visual misjudgement of UN patients with chiral objects (Baas et al., 2011; Coslett, 1998; Reinhart et al., 2012) consists in the production of more erroneous right responses when judging the laterality of left visual stimuli, than erroneous left responses when judging the laterality of right visual stimuli. This asymmetry in accuracy for left and right stimuli may be determined by an impairment of the egocentric reference frame and the resulting loss of stimulus-response coordination. It is therefore of paramount importance to determine the extent to which laterality judgment of chiral objects is influenced by the spatial attentive defect of UN for exploration and coordination of visuo-motor behaviour, as well as by representational space alterations.

In the present study I investigated the representation of stimulus laterality and its cerebral correlates by studying the UN left visual misjudgement together with the patients' spatial frames of reference for perception and imagery. Patients' performance on the hand laterality task was compared with performance on the visual laterality task. In the former task patients decided whether a rotated hand was left or right. In the visual laterality task (see also chapter 3) they were asked to decide on which side (left or right) a red marker placed on the same hand stimuli would be seen if the hand fingers were to point upward. With the visual laterality task I could test the hypothesis that the UN left misjudgement is determined by a failure in selecting spatial responses even when the stimulus does not possess particular representational qualities. If so, then UN patients should be less accurate when judging the laterality of left hands in the hand laterality task, as well as the laterality of left-located markers in the visual laterality task.

In addition, I employed standard tests to assess the patients' egocentric (i.e., cancellation tasks, line bisection) and allocentric frames of reference (i.e., the apple test) during the exploration of peripersonal space. Patients' ability to generate and represent the imaginative contralesional space of single objects (i.e., drawing objects from memory) was also assessed. In this way it was possible to check whether alterations of these perceptual and representational functions contribute to the UN left visual misjudgement.

To further evaluate this hypothesis, stimuli were presented to the left, central, and right visual space. I expected the lateralized presentation of visual stimuli to affect UN patients' performance following egocentric stimulus-response spatial codes. UN patients' performance should be affected by the incompatibility between the irrelevant spatial position of the stimulus in the visual space and the side of motor response.

Therefore, when stimuli were presented to the right visual space, UN patients' asymmetry in accuracy for left stimuli (i.e., more errors for left hands, and left-located markers) and right stimuli (i.e., less errors for right hands, and right-located markers) was expected to worsen compared to when these stimuli were presented to the central space. Stimuli were also presented to the left visual space. Here, UN patients were expected to omit responses more often than in the central and right visual field. Nevertheless, UN patients can elaborate information if cued to stimuli displayed on the contralesional visual space (e.g., Humphreys & Riddoch, 1993; Riddoch & Humphreys, 1983). One possible outcome of presenting stimuli to the left visual space was that the UN's asymmetry for left and right stimuli would not be significant. The absence of the left-right responses asymmetry in the left hemispace should reflect the advantage of responding with a compatible stimulus-response mapping, namely responding left to a stimulus presented in the left hemispace.

Differently from previous studies with UN patients (Baas et al., 2011; Coslett, 1998; Reinhart et al., 2012), hand stimuli were presented rotated in different angular departures as in the classic version of the hand laterality task (Sekiyama, 1982; Parsons, 1987). This manipulation allowed investigation of patients’ performance when stimuli were perceived with a CW rotation, and when they were perceived with a CCW rotation. In this way it was possible to investigate the characteristic mirror-reversal of RTs for the left, and the right hand stimuli (i.e., the MOLA effect). I looked at the interaction between direction of rotation and stimulus laterality to determine the MOLA, and compared patients’ performance on the hand laterality task with the visual laterality task. In the visual laterality task RTs monotonically increase with the angular departure of the stimulus but do not follow the MOLA effect (De Simone et al., 2013).

To summarize, following the stimulus-response integration hypothesis UN patients’ performance on left stimuli should be less accurate than performance on right stimuli when patients perform both the hand laterality task and the visual laterality task in the central visual space. When stimuli were displayed to the patients' right and left peripersonal space, UN patients' performance was expected to be influenced by the compatibility of stimulus' spatial position and the space of motor response (i.e., more errors for incompatible stimulus' spatial position and response's spatial position pairing).

6.1 Methods

6.1.2 Participants

Ten patients with right-hemisphere brain damage and left UN (UN+, six women; mean age 64.7 years, standard error of mean (SEM) 1.5; mean education 9.4 years, SEM 1; mean days from onset 73.7, SEM 16.7), ten patients with right-hemisphere brain damage with no signs of UN (UN-, six men; mean age 65.8, SEM 2.5; mean education 9.7 years, SEM 0.9; mean days from onset 77.3, SEM 14.4), and ten healthy age-matched controls (C, five women; mean age 65, SEM 1.3; mean education 9.2, SEM 0.9) took part in the study. Time from onset did not differ between UN+ and UN- patients, (t (1, 18) = .16 p = n.s.). Age and education of the three groups did not differ (age: F (2, 27) = .95 p = n.s.; education: F (2, 27) = .07 p = n.s.). All participants were right-handed. All patients had good language comprehension and could easily follow the instructions given by the experimenter. Patients were included in the UN+ group if they performed below cut-off either on cancellation tasks, or on the Line bisection test (i.e., egocentric neglect). The results of the neurological examination for the evaluation of visual field deficits together with demographic and clinical data are reported in Table 4. On the Line bisection sub-test the mean per cent deviation score (Schenkenberg et al., 1980) was computed from the bisection point of three bisected lines (cut-off ≥ 11% of rightward deviation). An aggregate score on Cancellation tasks was calculated for the Line crossing, the Letter cancellation, and the Star cancellation sub-tests of the B.I.T. (Wilson et al., 1987). The cut-off for the Cancellation tasks was ≤ 115/130. The Representational drawing score was computed for each of three drawings from memory (i.e., the image of a human body, of a butterfly, and of a clock), with a score of 0 assigned when the patient drew only the details of the left object side, or drew the left side of the object upon the right side of the drawing. The Figure copy score was calculated for each of three line drawings that was correctly copied (i.e., a star, a cube, and a flower) with a score of 0 given when the patient copied only the details of the left object side. The Shape copy score for each of three geometrical shapes copied had a score of 0 assigned in case the shape did not respect the geometrical proprieties of the model. The Figure copy and the Shape copy sub-tests served as control for the Representational drawing sub-test. It was considered as indicative of “allocentric” representational neglect only when left omissions in the Representational drawing were accompanied by good performance on the Figure copy and on the Shape copy sub-tests. For the Apple Test (Bickerton et al., 2011) the number of false alarms to distractors with a gap on the left, and number of false alarms to distractors with a gap on the right (false alarms for gap on the left / false alarms for gap on the right) were computed. This score represents the patient’s asymmetries in perceptual exploration when attention is allocated to the sides of a single stimulus (i.e., an apple) independently of where it is displayed on the page. The Shape detection task from the screening sub-test of the VOSP battery (Warrington & James, 1991) was used to exclude elementary deficits in visual processing. On a total of 20, a score of 1 was assigned for each detected shape.

Three patients in the UN+ group demonstrated allocentric neglect on the apple test (i.e., patients UN+/4, UN+/7, UN+/8). Three UN+ patients showed signs of allocentric

RN on the Representational drawing sub-test (i.e., patients UN+/3, UN+/6, UN+/8). One of them presented signs of allocentric neglect during both perception (the apple test) and imagery (the Representational drawing sub-test) (i.e., patient UN+/8). This patient presented also problems in the Figure copy sub-test. Similarly to patient UN+/8, also patient UN+/3 had problems in the Figure copy sub-test. For this reason it was not possible to attribute RN (i.e., imagery neglect) to these patients (i.e., patients UN+/3, UN+/8). Patient UN+/6 demonstrated allocentric RN on the Representational drawing sub-test, and had also good performance on the Figure copy and Shape copy sub-tests. Importantly, this patient performed the laterality tasks with behavioural asymmetries typical of the previously reported UN left visual misjudgement. However, also patients that did not show allocentric RN (i.e., patients UN+/2, UN+/7, UN+/10) performed the laterality tasks with the same behavioural asymmetries. In particular, results on the laterality tasks were comparable between patient UN+/6 with RN, and patient UN+/7 without RN. In the present study, the best predictor of the asymmetries on laterality judgments was the patients' performance on tests that assessed egocentric neglect, namely the cancellation tasks and the line bisection task.

Group/patient	Age/Sex	Days from onset	Line bisection	Cancellation tasks	Figure copy	Shape copy	Representational drawing	Apple test	Shape detection	Visual field deficit	% errors left stimuli CVS-RVS	% errors right stimuli LVS
UN+/1	63/f	34	25	106/130	2/3	3/3	3/3	0/0	18/20	+	5	17
UN+/2	63/f	141	26	116/130	1/3	0/3	3/3	0/0	20/20	-	18	16
UN+/3	67/f	24	47	54/130	0/3	1/3	1/3	1/1	18/20	+	17	15
UN+/4	55/m	64	38	118/130	3/3	3/3	2/3	32/1	19/20	-	13	15
UN+/5	73/f	166	22	119/130	3/3	3/3	2/3	1/3	19/20	+	6	7
UN+/6	66/m	34	38	95/130	3/3	3/3	0/3	0/0	20/20	-	24	22
UN+/7	62/f	58	18	113/130	3/3	3/3	3/3	42/8	19/20	+	22	22
UN+/8	68/f	136	42	54/130	0/3	3/3	0/3	13/2	18/20	+	19	18
UN+/9	68/m	47	19	126/130	3/3	3/3	2/3	3/4	19/20	-	23	17
UN+/10	62/m	33	42	98/130	3/3	3/3	3/3	0/0	20/20	-	16	18
UN-/1	68/m	78	7	130/130	3/3	1/1	3/3	0/0	20/20	-	7	4
UN-/2	71/m	145	9	119/130	1/3	1/1	3/3	1/0	20/20	-	8	15
UN-/3	72/m	138	8	130/130	3/3	1/1	2/3	0/0	20/20	+	10	10
UN-/4	69/f	64	1	130/130	3/3	1/1	3/3	0/0	n.a.	-	4	5
UN-/5	66/m	25	-2	130/130	3/3	1/1	3/3	0/0	20/20	+	4	2
UN-/6	64/m	39	-3	130/130	3/3	1/1	3/3	0/0	18/20	-	6	6
UN-/7	67/m	84	-2	129/130	3/3	1/1	3/3	0/0	20/20	-	2	0
UN-/8	45/f	37	3	130/130	3/3	1/1	3/3	1/0	20/20	-	11	15
UN-/9	72/m	35	5	130/130	3/3	1/1	3/3	0/0	19/20	-	10	5
UN-/10	64/f	128	6	128/130	3/3	1/1	3/3	1/0	20/20	-	12	9

Table 4. Demographic and clinical data. See section 6.1.2 for description of the neuropsychological tests.
% errors left stimuli CVS-RVS: The percentage of errors for left stimuli presented in the central and in the right visual space in both the hand laterality task and the visual laterality task. % errors right stimuli LVS: The percentage of errors for right stimuli presented in the left visual space in both the hand laterality task and the visual laterality task.

6.1.3 Experimental tasks and analysis

Each patient performed two experimental tasks: The hand laterality task and the visual laterality task. In the former task patients were asked whether a rotated picture of a hand was a left or right hand. In the visual laterality task patients had to decide whether a visual red marker was on the left or on the right side of a rotated hand picture. The laterality of the marker had to be judged as it would be seen if the hand had the fingers pointing upward. No explicit instructions were provided to participants as to which strategy to apply in order to perform the tasks. They were required to respond as accurate and fast as possible. In both tasks stimuli depicted a realistic picture of a hand that was the result of a rotation of two hand views (i.e., hand viewed from the back or from the palm). The location of the red marker could correspond either to the extremity of the stimulus hand's little finger, ring finger, index finger, or thumb. Each stimulus subtended a maximum extension in width that was ~12° of visual angle and was presented in six different angular departures (45º, 90º, 135º, 225º, 270º, 315º). All participants performed a block of the hand laterality task and a block of the visual laterality task. For each group the blocks' order was counterbalanced across participants. Each block consisted of 144 trials during which a fixation cross appeared in correspondence with the center of the monitor followed by the presentation of the visual stimulus that could appear to the left, the right or in the center of the screen. I initialized each trial making sure that the patient was looking at the computer monitor before starting the next trial. In order to obtain a sufficient number of responses from UN patients when stimuli were presented to the left visual space these patients were warned each time a stimulus had been displayed in the left hemispace. The stimulus remained visible on the monitor till a response was recorded. If no response was recorded within 11 seconds from stimulus presentation, a fixation cross appeared and remained visible until the initialization of the next trial. These trials were considered as omissions. Stimuli were presented in a pseudo-randomized order with the same type of stimulus that could not be presented within three consecutive trials. A custom button box consisting of two pads located horizontally next to each other was used to record left and right responses. Patients pressed the right pad for right responses with the middle finger, and the left pad for left responses with the index finger using their dominant, ipsilesional hand. Before each block started, patients performed twenty practice trials.

A first analysis of variance (ANOVA) on the number of omissions with spatial Position (left, LP; right, RP; and central, CP) as within-subjects factors, and Group (UN+/UN-) as between-subject factors returned a significant Position x Group interaction [$F(2, 36) = 3.85$, $p < .05$, $\eta^2 p = .18$]. Despite they were warned when a stimulus was presented in the left visual space, UN+ patients made significantly more omissions in the left space (mean 5.4 ± 2.1 SEM) than in the central (mean 1.2 ± .6 SEM) and in the right space (mean .3 ± .1 SEM, all ps < .05). UN+ patients in the left space made also more omissions than the UN- group (UN- mean omissions LP: 1 ± .8 SEM, CP: .9 ± .5 SEM, RP: .1 ± .1 SEM, all ps < .05).

Patients’ performance was investigated at the group level following the differential diagnosis of UN+ described in the methods section. Different mixed design analysis of variance (ANOVA) were conducted separately for data recorded on the left, central and right hemispace. Each ANOVA was conducted both on RTs and accuracy. For each participant, and each combination of the experimental variables, accuracy was computed as the percentage of errors made on the total number of responses collected excluding omissions. RTs were analyzed excluding responses with RTs < 1000ms, and RTs > 2SD of each participant mean in each task and the omissions. For accuracy data, each ANOVA had Task (hand laterality/visual laterality), Laterality (left/right), View (back/palm), and Orientation (CW/CCW) as within-subjects factors, and Group

(UN+/UN-/C) as between-subjects factor. For RTs data, each ANOVA had Task (hand laterality/visual laterality), Laterality (left/right), and Orientation (CW/CCW) as within-subjects factors, and Group (UN+/UN-/C) as between-subjects factor. Multiple comparisons were carried out using Scheffé's post-hoc test with the level of significance set at .05.

6.2 Results

6.2.1 Central space

6.2.1.1 Accuracy

The main analysis returned the significant main effect of Group [F (2, 27) = 32.66, p < .0001, $\eta^2 p$ = .71], which indicated that overall UN+ patients (UN+ mean errors 13.7% ± 3 SEM) performed less accurately than the group of UN- patients (UN- mean errors 6.7% ± 3.3 SEM), and the group of healthy controls (C mean errors 2.8% ± 1.8 SEM).

The significant interaction of Group and Task [F (2, 27) = 3.52, p < .05, $\eta^2 p$ = .21] showed that the UN+ group was less accurate in the hand laterality task as well as in the visual laterality task compared to the other groups' performance in both tasks (UN+ hand laterality mean errors 14% ± 3 SEM; UN+ visual laterality 13.3% ± 3.1 SEM; UN- hand laterality 6.2% ± 2.3 SEM; UN- visual laterality 7.2% ± 2.9 SEM; C hand laterality 5.5% ± 2.2 SEM; C visual laterality .13% ± .22 SEM; all ps < .05). Moreover, UN- patients made significantly more errors in the visual laterality task than C participants in the same task (p < .05).

The target interaction of Laterality and Group did not reach the significance level [F (2, 27) = 2.6, p = .09]. There was however a tendency (see Figure 42) for the UN+ patients to make more errors with left stimuli than right stimuli (UN+ left stimuli mean errors 16% ± 3.2 SEM; UN+ right stimuli 11.3% ± 2.7 SEM). The other participants did not show such a tendency (UN- left stimuli 6.4% ± 2.4 SEM; UN- right stimuli 7% ± 2.9 SEM; C left stimuli 3.2% ± 1.8 SEM; C right stimuli 2.5% ± 1.7 SEM).

6.2.1.2 Response times

The ANOVA on RTs returned the significant main effect of Task [F (1, 27) = 10.49, p < .005, η^2p = .28] with slower RTs in the hand laterality task than in the visual laterality task (hand laterality 2881ms ± 170 SEM; visual laterality 2405ms ± 254 SEM). The main effect of Group [F (2, 27) = 12.41, p < .0005, η^2p = .48], and the interaction of Group and Task [F (2, 27) = 6.45, p < .05, η^2p = .32] were significant. Overall, the UN+ group was slower than the C group and the UN- group, with the latter being also slower than the C group (UN+ 3459ms ± 407 SEM; UN- 2709ms ± 299 SEM; C 1762 ± 196 SEM; all ps < .05). Moreover, the UN+ patients were slower in the visual laterality task compared to the UN- patients in the visual laterality task and to the C participants in both tasks (UN+ visual laterality 3593ms ± 485 SEM; UN- visual laterality 2266ms ± 289 SEM; C hand laterality 2168ms ± 179 SEM; C visual laterality 1355ms ± 289 SEM; all ps < .05). UN- patients were slower in the hand laterality task compared to the visual laterality task, as well as compared to the performance of the C group in the visual laterality task (UN- hand laterality 3152ms ± 239 SEM; both ps < .05). Finally, the UN+ group performed the hand laterality task slower than the C group in the visual laterality task (UN+ hand laterality 3323ms ± 311 SEM; p < .005).

The interactions of Laterality and Orientation [F (1, 27) = 9, p < .05, η^2p = .25], and of Task, Laterality, and Orientation [F (1, 27) = 12.66, p < .005, η^2p = .32] were also significant. These effects were accounted for by the MOLA effect: In the hand laterality task, RTs were faster for right hand stimuli with CCW orientation than right hand stimuli in CW orientation, and were faster for right stimuli with CCW orientation than left hand stimuli with CCW orientation (right hand CCW 2549ms ± 165 SEM; right hand CW 3087ms ± 193 SEM; left hand CCW 3085ms ± 157 SEM; left hand CW 2804ms ± 151 SEM; both ps < .05). Finally, the right hand stimuli with CW orientation and the left hand stimuli with CCW orientation were judged slower than all other stimuli of the visual laterality task (left-sided marker CW 2498ms ± 274 SEM; left-sided CCW 2390ms ± 249 SEM; right-sided CW 2364ms ± 254 SEM; right-sided CCW 2367ms ± 250 SEM; all ps < .05).

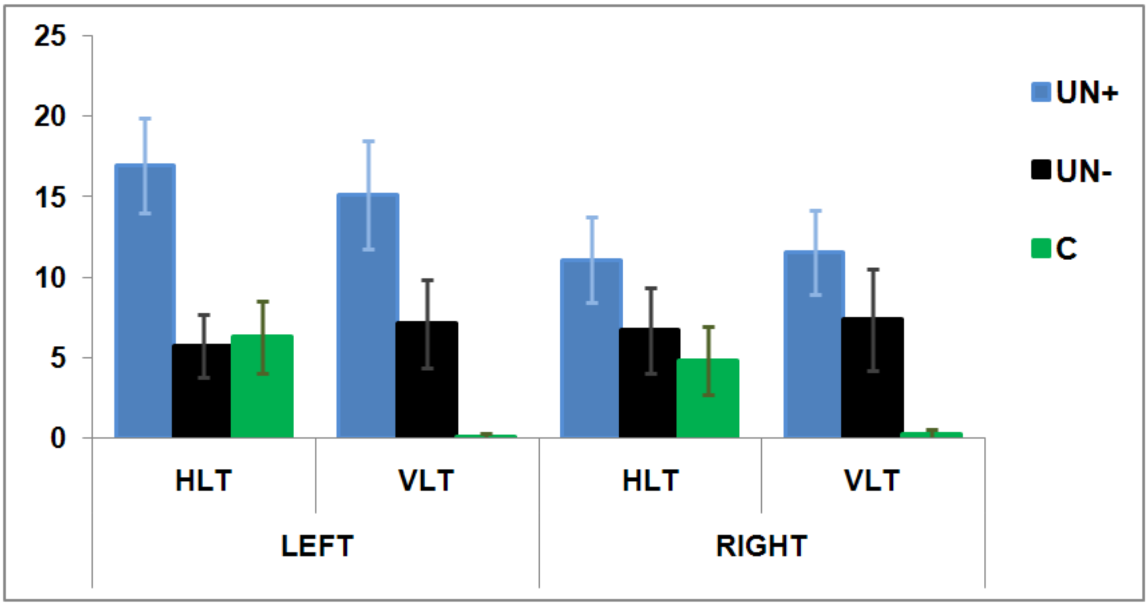

Figure 42. Mean percentage of errors of the three groups (UN+, UN-, C) for right and left stimuli (LEFT-RIGHT) in the hand laterality task and in the visual laterality task (HLT-VLT). Central space data. Error bars depict the standard error of the mean.

6.2.2 Right space

6.2.2.1 Accuracy

The ANOVA on accuracy data relative to the right peripersonal space returned a significant main effect of Group [F (2, 27) = 18.8, p < .0001, η^2p = .58]. The UN+ group made significantly more errors than the C group, and the UN- group, which in turn made more errors than the C group (UN+ mean errors 13.88% ± 3.1 SEM; UN- 7.55% ± 3.8

SEM; C 2.9% ± 2 SEM; ps < .05). The significant main effect of Laterality [F (1, 27) = 5.9, p < .05, η^2p = .18] indicated that the left responses were associated with more errors than the right responses (left responses mean errors 9.13% ± 2.1 SEM; right responses 7.1% ± 1.78 SEM).

The interaction of Group and Laterality was significant [F (2, 27) = 4.89, p < .05, η^2p = .26]. Coherently with the experimental hypotheses, in the right peripersonal space the UN+ group made more errors with left stimuli than right stimuli (UN+ left stimuli mean errors 16.71% ± 3.95 SEM; UN+ right stimuli 11% ± 3.45 SEM; p < .05). The UN+ group made more errors with left stimuli (see Figure 43) also compared to the other groups' performances with both left and right stimuli (UN- left stimuli mean error 8.12% ± 3.1 SEM; UN- right stimuli mean error 7% ± 3.1 SEM; C left stimuli 2.55% ± 2.1 SEM; C right stimuli 3.16% ± 2 SEM; all ps < .05). Moreover, the UN+ patients made significantly more errors with right stimuli than the C group with left and right stimuli (ps < .05).

The significant interaction of Task and Group [F (2, 27) = 3.85, p < .05, η^2p = .22] revealed that the UN+ group made more errors in the hand laterality task compared to the UN- in the same task, as well as compared to the C group in the hand laterality task and in the visual laterality task (UN+ hand laterality mean errors 15.5% ± 4.1 SEM; UN- hand laterality 6.35% ± 2.91 SEM; C hand laterality 5.62% ± 2.57 SEM; C visual laterality .08% ± .14 SEM; all ps < .05). Furthermore, both the UN+ and the UN- group made more errors in the visual laterality task compared to the C group in the same task (UN+ visual laterality mean errors 12.23% ± 3.4 SEM; UN- visual laterality 8.75% ± 3.24 SEM; both ps < .05).

The interaction of Laterality and Orientation [F (1, 27) = 9.81, p < .005, η^2p = .27] was significant but the three-way interaction of Task, Laterality, and Orientation did not reach the significance level [F (1, 27) = 3.93, p = .058]. These interactions describe the

MOLA effect on the hand laterality task. There were more errors for left stimuli with CCW orientation (mean errors 10.3% ± 2.4 SEM) than for right stimuli with CCW orientation (mean errors 4.9% ± 1.3 SEM; $p < .05$).

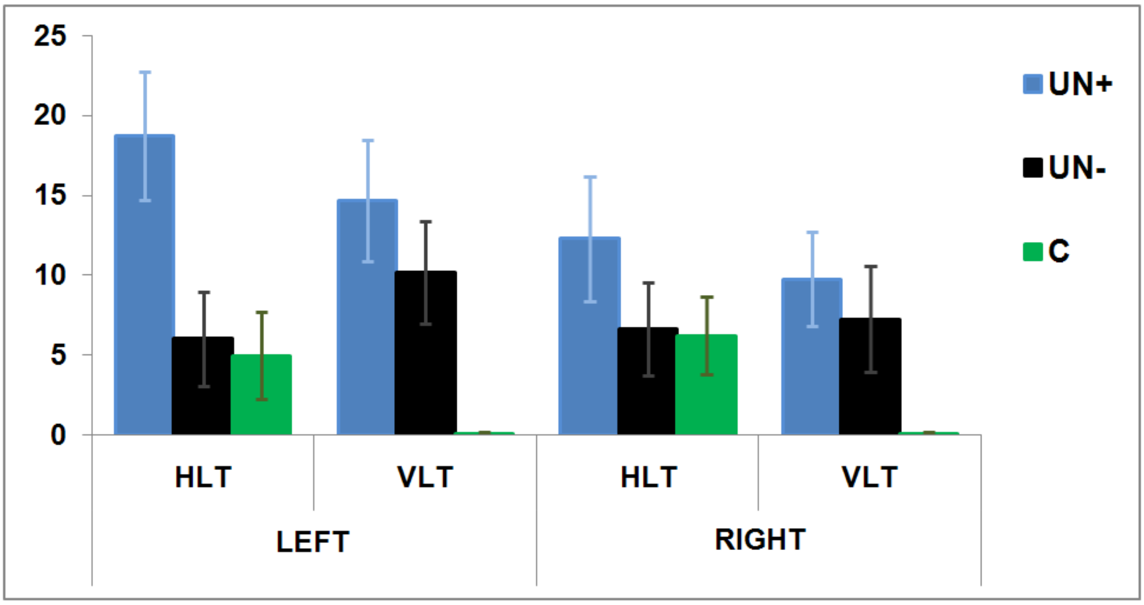

Figure 43. Mean percentage of errors of the three groups (UN+, UN-, C) for right and left stimuli (LEFT-RIGHT) in the hand laterality task and in the visual laterality task (HLT-VLT). Right space data. Error bars depict the standard error of the mean.

6.2.2.2 Response times

The ANOVA on RTs highlighted the significant main effects of Group [$F(2, 27) = 10.7$, $p < .0005$, $\eta^2p = .44$], Task [$F(1, 27) = 17.46$, $p < .0005$, $\eta^2p = .39$], and Laterality [$F(1, 27) = 7.28$, $p < .05$, $\eta^2p = .21$]. The former effect revealed that the UN+ and the UN- groups were slower than the C group (UN+ 3330ms ± 380 SEM; UN- 2784ms ± 301 SEM; C 1868 ± 212 SEM; both ps < .05). The main effect of Task indicated faster RTs in the visual laterality task than in the hand laterality task (hand laterality 2934ms ± 171 SEM; visual laterality 2387ms ± 227 SEM), while the main effect of Laterality reported faster RTs for right responses than left responses (left responses 2734ms ± 217 SEM; right responses 2586ms ± 196 SEM).

There was a significant interaction of Task and Group [F (2, 27) = 8.24, p < .005, η^2p = .38] which indicated that the UN- group performed the hand laterality task slower than the visual laterality task (UN- hand laterality 3284ms ± 241SEM; UN- visual laterality 2285ms ± 273 SEM; p < .05). Furthermore, the UN+ group was slower in the hand laterality task and in the visual laterality task compared to the C group in the hand laterality task and in the visual laterality task respectively (UN+ hand laterality 3230ms ± 320 SEM; UN+ visual laterality 3429ms ± 433 SEM; C hand laterality 2289ms ± 209 SEM; C visual laterality 1448ms ± 105 SEM; both ps < 005).

Finally, the significant interactions of Task and Orientation [F (1, 27) = 4.8, p < .05, η^2p = .15], of Laterality and Orientation [F (1, 27) = 11.11, p < .005, η^2p = .29], and of Task, Laterality and Orientation [F (1, 27) = 27.9, p < .0001, η^2p = .51] were consistent with the MOLA effect. Indeed, only in the hand laterality task, right hand stimuli with CCW orientation were judged faster than right hand stimuli with CW orientation, and right hand stimuli with CCW orientation were judged faster than left stimuli with CCW orientation (right hand CCW 2505ms ± 139 SEM; right hand CW 3141ms ± 144 SEM; left hand CCW 3265ms ± 199 SEM; both ps < .05). Moreover, the right hand with CW orientation and the left hand with CCW orientation were judged slower than any other type of stimulus in the visual laterality task (left-sided marker CW 2210ms ± 235 SEM; left-sided CCW 22491ms ± 232 SEM; right-sided CW 2439ms ± 189 SEM; right-sided CCW 2408ms ± 259 SEM; all ps < .005).

6.2.3 Left Space

6.2.3.1 Accuracy

The significant main effect of Group [F (2, 27) = 25.99, p < .0001, $\eta^2 p = .66$] showed that the UN+ group was slower than the UN- group, which in turn was slower than the C group (UN+ mean errors 15.15% ± 2.8 SEM; UN- 7.22% ± 3.9 SEM; C 2.7% ± 2 SEM; both ps < .005).

The main effect of Laterality [F (1, 27) = 9.45, p < .005, $\eta^2 p = .26$] was significant with more errors for right than left responses (right responses mean errors 9.34% ± 2.16 SEM; left responses 7.35% ± 1.77 SEM). The interaction of Group and Laterality (see Figure 44) that was targeted by the experimental hypotheses was also significant [F (2, 27) = 6.21, p < .05, $\eta^2 p = .31$]. Surprisingly, on the left visual space the UN+ group made significantly more errors with right responses than left responses (UN+ left responses mean errors 12.55% ± 3.63 SEM; UN+ right responses 17.7% ± 4 SEM; p < .05). The UN+ participants ' performance with right responses was also less accurate than the other groups' performance on both left and right responses (UN- left responses mean errors 7.21 ± 2.7 SEM; UN- right responses 7.23% ± 2.9 SEM; C left responses 2.29% ± 1.6 SEM; C right responses 3% ± 2.41 SEM; all ps < .0005). Furthermore, the UN+ patients' performance with right responses was more error prone than the C participants' performance on both left and right responses (both ps < .0001). Therefore, on the left hemispace not only UN+ patients did not show the left visual misjudgement but the asymmetry of lateral responses was reversed relative to the central and right hemispace presentation. Indeed on the left hemispace UN+ patients made more errors for right stimuli than left stimuli.

There was a significant interaction between Task and Laterality [F (1, 27) = 8, p < .05, $\eta^2 p = .23$] with right responses in the hand laterality task being associated with more errors than left responses in the same task and also with left and right responses in the visual laterality task (hand laterality left responses mean errors 7.34% ± 1.74 SEM; hand laterality right responses 11.39% ± 2.23 SEM; visual laterality left responses

7.37% ± 1.8 SEM; visual laterality right responses 7.3% ± 2 SEM; all ps < .05). Finally, the significant interaction of Task, Laterality, and Orientation [F (1, 27) = 4.56, p < .05, η^2p = .14] showed that in the hand laterality task there were more errors for right hand stimuli with CW orientation compared to left hand stimuli CW orientation, as well as compared to right-sided markers in the visual laterality task with CW orientation (right hand stimuli in CW mean errors 13.38% ± 2.4 SEM; left hand stimuli in CW 6.64% ± 1.7 SEM; right-sided markers in CW 6.5% ± 1.9 SEM; both ps < .05).

6.2.3.2 Response times

The ANOVA on RTs on the left peripersonal space returned the main effect of Group [F (2, 27) = 16.6, p < .0001, η^2p = .55] with the UN+ group and the UN- group performing slower than the C group (UN+ 3557ms ± 373 SEM; UN- 2826ms ± 315 SEM; C 1828ms ± 205 SEM; both ps < .05). The main effect of Task [F (1, 27) = 18, p < .0005, η^2p = .40] with slower RTs in the hand laterality task than in the visual laterality task (hand laterality 3012ms ± 181 SEM; visual laterality 2461ms ± 240 SEM) was significant. The interaction of Group and Task [F (2, 27) = 12.6, p < .0005, η^2p = .48] was also significant. This interaction showed that the UN+ group in the visual laterality task was slower compared to the UN- group in the same task, as well as compared to the C group in both tasks (UN+ visual laterality 3732ms ± 408 SEM; UN- visual laterality 2248ms ± 261 SEM; C hand laterality 2252ms ± 199 SEM; C visual laterality 1403ms ± 93 SEM; all ps < .05). The UN- patients were slower in the hand laterality task compared to the visual laterality task, as well as compared to the C participants in the visual laterality task (UN- hand laterality 3403ms ± 253 SEM; both ps < .005). The UN+ patients were slower in the hand laterality task than C participants in the visual laterality task (UN+ 3381 ± 330 SEM; p < .0005).

The significant interaction of Task, Laterality and Orientation [F (1, 27) = 15, $p < .001$, $\eta^2p = .36$] was accounted for by the MOLA. Post-hoc comparisons showed that only in the hand laterality task right hand stimuli with CW orientation were judged slower than all stimuli in the visual laterality task (right hand in CW 3308ms ± 192 SEM; left-sided markers in CW 2559ms ± 262 SEM; left-sided markers in CCW 2350 ± 227 SEM; right-sided markers in CW 2355ms ± 226 SEM; right-sided markers in CCW 2582ms ± 252 SEM; all ps < .05). Furthermore, left hand stimuli in CCW were judged slower compared to right-sided markers in CW, as well as compared to left-sided markers in CCW (left hand stimuli in CCW 3105ms ± 185 SEM; both ps < .05).

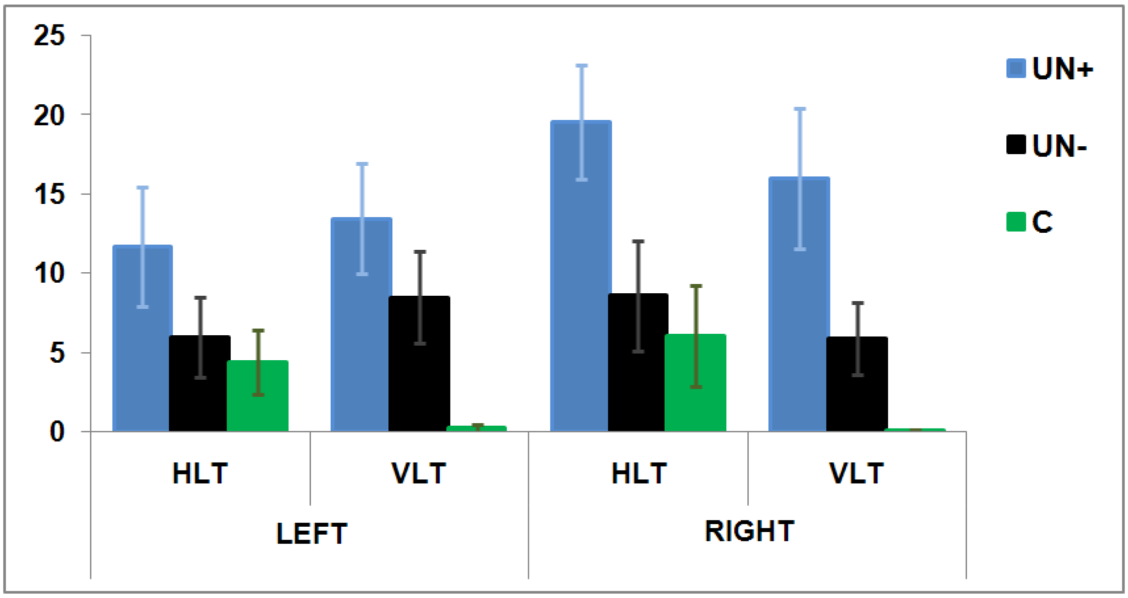

Figure 44. Mean percentage of errors of the three groups (UN+, UN-, C) for right and left stimuli (LEFT-RIGHT) in the hand laterality task and in the visual laterality task (HLT-VLT). Left space data. Error bars depict the standard error of the mean.

6.3 Lesion reconstruction and analysis

Neuroradiological examinations were available for all patients. They all had brain damage of vascular aetiology. The location of each patient lesion was defined by an expert neuroradiologist using the MRIcron software (http://www.mccauslandcenter.sc.edu/mricro/mricron). The normalization of the T1 MRI images and CT scans was done using the “Clinical Tool box” (http://www.mccauslandcenter.sc.edu/CRNL/clinical-toolbox) for SPM8 (www.fil.ion.ucl.ac.uk/spm) (Rorden et al., 2012). The resulting volumes of interest (VOIs) were plotted on the T1-weighted template MRI scan from the Montreal Neurological Institute – MNI. Figure 45 shows the statistical maps given by the overlap of brain regions damaged in the two groups of patients [Lesion volume (cm^3): UN+ 94.3 ± 18.6, UN- 95.1 ± 17.2; Center of mass (MNI x/y/z): UN+: 133/110/88, UN-: 133/103/81]. From the lesion overlaps of the UN+ patients the lesion overlaps of the UN- patients were subtracted in order to highlight the brain regions most frequently associated with UN. Figure 45 (UN+>UN-) shows the regions with at least 40% greater incidence of damage in the UN+ group. The displayed regions correspond to the inferior parietal lobule, including the supramarginal gyrus and the angular gyrus, as well as the basal ganglia. The relevance of damage of these brain regions in determining UN is confirmed by previous reports that converged on these same regions using more numerous groups of patients (e.g., Karnath et al., 2002, 2004; Mort et al., 2003; Vallar & Perani, 1986).

Voxel-based lesion symptom mapping (VLSM, Bates et al., 2003) was used to characterize the neural correlates of the behavioural asymmetries on laterality judgments on the central and right hemispace, and separately for data collected on the left hemispace. VLSM allows investigation of the voxel-by-voxel statistical dependence between patients’ behaviour and their brain damage. In the first analysis, the proportion of the number of correct responses for left stimuli presented in the central and right hemispace was used as continuous behavioural measure of UN+ and UN- patients’ performance. In the second analysis the proportion of the number of correct responses for right stimuli presented in the left hemispace was entered as behavioural measure of patients' performance. Only voxels damaged in at least 10 patients were tested. The nonparametric Brunner-Munzel test was used to carry out comparisons on a voxel-by-voxel basis. The results showed that for both the analysis on the central and right hemispace (coordinates, 29, -12, 14), and the analysis on the left hemispace (coordinates, 28, -6, 15) damage to the right putamen was the best predictor of the behavioural asymmetry on the laterality judgments.

6.4 Discussion

The present study sought to investigate the hypothesis that UN can be associated with neglect of the space of response, and that this impairment can make UN patients appear as having representational deficits in the identification of left-handed objects. My hypothesis was that the previously reported UN left visual misjudgement is due to disturbed integration of visual information with the spatial codes of the response, rather than being an impairment of representational abilities. I took advantage of a visual laterality task employed elsewhere (Tomasino et al., 2011) and showed that UN patients frequently fail to translate stimuli into spatially organized responses even when the task does not rely on representational functions. In the visual laterality task the left-right response identified the location of a red marker in stimulus-centerd coordinates and did not involve the identification of a stimulus trough the access to stored visual representations. The results showed that for UN+ patients there were no differences in the responses' asymmetry between the hand laterality task and the visual laterality task. The UN+ performance for left and right stimuli followed the same pattern of errors in both tasks. In this respect the present data demonstrated that the UN left visual misjudgement should not necessarily be considered a disturbance of body representation because it can emerge in a task where there are no representational attributes to be judged.

By presenting the stimuli also to the patients' left and right visual space it was possible to check if the egocentric configuration of stimuli and responses influenced the pattern of behavioural asymmetries on the laterality judgement tasks. The right-space presentation was expected to increase the asymmetry between left and right responses with increasing errors for left stimuli than right stimuli. On the other hand, if the sensorimotor integration hypothesis is effective the left-space presentation should have made left responses easier to be selected than right responses. Thus, the compatibility between the stimulus position in the left hemispace and the left side of the response should have attenuated the asymmetrical difference between left and right response errors.

All the prediction made by the sensorimotor integration hypothesis were confirmed. In the case of stimuli presented to the central space, there was a clear tendency towards significance with more errors made by the UN+ group when judging the laterality of left stimuli than right stimuli. However, as in the study by Reinhart et al. (2012), the interaction between Group and Laterality was close but statistically significant. When stimuli were presented to the right space the UN+ group made more errors when judging left stimuli than right stimuli. As predicted, the irrelevant right-spatial position of the stimulus influenced the asymmetry of responses increasing errors for left stimuli. This pattern of results can be interpreted as reflecting the tendency of UN+ patients to respond erroneously with a right key press when the stimulus is instead a left one (i.e., neglect for the space of response). However, when stimuli were presented to the left visual space the asymmetry of responses was inverted, with more errors for right stimuli than left stimuli.

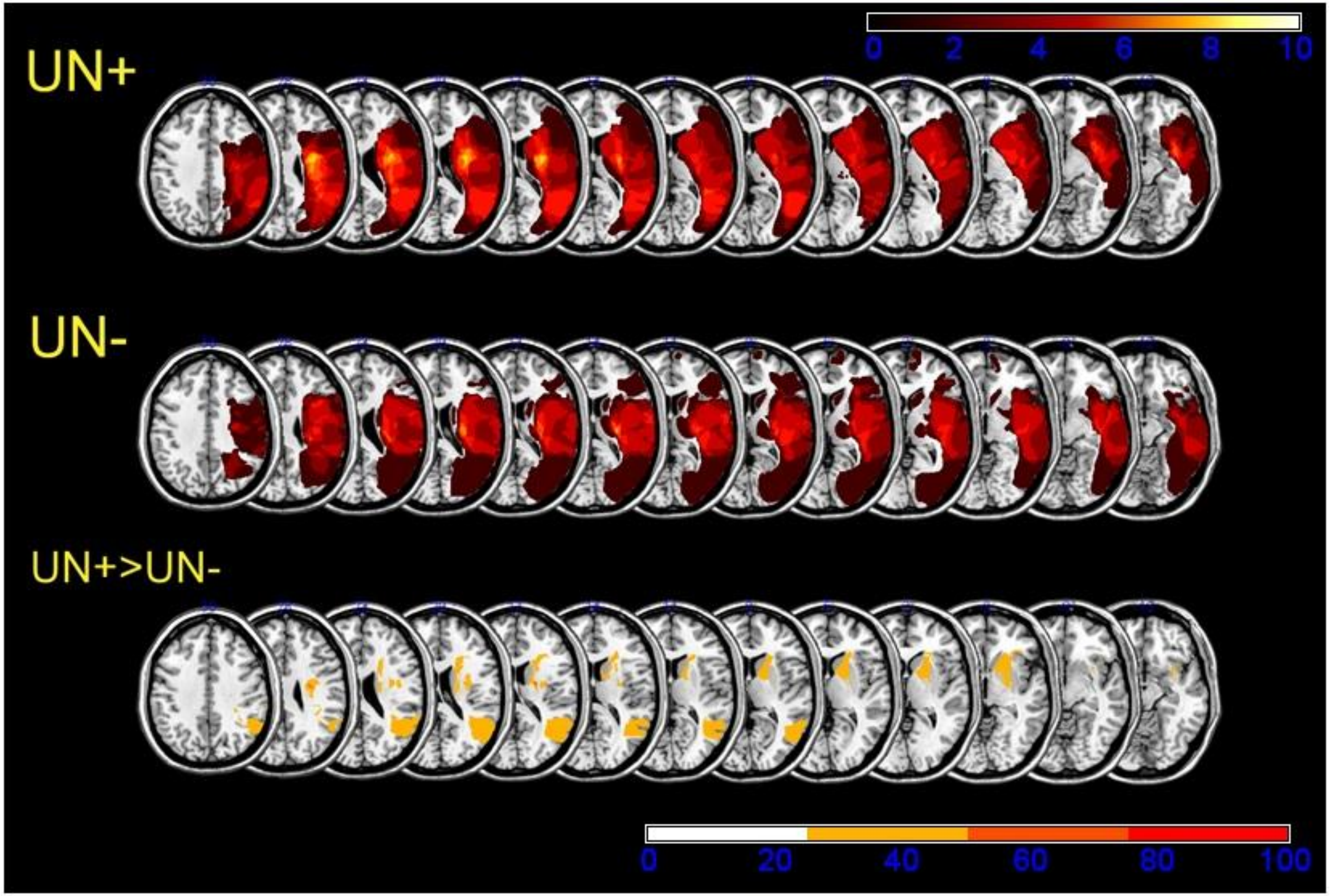

Figure 45. Axial brain sections of the MNI template displayed in descending order. (UN+): Lesion overlap of the UN+ group. (UN-): Lesion overlap of the UN- group. The color scale indicates the number of overlapping regions. (UN+>UN-): Subtraction plot displaying regions associated with at least 40% greater prevalence in the UN+ group. The color scale indicates the relative incidence of damaged regions in the UN+ group.

Therefore, not only the responses' asymmetry changed favouring the spatial compatible mapping on the left hemispace as predicted by the experimental hypothesis, but the pattern of errors for left and right stimuli changed direction entirely. This result demonstrates that the underlying cognitive deficit of the UN left visual misjudgement is related to a failure in the integration of the spatial codes of the stimulus and of the response. This effect strongly suggests that UN is accompanied by a failure in the integration of visual information with the spatial codes of the response.

Furthermore, patients suffering from left UN+, and right brain damaged patients without UN- were assessed for alterations of spatial frames of reference during visual perception, and for deficits in representing mental images of single objects (i.e., allocentric representational frame). The results of the clinical test that assessed the presence of "allocentric neglect" during visual perception (i.e., the apple test) and imagery (i.e., the Representational drawing) could not predict the patients' performance on the hand laterality task. This was expected because, as previously noticed by Coslett (1998), an object-centerd "allocentric neglect" would have implied difficulties in recognizing hands regardless of their laterality. In that case, allocation of visual attention only to the right side of the hand stimulus should have prompted UN+ patients to perform poorly also when judging right hands viewed from the back because, as for left hands seen from the palm, the thumb might not be consciously perceived.

It was suggested that a distortion of the body schema (Coslett, 1998, Reinhart et al., 2012), or of the general representational space (Baas et al., 2011) creates the basis of the UN left misjudgement. In the present study, performance on the laterality tasks was comparable between the patient that showed signs of RN (i.e., UN+/6) and patients that did not (e.g., UN+/7). Thus, the asymmetries on laterality judgments could emerge independently of whether the patient failed to mentally represent the left side of a visually memorized object, thus independently of the object visuo-spatial coordinates updated in allocentric frames. This result strengthens the interpretation of disturbed stimulus-response integration in UN and challenges the notion that the left visual misjudgement would be determined by alteration of the representational medium. Nevertheless, other considerations about RN should be made. Different accounts of RN have been proposed. RN was firstly interpreted as the result of “a representational map reduced to one half” (Bisiach et al., 1981), with degraded generation of the left side of mental representations (Bisiach et al., 1981; Bisiach & Luzzatti, 1978). Coherently with this view, it has been proposed that RN derives from spatial working memory deficits (e.g., Della Sala et al., 2004; Denis et al., 2002). Other views of RN consider it due to a bias in the exploration of mental images (Grossi et al., 1989), or also to a disengagement deficit from the ipsilesional representational space (Loetscher & Brugger, 2007). More recently, RN has been linked to problems related to the patients' spatial re-orientation in representational space because RN patients fail to use cognitive maps of the environment for navigation (Guariglia et al., 2005; Palermo et al., 2010). These findings have demonstrated the distinction between the so-called topological and non-topological types of mental images. Topological mental images are mental representations that are built upon an egocentric spatial frame of reference, and serves navigation skills. Non-topological mental images reflect an allocentric spatial frame of reference in representational space, and are linked to the mental representation of objects. In a study including a large series of right brain damaged patients, Guariglia et al. (2013) have demonstrated that these two types of mental images can be selectively affected with RN. Patients suffering from RN could either show asymmetry scores on the Familiar Square Description Test (Bisiach & Luzzatti, 1978), or on the O' Clock test (Grossi et al., 1989), indicating dissociations in representational space for topological and non-topological mental images respectively. Around a fifth of the RN patients presented asymmetries on both tests. The study also found that the prevalence of RN for topological images was significantly higher than RN for non-topological images. For these reasons, it is still open the possibility that our patients suffered from RN of the egocentric representational space as we only tested RN for non-topological (allocentric) mental images. Neither were they tested for the presence of PN. In order to demonstrate that the UN left-visual misjudgement corresponds to a malfunctioning of the patients' representational space it is necessary to show that this phenomenon is present when stimuli do not call directly upon a left-right response. However, employing vocal RTs (e.g., Baas et al., 2012; Bourlon et al., 2011) for responses that are coded spatially will not solve the problem, because stimulus-response compatibility effects work also in this response modality (Proctor and Vu, 2002; Wühr, 2006).

By employing plane rotated stimuli, the ability of UN+ patients to perform mental rotation when the to-be judged stimulus was presented rotated with a CW or with a CCW rotation was tested. The results indicate that UN+ patients’ performance was comparable for judgments of stimuli presented with a CW rotation and with a CCW rotation. Moreover, the present results show also that the MOLA effect is present when judging hand laterality and that there was no specific difficulty for UN+ patients in judging medially-oriented or laterally-oriented stimuli. The visual laterality task instead did not produce such an interaction between stimulus laterality and its orientation, a result that replicates my recent work (De Simone et al., 2013).

The present study is in line with the idea that sensorimotor integration in stimulus-response compatibility tasks can be hardly differentiated from spatial attention. Even in basic stimulus-response compatibility tasks like the Simon-task, it is the covert shift of saccades that determines the direction of the effect on spatial compatible and incompatible trials (Nicoletti & Umiltà, 1994). Indeed spatial attention can be analyzed at the level of processing of the brain’s sensorimotor areas. There is ample evidence that the neuro-cognitive bases of spatial attention, saccades, and sensorimotor integration overlap extensively. Overt saccades and covert shift of spatial attention activates the same network of premotor and parietal regions (e.g., Corbetta, 1998; Corbetta et al., 1998). At the same time, basic sensorimotor coupling in the context of stimulus-response compatibility correlates with increased activity in the very same fronto-parietal regions (e.g., Iacoboni et al., 1996). Furthermore, the well-known attentional phenomenon of inhibition of return can be instantiated by the overt execution of a saccade (Reuter-Lorenz & Rosenquist, 1996). This attentional inhibition for previously attended locations is paralleled by the dynamics of ocular movement's execution, with directional saccades being slower if a previously executed saccade is performed in the same direction (Juttner & Wolf, 1994). Coherently, it has been shown that lesion of the parietal cortex (Posner et al., 1984), usually associated with UN (Morrow & Ratcliff, 1998), interferes with disengagement of spatial attention from previously attended locations.

Attentional processing can be related to goal-directed endogenous orienting or to the automatic, exogenous orienting of attention. UN patients have deficits primarily in orienting spontaneously to the stimulus and are relatively preserved in attending voluntarily towards the portion of space contralateral to the cerebral damage (for a review see Bartolomeo & Chokron, 2002). Thus, UN patients appear to be constantly attracted to stimuli present on the same side of space of the brain damage. A novel finding of the present study is that when the UN patients were warned of stimulus presentation in the left hemispace they showed an opposite pattern of errors for lateral responses. Once the habitual difficult stimulus detection in the contralesional space was overcome, UN patients seemed not to neglect the left-contralateral side of motor's response space but the right-ipsilesional side of response space. I suggest that this behaviour reflects a deficitary re-coding of the stimulus spatial attributes with the response spatial attributes supported by the network of brain regions damaged in the present sample of patients. Previous research suggest that UN should be understood as dysfunction of a distribute cerebral network (Bartolomeo et al., 2007; Corbetta & Shulman, 2011) including the premotor cortex, the parietal lobule, and subcortical structures such as the basal ganglia and the thalamus (Vallar 2001; Karnath et al. 2002).The results of the VLSM on the behavioural asymmetry of responses converged on the right putamen for both the analysis on the central and right visual space, and the analysis on the left visual space. This preliminary evidence points to a functional implication of the putamen in relation to the disturbed selection for action between compatible and incompatible stimulus-response mappings. The present data extends previous findings concerning neglect for the space of response (Làdavas et al., 1994) and the UN's disturbed functional association between spatial attention deployment and the integration of stimulus and response (Behrmann et al., 1995).

I argue that neither a form of body representational disorder, nor of a general representational deficit can fully explain the left visual misjudgement. It is concluded that the attentional deficits of the present UN patients depend on a failure in sensorimotor integration of visual stimuli and spatially organized responses.

7. General discussion

The project described in this thesis set out to define the cognitive and neural correlates of hand laterality visual identification. For almost thirty years the dominant *motor imagery account* (Parsons, 1987; Sekiyama, 1982) has stimulated a significant number of experiments on body parts' laterality identification as a form of implicit motor simulation. Several experiments have adopted the hand laterality task as means to test motor imagery and the related capacity to represent the position of the body in space (i.e., the body schema). Only recently this view has been challenged on both theoretical and empirical grounds. The *multisensory integration account* (Grafton & Viswanathan, 2014; Viswanathan et al., 2013) and the *disembodied account (*Vannuscorps & Caramazza, 2015) have casted profound doubts on the widely accepted notion that perceptual judgment of plane-rotated hands rely on action simulation abilities. The present work was motivated by the need to explain the discrepancies present between the different interpretations put forward by these accounts and the data they have provided. Differently from previous research, the approach I have adopted was not limited to the unique contribution of sensory or motor components. Object's laterality identification was studied in terms of integration of sensory and motor features by manipulating key aspects of the stimulus, the current state of the observer's body, and the relevant task sets.

In experiment 1 I have demonstrated a new spatial compatibility effect in which the orientation of a stimulus in the vertical plane automatically influences the time for left-right responses. This experiment confirms that perception of misoriented objects involves spatial shifts in visual processing that follow the direction towards which the rotated stimulus points in space. This automatic orienting of attention can give rise to effects of spatial compatibility affecting RTs in a systematic fashion. In experiment 1, the orientation of a rotated hand image influenced the time for lateral responses even if orientation was an irrelevant stimulus-dimension. The temporal properties of this simple sensorimotor integration task followed a pattern coherent with the spontaneous deployment and disengagement of attention in the external space. At the short SOA there was facilitation for responses compatible with the direction of stimulus rotation (i.e., a standard compatibility effect), while at the long SOA there was facilitation for the side of response that was spatially opposite to the direction of stimulus rotation (i.e., a reversed compatibility effect). This result suggests that the mirror-reversed configuration of RTs in the hand laterality task is an attentional phenomenon related to the integration of sensory information with the appropriate response.

RTs for hand laterality judgments increase linearly with the degree of stimulus' rotation (e.g., De Simone et al., 2013) but the functions relating the RTs curves for left and right hand stimuli are mirror-reversed (i.e., the MOLA). In this task, upon stimulus presentation, attention moves in the direction of rotation of the hand image towards the hand's fingers, particularly on the thumb. In experiment 2 I have shown that observers rely on the thumb as the most informative feature for making correct identifications of left and right hand images: During hand laterality identification the average fixation durations on the thumb were longer than on the other stimulus' parts. In experiment 1 I have shown that the MOLA can be explained as a stimulus-response compatibility effect triggered by the allocation of attention towards the direction of rotation of the hand stimulus. In the long SOA condition, when the stimulus was rotated in a CW orientation (i.e., to the right) attention was firstly allocated in this direction and then was disengaged from it (i.e., to the left). This attentional modulation favored the selection of faster left responses than right responses. When the stimulus was rotated in a CCW orientation (i.e., to the left) attention was firstly allocated in this direction and then was disengaged from it (i.e., to the right). Therefore there were faster right responses than left responses. However, differently from experiment 1, in the hand laterality task the response is coded explicitly as left or right. Thus, the effect of orientation on lateral responses is much larger in the hand laterality task than in tasks such as the one described in experiment 1. The results of experiment 1 explain also why in the study of Jolicoeur with misoriented objects the RT curve was asymmetrical for left and right facing stimuli (Jolicoeur, 1988). As in the hand laterality task, in Jolicoeur's study (1988) left responses were faster when the object was rotated in CW orientation than in CCW orientation, and right responses were faster when the object was rotated in CCW orientation than in CW orientation. These findings support the notion that the mirror-reversal of RTs does not reflect the integration of information from different sensory modalities or even an improbable illusion of hand movements, as proposed by the multisensory integration account.

Experiment 3 also supports the idea that the MOLA is mainly an attentional phenomenon. In this experiment the stimulus that was judged was not a body part but an object (i.e., the shape of a rear-view mirror). Also with this type of stimulus it was possible to observe both the modulation of RTs as function of the angle of rotation, and the asymmetry of the RTs distribution for left and right stimuli. Moreover, the key aspect that determined the instantiation of the RTs mirror-reversal was not the functional propriety of the object but the specific configuration of two spatial features of the stimulus (i.e., stimulus' laterality and location of the informative feature). For this reason the present work suggests that the MOLA cannot be ascribed to the way the perceptual system process images of bodies and body parts (e.g., Tessari et al., 2010; Vannuscorps & Caramazza, 2015; Vannuscorps et al., 2012). These results explain also why patients with congenital absence of upper limbs can perform the hand laterality task with the same MOLA as healthy individuals (patient A.Z.: Brugger et al., 2000; Funk & Brugger, 2008; patient P.M.: Vannuscorps & Caramazza, 2015; patient D.C.:

Vannuscorps et al., 2012). Altogether, the present work indicates that the available theoretical accounts of hand laterality identification fail to describe the strategy adopted by human observers in performing the hand laterality task. Despite the different approaches, both accounts assume that the MOLA is indicative of the *correct-hand-effect*, an unconscious pairing preceding object identification between the stimulus and the observer's “correct” own hand. This *correct-hand-effect* is an explanatory concept of the RTs mirror-reversal that is common in the *multisensory account,* in the *motor imagery account,* and in the *disembodied account*. A clear demonstration of the inconsistence of this explanation has been given in experiment 3, where the same configuration of RTs was obtained with other types of stimuli than body parts. However, it is important to discuss further how this systematic alteration of the RTs distribution is formed and its significance for visual object identification processes. A key aspect of experiment 3 and 4 is that, even though there was no manual response required and the response did not call upon a left-right selection, it was possible to obtain asymmetric responses between left and right stimuli. This observation indicates that the actual motor response is not necessary to generate the compatibility effect between stimulus laterality and orientation. The mirror-reversal of RTs depends on attentional processing that change following the spatial characteristics of the stimulus, independently of response modality. Coherently, the temporal and spatial fluctuations in the deployment of spatial attention have been classically studied with detection tasks involving a central motor response with no left-right spatial codes (e.g., Posner, 1980; Posner and Cohen, 1984). The presence of compatibility effects when no motor response is executed resemble the stimulus-stimulus congruence effect found in spatial Stroop tasks. In these cases a perceptual event influences RTs because two spatial features of the stimulus are congruent or incongruent. For example it has been shown that discrimination of targets presented in different irrelevant locations is associated with Stroop-like interactions between the left and right hemispace of presentation and the relative left-right position of the stimuli within the stimulated visual hemifield (Lamberts et al., 1992). This is in line with theories of attention composed by multiple frames of reference for egocentric and allocentric spatial processing (e.g., Egly et al., 1994; Vecera & Farah, 1994). Therefore RTs increased with stimulus' orientation because its spatial coordinates were gradually coded in the observer's egocentric spatial frame of reference. This view fits well with the incremental component on RTs found when the angle of rotation of the stimulus points downward (i.e., +120° and -120°), thus when the object-centered coordinates of the shape's visual features are inverted relative to the viewer-centered reference frame. These data indicate that the effect of orientation and the interaction of orientation and shape's type in experiment 3 represent an automatic spatial coding of visual features from allocentric to egocentric coordinates. It has been recently shown that mental rotation involves tracking of single visual features in the picture plane (Xu & Franconeri, 2015), and that spatial attention is implicated in binding of visual features (Corbetta et al., 1995) between retinotopic and spatiotopic locations (Golomb et al., 2014). Thus, spatial attention might play an important role for visual object constancy favoring the binding of stimulus' features with the visual representation of the object stored in egocentric coordinates.

The present results suggest that the RTs mirror-reversal reflects stimulus-response and stimulus-stimulus features bindings. In the light of an information processing view of cognition, the stimulus-response compatibility effects for rotated pictures of hands would be interpreted as related to the response selection stage, thus these effects would emerge from low-level cognitive processing that occurs between stimulus identification and the actual response. For example, in the first study on the hand laterality task (Cooper & Shepard, 1975) it was acknowledged that RTs depended on the decision making process that involved the identification of the stimulus as well as the response selection process. However, stimulus-response bindings are not just the mere selection of the motor response that occurs after stimulus identification. Indeed, it has been shown that stimulus-response bindings can encode information at different levels of abstraction. For example, in priming studies stimulus-response compatibility effects have been found when switching from pictures to written object names (Horner & Henson, 2011), or when switching from object pictures to object sounds (Frings et al., 2013). This suggests that stimulus-response bindings can represent the identity of perceived objects. There is also evidence that stimulus-response bindings underlie priming effects for semantically congruent stimuli (e.g., Waszak et al., 2004). Bindings of stimulus' features is part of the formation of the so called “object file”, a memory structure that integrates all the information relative to an object (e.g., Kahneman & Treisman, 1984). It has been shown that object files are not exclusively perceptual structures but that they are better described as “event files”, including information about actions and response codes as well (Hommel, 1998). This implies that stimuli and responses are coded in the same format (i.e., the common coding principle, e.g., Hommel et al., 2001), and that visual selection arises from the mental architecture that governs also action selection (e.g., Hommel et al., 2001; Schneider & Deubel, 2002).

In experiment 3, the RTs mirror-reversal was present when the laterality of the stimulus and the position of the informative feature described opposite lateralities, namely for glass judgments of H shapes and for plastic judgments of R shapes. However the direction of the orientation effect was inverted between glass view and plastic view judgments. In the glass view judgment of H type shapes RTs were faster for CW orientations when the stimulus was left (with the informative feature on the right), and were faster for CCW orientations when the stimulus was right (with the informative feature on the left). This effect corresponds to the MOLA found with hand shapes: Medial orientations (i.e., left stimulus in CW and right stimulus in CCW) are faster than lateral orientations (i.e., left stimulus in CCW and right stimulus in CW). In the plastic view judgment of R type shapes, RTs were faster for CW orientations when the stimulus was right (with the informative feature on the left), and were faster for CCW orientations when the stimulus was left (with the informative feature on the right). Therefore, for plastic judgments of R shapes the RTs' distribution was mirror-symmetric relative to the RTs' distribution for glass judgments of H shapes: In the former case lateral orientations were faster than medial orientations. The different direction of the interaction between shape, view and orientation in the glass judgment of H shapes, and in the plastic judgment of R shapes indicates that in both cases stimuli were matched against the corresponding “canonical” shape stored in glass view. Indeed, in the glass view judgment of H type shapes there were faster RTs when the stimulus was physically rotated to the right and the corresponding stored shape in glass view had the informative feature on the right (i.e., H type shape 1 in CW orientation), and when the stimulus was physically rotated to the left and the corresponding stored shape in glass view had the informative feature on the left (i.e., H type shape 2 in CCW orientation). Coherently, in the plastic view judgment of R type shapes RTs were faster when the stimulus was physically rotated to the right and the corresponding stored shape in glass view had the informative feature on the right (i.e., R type shape 1 in CW orientation), and when the stimulus was physically rotated to the left and the stored shape in glass view had the informative feature on the left (i.e., R type shape 2 in CCW orientation). Thus, the stimulus was transformed into congruence with the stored shape in frontal view that had the same laterality of the stimulus, taking as reference the position of the informative feature of this “canonical” mental image. Therefore, the inversion of the effect between glass judgments of H shapes and plastic judgments of R shapes reflects the spatial coding of the stimulus in visual imagery. Indeed, the direction of the interaction between shape, view and orientation depended on the relationship between the orientation of the stimulus and the location of the informative feature of the canonical shape stored in frontal view (i.e., in glass view).

The overall longer RTs for plastic judgments than for glass judgments with both types of shapes strongly support the notion that each shape was matched against a canonical visual representation of the stimulus. In mental rotation tasks, two visual stimuli are presented and participants judge if the two objects are the same or if they are different. One object pair is presented misoriented by some degree of rotation (usually in the picture-plane) relative to the other object. In half of the trials the two objects are the same, while in the remaining trials the two objects are mirror-reflections and are therefore different. In this type of task RTs for judgments of different objects' pairs are slower than judgments of same objects' pairs. This result has been consistently obtained with abstract 3D (e.g., Just & Carpenter, 1976; Shepard & Metzler, 1971) or 2D objects (e.g., Cooper, 1975), as well as with alphanumeric characters (e.g., Cooper & Shepard, 1973; Hamm et al., 2004). Hence, the incremental component on RTs observed for plastic judgments in experiment 3, and for palm judgments in experiment 4, suggests that stimulus identification relies on a mental spatial transformation of the image in order to match it with a stored visual representation. This explains why in the hand laterality task RTs for stimuli in palm view are slower than for stimuli in back view (e.g., De Simone et al., 2013), even when the observer's hand posture is in supine position (i.e., the palm up posture; see Figure 3 from Shenton et al., 2004). The long-term visual and somatic association that exists between the vision of the hands from the back with the left hand having the thumb on its right, and with the right hand having the thumb on its left, makes it easier to identify hand images when they are shown from the back. This has also been shown in the study of Ottoboni et al. (2005), in which judgments for a target color presented on hand images were faster with left responses when the target appeared on shape1 (with the thumb on the right) relative to shape2 (with the thumb on the left), and faster with right responses when the target appeared on shape2 relative to shape 1. Critically, the same association of lateral responses with the two different hand shapes was found when the hand images displayed were seen from the palm. Thus, back view hands are easier to be identified because their shapes match directly the more vivid visual representation of the left and of the right hand stored in long-term memory.

In the mental rotation literature the slower RTs for “different” judgments has not been interpreted in a unique way. It has been proposed that on trials with different objects pairs the observer would not only rotate the stimulus in the picture-plane but also in the horizontal plane, that is, the observer would also “flip” the to-be-rotated stimulus on the other, upright stimulus (e.g., Hamm et al., 2004; Nunez-Pena & Aznar-Casanova, 2009). This was also the idea I had expressed in the hypotheses of experiment 3, for which an inversion of the RTs pattern between glass view judgments of H shapes and plastic judgments of R shapes was expected. Cooper and Shepard (1973) proposed that the incremental component of RTs on “different” trials is due to a bias in response selection: The observer would be prepared for “normal” judgments and should thus inhibit this prevalent response when a pair of stimuli has different objects, causing a delay in response execution. A recent fMRI and eye-tracking study (Paschke et al., 2012) found smaller saccade amplitude for mirrored stimuli (i.e., different stimuli), and also less activation of early visual areas compared to normal stimuli (i.e., same stimuli). This finding suggests that the processing of mirrored stimuli would diverge from that of “normal” stimuli already at the perceptual level. In this respect, another relevant finding is that of Gardony et al. (2014). They studied mental rotation and physical rotation of Shepard-Metzler figures (see section 1.1.3) and found very similar results for the mental rotation and the physical rotation task. Moreover, these authors used the physical rotation data (i.e., the real-time angular disparity between the stimuli in each pair) to reveal important aspects of mental rotation. Results showed that participants did not rotate the stimulus to achieve a perfect match with the other stimulus of the pair in either same or different trials. Specifically, on same trials the to-be-rotated stimulus was transformed to a *canonical difference,* while on different trials the to-be-rotated stimulus was transformed to a *distinct view*. The *canonical difference* was defined as “an off-axis rotation that affords an optimized view for perception and comparison of stimuli features” consistent with the preference for off-axis views found in perception research (Palmer et al., 1981). Indeed, on same trials the angular disparity of stimuli for physical rotation data converged, at the time of response, around 49° of angular disparity. On different trials the angular disparity converged around 113° at the time of response, thus to a *distinct view* relative to the other stimulus of the pair. This result indicates that different strategies are adopted on same and different trials in mental rotation tasks, and that these differences may have affected also RTs for plastic and palm view judgments of experiment 3 and 4.

Experiment 4 was another critical test of the *multisensory integration account.* In this experiment participants' hand posture was varied from prone to supine (i.e., the palm-up, palm-down posture conditions) while they performed the view judgment task of Viswanathan et al. (2013) with vocal responses. In Viswanathan et al.' study (2013) the MOLA was present for back view judgments but it was absent for palm view judgments. Given that participants held their hands in a palm-down posture, the emergence of the mirror-reversal exclusively for back view judgments was explained by the binding of the visual hand stimulus with the congruent proprioceptive information of the observer's felt hand in the palm-down posture. In experiment 4 it was shown that with the palm-up posture participants judged stimuli in back view with the same RTs' mirror-reversal that was present in the palm-down posture condition. This result clarified that the congruence between the proprioceptive information of the observer's own hand with the visual hand stimulus is not a necessary condition for the emergence of the MOLA.

There are two aspects of the RTs distribution for palm view stimuli in the palm-up posture condition suggesting that observers exploited the actual position of their hands to perform palm view judgments. Firstly, RTs for palm view stimuli were not markedly slower than for back view stimuli, as can be observed by comparing RTs at 0° of rotation for back and palm view judgments. This is in contrast with the palm-down posture condition where RTs for palm view stimuli were slower than RTs for back view stimuli. Also for the rear-view shapes of experiment 3, plastic view judgments were always slower than glass view judgments. I have discussed how this incremental component of RTs might reflect an additional “flip” of the visual image to compare it with the stable visual representation of the stimulus stored in long-term memory. Therefore, the absence of this incremental component in the palm-up posture condition indicates that the stimulus was compared with the representation of the felt hand, making the additional mental transformation on the horizontal plane unnecessary. Indeed, in the palm-up posture condition the representation of the felt hand and the stimulus differed only relative to the degree of rotation in the vertical plane. Moreover, differently than in the palm-down posture condition there was a mirror-reversal of RTs for palm view stimuli. The emergence of the RTs' mirror-reversal in the palm-up posture condition with palm view stimuli also suggest that it was the allocation of attention towards the position of the observer's "felt thumb" that generated the MOLA. Indeed, differently from the palm-down posture condition and from experiment 3, the effect was significant for stimuli with spatial codes that described the same laterality. Thus, when stimulus laterality (left-right) and the to-be-judged shape (shape1-shape2) were congruent with one of the observer own hand in palm-up posture, this dimensional overlap made the observer shift attention on the felt position of the thumb. It was this attentional shift that created the condition for the emergence of the mirror-reversal, similarly to the attentional modulation given by the contrasting spatial codes of the stimulus in experiment 3. Left stimuli (shape 2) were judged faster when rotated in CW orientation and right stimuli (shape 1) were judged faster when rotated in CCW orientation. Indeed, in the former case RTs were faster because attention moved from the position of the left felt thumb towards the rightward oriented stimulus (i.e., CW orientation), and in the latter case RTs were faster because attention moved from the position of the right felt thumb towards the leftward oriented stimulus (i.e., CCW orientation).

The present work supports the role of spatial attention in mental imagery and object cognition. Indeed, the effects of facilitation on RTs for perceptual judgments of misoriented objects reported here depended mostly on the modulation of spatial attention given by the contrasting spatial codes of the stimulus, or by the dimensional overlap between the stimulus and the position of the observer's hand. How is attention conceived within the framework of the present studies? Attention has been classically studied as an abstract mental function that allows selecting and controlling the relevant information that needs to be processed by the observer. This view considers that attention correlates with the functioning of a dedicated brain network, such as an anterior system for controlling complex cognitive tasks, and a posterior system linked to spatial attention (Posner & Dehaene, 1994). In contrast with an abstract representation of attentional functions, recent functional imaging studies and neurophysiological recordings have demonstrated that spatial attention is associated with activity of premotor regions that are crucial for planning and executing eye movements, such as the frontal eye fields (e.g., Corbetta et al., 1998; Moore & Fallah, 2001; Thompson et al., 2005). Moreover, other studies have shown that attentional modulation of sensory processing correlates with brain activity in a network of premotor, parietal, and sensory regions (e.g., Siegel et al., 2008). These findings support the premotor theory of spatial attention according to which shifts of attention in space are generated together with the programming of covert saccades (Rizzolatti et al., 1987). Therefore selective attention is related to the activation of the same spatial cortical maps used to perform actions (Rizzolatti & Craighero, 1998; Rizzolatti et al., 1994). Within the fronto-parietal circuit for visuo-motor integration two main networks can be distinguished on the basis of the type of space coding they represent. A dorsal network for oculomotor space coding is associated with saccades in far space and with perception of simple visual stimuli. This network is formed by the superior colliculus, the superior parietal lobe, and the dorsal premotor cortex (e.g., Colby & Goldberg, 1992; Rizzolatti et al., 1994). A ventral network for peripersonal and personal space coding is associated with perception of 3D objects, with actions of the hand, and of the arm. This network is formed by the inferior parietal lobe and the ventral premotor cortex (Gentilucci et al., 1983; Rizzolatti et al., 1988; Sakata et al., 1995). Coding of space involves receptive field activity that is gaze-view-dependent in the former network and gaze-view-independent in the latter, with bimodal receptive fields formed by visual receptive fields located near tactile receptive fields (e.g., Graziano et al., 1994). Interestingly, when the hand laterality task was performed with stimuli presented in the peripersonal space, the mirror-reversal of RTs between left and right stimuli was present (ter Horst et al., 2011). However, when the stimuli were displayed in the far space there was no mirror-reversal of RTs. The same effect was obtained for laterality judgments about which hand (left or right) would grasp the handle of a rotated mug's picture. Also in this task the RTs mirror-reversal was present in peripersonal space but not in the far space presentation.

In chapter 6 I have described a study with a group of UN patients, a group of right brain damaged patients, and a group of age-matched controls. They performed the hand laterality task and a visual laterality task, in which the laterality of a red marker placed on the same hand pictures used in the former task had to be judged. Previous studies indicated that UN (Coslett, 1998), especially if with PN (Baas et al., 2011;

Reinhart et al., 2012), is associated with asymmetries in accuracy with more errors when judging the laterality of left hand pictures than right hand pictures. It was concluded that UN patients suffer from a disturbance of the body schema (Coslett, 1998), or of the general representational space (Baas et al., 2011). In contrast with these proposals, I have reported that UN patients show asymmetries in accuracy for judgments of hand laterality but also for judgments of visual laterality. This result suggests that the asymmetric pattern of errors for chiral stimuli can be explained by neglect for the space of response, that is an impairment in the integration of the spatial codes of the stimulus with the spatial codes of the response. Indeed, UN patients were influenced by the irrelevant location of the stimuli showing neglect for the contralesional space of response for stimuli presented centrally or in the right hemispace, and with neglect for the ipsilesional space of response when stimuli were presented in the left hemispace. In the central presentation and in the right hemispace presentation they made more errors with left stimuli, thus when the response was wrong they pressed the right key more often than the left key. In the left hemispace presentation they made more errors with right stimuli, thus when the response was wrong they pressed the left key more often than the right key. The study demonstrated that patients suffering from UN fail to integrate visual information with the production of spatially organized responses and confirmed that disturbance of peripersonal space exploration result in deficits of sensorimotor integration. Do these results indicate that the UN's error asymmetry is a response-related phenomenon that has nothing to say about object cognition? Should we consider the behavior of UN patients as due to an impairment of low-level processing in response selection and execution? A previous study with UN patients found evidence for a response-related dissociation of consciousness (Bisiach et al., 1985). On a panel placed in front of the patient there were two rows of diodes that could emit either a red light or a green light. In the first task, patients were instructed to name the color in which the diodes lighted. In the second task they were instructed to press a key of the same color that lighted simultaneously with the diode on the panel. In this task the light stimulus could appear on the left or on the right of a central point where patients had to maintain ocular fixation. The response could be executed on a key that lighted on the same side of the stimulus or on the opposite side (i.e., on the left or on the right). In the first task patients could always name the color of the diode that lighted on the right side of the panel. In the second task patients responded to all diodes that lighted on the right side when the response key also lighted on the right. However, when was the left key that had to be pressed in response to a right stimulus, patients often made incorrect responses by pressing the key on the right side. In this situation, on some trials patients also denied that a stimulus had been presented in the right space. Therefore these patients could be aware of the stimulus when it followed a full stimulus-response cycle but they were unaware of it when the same stimulus could not be fully integrated in the stimulus-response chain.

A final consideration should be made about the study described in chapter 3. The main result was that a group of elderly individuals were slower and made more errors than a group of young participants when they judged the laterality of hand pictures shown with lateral orientations (i.e., left hands with CCW orientations and right hands with CW orientations). It was concluded that elderly individuals are impaired in imagining complex hand movements (De Simone et al., 2013). This interpretation of the data followed the idea that hand laterality judgments rely on action simulation of hand movements. Nevertheless, in chapter 5 I have shown that the RTs differences between medial and lateral orientations are determined by spatial stimulus-response compatibility between the direction of stimulus rotation and the side of the motor response. Therefore, the slower RTs and the less accurate performance for hands shown with lateral orientations demonstrated by the elderly participants were likely due to the increased difficulty experienced with aging when stimuli and responses are spatially incompatible. There is indeed ample evidence that aging entails slower performance with incompatible spatial stimulus-response mappings (e.g., Diggles-Buckles & Vercruyssen, 1990; Proctor et al., 2005; Simon, 1967).

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