Chapter 6
Rethinking the Role of Motor Simulation in Perceptual Decisions

Scott T. Grafton and Shivakumar Viswanathan

6.1 Introduction

Goal-oriented action demands a constant ebb and flow of information processing between perception and movement. Decisions about whether or not a task can be executed, such as jumping over a gap or reaching to switch a light, demand reliable perceptual evidence. Likewise, perceptual decisions that are particularly subject to optical distortion might benefit from physical knowledge gained through motor experience. For example, the inaccurate estimation of angles and azimuths during navigation could benefit from a motor-based simulation of the body moving in the world. One of the ways these kinds of decisions can be achieved is by conscious access to the motor system to form virtual movements. We can imagine jumping over the gap, and use this to influence our decision to act. Or we can imagine turning ourselves in the environment to get a better estimate of the relative bearing between locations. Increasing evidence suggests that motor simulation of this sort can aid subsequent overt motor performance, increase the rate of skill acquisition, and potentially be used to solve cognitive or perceptual problems involving the physical environment (Holmes and Collins 2001; Mulder et al. 2004). Understanding what behavioral or neural signatures constitute a motor simulation is an essential step for understanding how simulation might actually influence overt motor behavior or enhance perception. In this chapter, we consider a widely used experimental protocol that is broadly assumed in the literature to represent motor simulation, the hand judgment or laterality task (Cooper and Shepard 1975; Parsons 1987a). We provide overwhelming evidence that the behavioral phenomena associated with this task are not a result of motor simulation, and provide an alternative interpretation of these studies. The point of this review is not to undermine motor simulation as an important process or concept. Rather, we argue that progress in motor simulation

---

S. T. Grafton (✉) · S. Viswanathan
Department of Psychological Brain Sciences, University of California,
Santa Barbara, CA 93106-9660, USA
e-mail:grafton@psych.ucsb.edu

M. F. Levin (ed.), *Progress in Motor Control,* Advances in Experimental Medicine
and Biology 826, DOI 10.1007/978-1-4939-1338-1_6

research requires a higher standard of confirmatory evidence for what constitutes motor simulation and that the behavioral effects that are commonly reported are not necessarily sufficient to conclude that a motor simulation is occurring.

The general concept of simulation emerged in the 1970s during an explosion of cognitive science directed at understanding how mental representations were manipulated to solve problems (Shepard 1978). Simulation is now widely acknowledged to be an integral component of cognition (Barsalou 2008) and as a mechanism for manipulating or transforming internal representations to new states (Kosslyn et al. 2001). A classic example of how simulation is used in perceptual problem solving is the mental rotation of complex visual objects in matching tasks. In this case, reaction times (RTs) typically correlate with the rotation angle needed to match the orientation of one object to another, revealing a mental operator with analog properties acting on the internal representation of the object (Moulton and Kosslyn 2009). The concept of motor simulation followed suit. In this form of simulation, knowledge derived from the motor system might be used to organize virtual behavior. Motor simulation has links to explicit motor imagery or emulation, where we can imagine moving our body without actually displaying any overt action (Jeannerod and Decety 1995; Decety 1996; Jeannerod and Frak 1999; Jeannerod 2001). Similar to object rotation, the time to complete imagined movements also displays analog properties corresponding with real movement (Decety et al. 1989). However, in all of these early studies of motor simulation (or equivalently, imagery and emulation), there was no cognitive or motor problem in the experiments that actually needed to be solved by the participant. Thus, it was unclear whether motor simulation is actually a meaningful operation for solving cognitive problems. While one can imagine moving one's hand, it is challenging to find real examples where this sort of action imagery is utilized for planning or execution of everyday behavior let alone for virtual motor simulation.

One of the earliest and most widely cited examples of a motor simulation process that might actually be used to solve a perceptual problem is the laterality task (Cooper and Shepard 1975). In this wonderfully simple paradigm, the subject must decide if a visual image of a hand constitutes an image of a right or left hand, and then report their choice with a button press using their own right or left hand (Luria 1966). The three-dimensional (3-D) mirror symmetry of the two hands makes them chiral objects, which could be potentially difficult for the visual system to distinguish from each other. In the laterality task, also referred to as the hand judgment task, RTs depend on the angle of rotation between the hand stimulus and an unseen vertically oriented "virtual" hand (palms directed away from the subject with the fingers pointing upward). The analog property of RTs in the laterality task created a strong conceptual link with other forms of simulation such as object rotation, suggesting there is an internal representation of the hand stimulus that is transformed to a new orientation. Cooper and Shepard interpreted the analog delay in the laterality task as part of a decision-making process involving both perceptual discrimination and response selection. They proposed that the visual system was making a holistic analysis of the object, reorienting it, and comparing it to a canonical virtual left or right hand. They wanted to know if right versus left discrimination could be solved

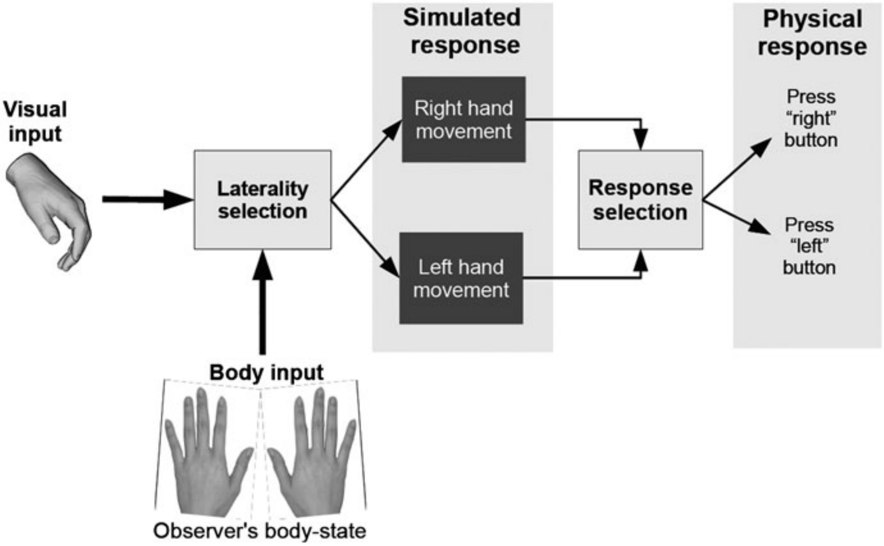


Fig. 6.1 Traditional model of motor simulation in the hand judgment task: Laterality of the visual hand stimulus is determined by comparing it to either of the "felt" hands, which are rotated by covert motor activity to a matching spatial orientation. This provides a mapping between each stimulus and the corresponding hand used to make the physical response

"without having either to preserve or to search through a store of fixed 2-D templates corresponding to all possible retinal projections." Mental rotation of the object (in this case a hand) provided an algorithm for reducing the storage and search requirements, as shown in Fig. 6.1. The simulation (and virtual hand rotation) provided new information that could be used to improve the decision-making process. While compelling as a possible cognitive mechanism, the authors fully acknowledged the fragilities of this interpretation. First, it was possible that the analog property in the laterality task was not sufficient evidence on its own to demonstrate that an object rotation was invoked to make the perceptual decision. Second, they acknowledged that if it could be demonstrated that a parts-based analysis was sufficient to solve hand identification then the use of simulated hand rotation to aid in the perceptual decision was less likely. In parts-based analysis, the observer can use local features of the object, such as the wrinkles on the palm or the pattern of the fingernails to make the identification. The alternative, a whole-based analysis, relies on understanding the complete 3-D structure of the object.

6.2 Motor Simulation and the Birth of a Conundrum

Uncertainties about what was actually being simulated or judged in the laterality task appeared early in the literature. In an experiment testing the influence of head position on laterality judgments, Sekiyama noticed that when the RTs, as a function of angle

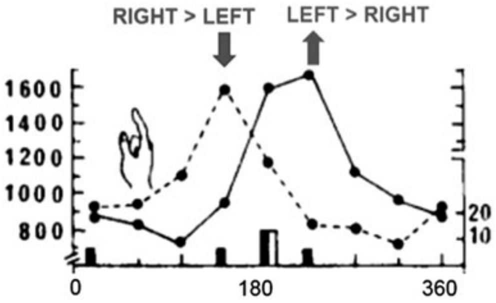


Fig. 6.2 An example of the correct-hand effect: The distribution of reaction time is different for right- and left-hand stimuli. This can only occur if the subject could distinguish the stimuli perceptually. (The plot is from Fig. 2 in Sekiyama 1982)

of rotation, were plotted separately for each hand, the profiles were not symmetric (Sekiyama 1982). They were skewed such that the RT profiles were mirror patterns for right- and left-hand responses, as shown in Fig. 6.2. This pattern was not apparent in the data from Cooper and Shepard, because they averaged the RTs for the two hands together (Cooper and Shepard 1975). The pattern of separate RT data for each hand in Sekiyama's data raised a critical issue. It could only occur if the subject was using a different mental process for each hand. This in turn implied that there was already sufficient perceptual information in the stimuli for subjects to be able to discriminate left and right hands. This possibility in turn raised the question of how if at all mental rotation of the hand actually contributed to the perceptual decision-making process. Sekiyama did not provide a clear answer. She interpreted the results from a kinesthetic framework, such that the "felt" position of the hands might be used to aid in the judgment.

The kinesthetic properties of the laterality task provided by Sekiyama were subsequently overshadowed by Larry Parsons' elegant experiments showing a range of new effects that were interpreted as overwhelmingly motoric in nature (Parsons 1987a). First, he demonstrated a remarkable sensitivity of the RTs to biomechanical constraints (Parsons 1994). RTs were highly sensitive to extreme positions such that hand stimuli in postures that normally are not comfortable led to slower RTs. Second, the analog properties of the laterality task were generalized to other body parts. They were also observed in a foot version of the task (Parsons 1987b). Third, many subjects (including the authors of this chapter) reported a sense of body motion when performing the task. Fourth, the RTs for judging hands at different rotations were proportional to the time to make actual movements from that position to a neutral point with the joint angles at mid-position. These effects led Parsons to note, "These imagined paths seemed to simulate the paths used for physically moving the hand or foot between their task orientation and the orientation of the stimulus" (Parsons 1987a). All of these findings have stood the test of time and continue to be replicated 25 years later. In addition, follow-up studies demonstrated that the RTs were sensitive to the posture of the participant as they performed the task (Sirigu and Duhamel 2001; Ionta et al. 2007). For example, placing the left hand behind the back would slow the RTs for left-hand judgments. They entrench the notion that the perceptual decision making in the laterality task is based on motor simulation (Ionta et al. 2007; ter Horst et al. 2010; Ferri et al. 2011; Ní Choisdealbha et al. 2011), motor imagery (Grush 2004) or motor emulation (Moulton and Kosslyn 2009). The motor simulation mechanism continues to be used to interpret findings in a variety of patient populations as well (Deconinck et al. 2009; Helmich et al. 2009; Williams et al. 2011).

However, as with Sekiyama's data, Parsons' work also reveals the remarkable skewing of RT profiles when the two hands are plotted separately. This skewing can only occur if the participants knew which hand to covertly rotate on each trial. This correct-hand effect shows that perceptual identification of hand chirality is orientation-invariant, even in the face of the added challenges imposed by the visual mirror symmetry of the hand stimuli. Despite the seemingly impregnable interpretation that a motor simulation is used in the laterality task, the correct-hand effect observed in data from Sekiyama, Parsons, and countless follow-up studies introduces a fundamental conundrum. A consistent limb-specific mirror skewing of the RT profiles could only occur if subjects identified the correct hand, invariant to orientation, prior to any putative motor simulation. *If simulation is used in perceptual decision making, then how does the motor simulator always choose the correct hand in the first place and, more importantly, why bothr with motor simulation at all?* The conundrum clearly speaks to Cooper and Shepard's original concern that if local perceptual features could be used to discriminate the stimulus, then the argument that simulation is used for perceptual decision making is flawed. In the face of this uncertainty, Parsons proposed an alternative explanation that could sustain motor simulation as a putative mechanism, as shown schematically in Fig. 6.3. He noted that "Performance in the left-right judgment task appears to involve these operations, some of which may occur concurrently: (a) analysis of the orientation and handedness of the stimulus; (b) analysis of the orientation of the internally represented corresponding hand; (c) planning a path for the internally represented hand to move (within its joint constraints) to the orientation of the stimulus; (d) mental simulation of planned action; and (e) exact-match confirmation of shape of imagined and perceived hands" (Parsons 1994). His final point addresses the conundrum by invoking a post hoc confirmation mechanism. This mechanism could take two forms. One would be a direct confirmation of the percept. However, the entire notion of a post hoc motor simulation to confirm what is already perceived is deeply problematic. It is difficult to find any other examples in the cognitive science literature where motor simulation or imagery is used to directly confirm an already correct percept. The other explanation for the post-hoc confirmation step proposes that mental rotation is needed to map the correctly perceived hand into the appropriate motor response, that is, there is uncertainty in the mappings between "right" and "left," and the sides of the body used to make the response. In a recent set of experiments where local features of the hand stimuli were manipulated, we discovered that neither of these post-hoc confirmation mechanisms is tenable (Viswanathan et al. 2012).

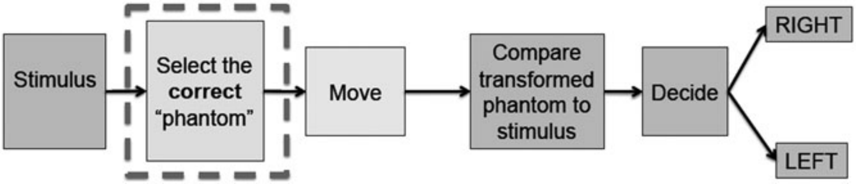


Fig. 6.3 The conundrum introduced by the correct-hand effect. A correct percept of the visual stimulus is always used as the referent for comparison in the motor simulation. Thus, it is unclear what the subject is actually deciding since they already recognize the chirality of the stimulus

6.3 Multisensory Hand Binding

We propose that the behavioral properties of the laterality task are not due to motor simulation. Instead, the analog and biomechanical features of the laterality task are a consequence of what we refer to as "multisensory hand binding." At the onset of the stimulus, the observer has simultaneous access to sensory information about the same entity (i.e., a hand) from different modalities—the visual representation of the seen hand depicted by the stimulus, and the proprioceptive representations of the observer's own felt hands (Shenton et al. 2004). There are more than enough local features in the visual stimulus used in a typical laterality experiment to uniquely identify it as the front or back of the hand. According to the multisensory hand-binding hypothesis, there is a simultaneous, (orientation-invariant) cross-modal comparison of the seen hand to the proprioceptive representation of the corresponding hand, as shown schematically in Fig. 6.4. The outcome of cross-modal comparison is not a match/mismatch signal that is used for perceptual decision making. Instead, it results in a binding of the visual representation of the seen hand to the proprioceptive representation of the "matching" felt hand or vice versa. Successful binding produces an intermodal discrepancy due to the differing orientations of the bound seen- and felt-hand representations (in a body-centered reference frame). This discrepancy automatically initiates a sensorimotor recalibration process to align the spatial representation of the felt hand to that of the seen hand—an aftereffect that can cause a feeling of moving. Critically, the motor response that is required in the laterality task is delayed until this intermodal conflict is resolved. This delay leads to the laterality specificity of the RTs. We speculate that the need to perform this recalibration between the seen and felt hand is evidence that the motor system requires an internally consistent and unique representation of body position (or state) as part of generating a motor command, although this consistency argument remains to be tested directly. Critically, the recalibration in multisensory hand binding is achieved by relating representations in different sensory reference frames with respect to each other. A critical prediction is that this occurs without requiring a motor signal from either premotor or motor cortex and does not require any sort of motor simulation, emulation, or explicit strategy. With multisensory hand binding, the response delay is related to recalibration of body position as a part of planning a normal movement and not related in any way to perceptual decision making. Thus, there is no conundrum as arises with the standard motor simulation account of laterality judgments.

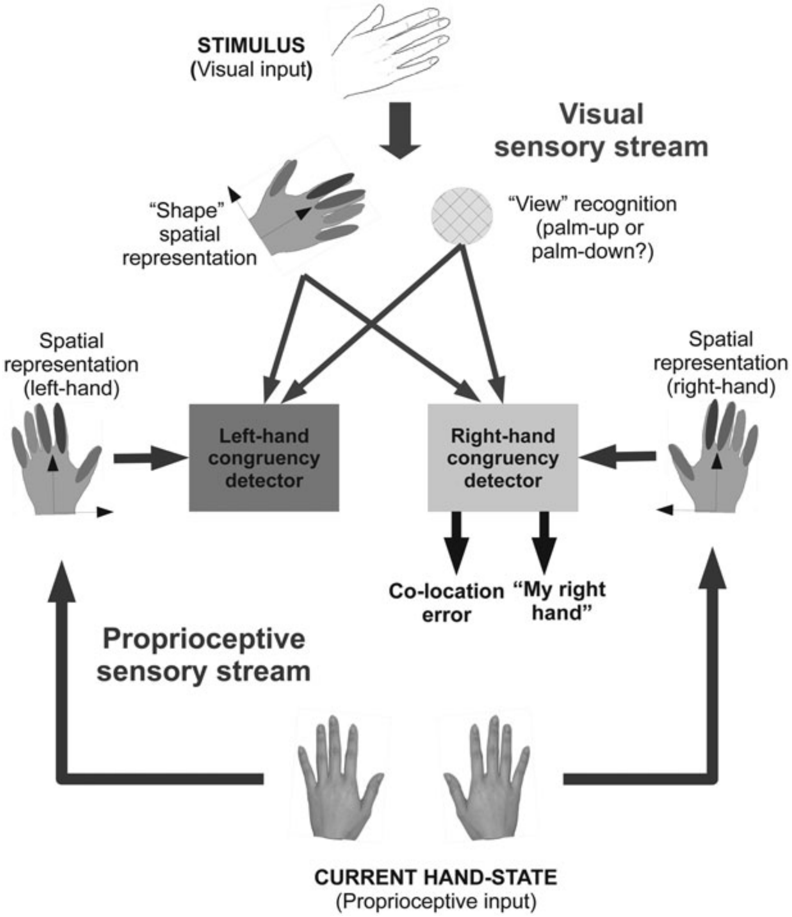


Fig. 6.4 The multisensory binding process: In the laterality task, a visual stimulus of the hand is evaluated in terms of hand shape and orientation (palm up/down) and this information is used to establish chirality of the visual stimulus. This is matched to the spatial representation of the corresponding felt hand. The planning of a motor response requires that this spatial discrepancy between two estimates of body position be reconciled

6.4 Experimental Evidence for Multisensory Hand Binding

Unlike the traditional motor simulation and confirmation model, the multisensory hand-binding hypothesis imposes strong constraints on when and whether the correct-hand effect will occur. Here, we summarize a study that used an attention manipulation to selectively induce a "wrong-hand effect" (Viswanathan et al. 2012). The experiment selectively extinguished the correct-hand effect by eliminating the contextual relevance of the proprioceptive inputs. Neither effect is plausible with

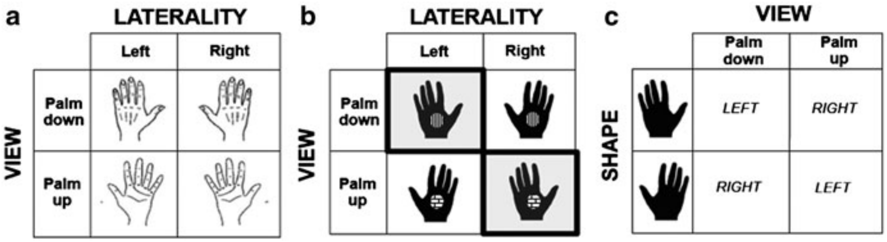


Fig. 6.5 Stimuli in the standard form of the laterality task have sufficient local features to determine chirality (**a**). In an ambiguous silhouette, each shape can correspond to either hand (**c**). With simple symbolic cues, chirality can be restored (**b**)

motor simulation. Finally, we describe a recent study that requires a simple perceptual decision of determining if two ambiguous hand silhouettes have the same or different outlines. The results show that there is an obligatory multisensory binding of the stimuli to the observer, even in a task when no right/left judgments are required.

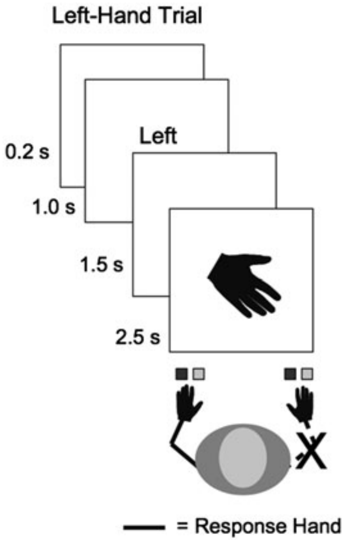
Inducing the Wrong Hand According to the hand-binding hypothesis, only sensory information about the spatial configuration ("shape") of the visual hand representation can be correlated with the proprioceptive hand representations. The afferent proprioceptive representation of a hand codes the relative spatial position of the digits and hand, but does not itself contain information about visual attributes such as the color, lines, and textural patterns of the skin covering that hand. Therefore, the "shape" of the seen hand and the "patterns" on the seen hand should have dissociable effects on laterality identification. To test this prediction, we exploited the fact that visual hand "patterns" are indispensable in identifying the laterality of certain hand shapes. In Fig. 6.5a, the visual patterns on each hand are diagnostic of whether the palm or the back of that hand is being viewed. Without these patterns, the 2-D hand shapes exhibit multiple symmetries. The shapes of the palm-up and palm-down views of the same hand are mirror-symmetric, as are the shapes of the right and left hands having the same view as shown in Fig. 6.5c. Furthermore, the palm-up view of one hand has the same shape as the palm-down view of the other hand. Due to these symmetries, the laterality of a hand cannot be uniquely determined based on shape alone, without the view information from the visual patterns. The Cooper–Shepard paradigm was altered to include a task-set manipulation, using the hands in Fig. 6.5b as stimuli. Black silhouettes depicted hand shapes and colored dots were used to denote hand orientation. A red dot indicated a palm-down view of the hand, and a green dot indicated the palm-up view. Participants readily learned to recognize this color-to-view mapping before the experiment. The paradigm involved two independent conditions—the View-first condition and the Shape-first condition.

Each condition consisted of cued and uncued trials that occurred with (approximately) equal frequency. On the cued trials of the View-first condition, participants first saw a colored dot (red or green) indicating the view of the forthcoming test stimulus. After a brief offset, a test stimulus depicting a hand shape (without view information) was presented at a variable picture-plane orientation. On the uncued trials, the advance cue (a gray dot) did not provide any task-relevant information, and the subsequent test stimulus contained both view and shape information together. Participants had to combine view and shape information, whether presented serially (cued trials) or simultaneously (uncued trials), to identify the laterality of the hand. The stimulus ordering on the cued trials was reversed in the Shape-first condition—the advance cue was a hand shape, followed by a test stimulus depicting that hand's view. Critically, the uncued trials were identical in the Shape-first and View-first conditions. We assumed that participants would selectively attend to one and then the other visual attribute of the stimulus in the same sequence used in the cued trials of that condition. With this assumption, the hand-binding hypothesis predicts that response times on the *uncued* trials should differ in a very specific manner between the View-first and Shape-first conditions. On the View-first condition, "view" should be processed before "shape." According to the hand-binding hypothesis, view representations should therefore be available to mediate the subsequent perceptual correlation of hand shape to the proprioceptive hand representations, thus leading to a unique and "correct" laterality binding solution. Consistent with this, the RT profiles for these stimuli were mirror-reversed in the View-first condition, consistent with the correct-hand effect reported by previous studies. On the Shape-first condition, "shape" would be processed before "view." A hand shape without view information has an ambiguous laterality. Due to the *participant's* palm-down hand position, each shape should be correlated with the spatial configuration of a unique proprioceptive hand representation. Consequently, the ambiguous hand shapes are automatically bound to the correlated felt-hand representation, according to the hand-binding hypothesis. This "premature" binding, without incorporating stimulus-defined view information, leads to a critical result. Stimuli having identical shapes but different views were bound to the very same felt hand. RT profiles for these stimuli were *not* mirror-reversed in the Shape-first condition, unlike the predictions for the View-first condition. Due to this premature binding, palm-up stimuli were consistently bound to the "wrong" felt hand, in violation of the correct-hand effect. Note that this "wrong-hand effect," while eliminating the asymmetry of RT profiles, does not necessarily result in "wrong" laterality judgments. When the binding enters awareness, participants can evaluate whether the stimulus-defined view corresponds to a palm-down or a palm-up view, and respond accordingly with either the bound hand or the opposite hand.

Binding Without Laterality Judgments We performed a variant of the Cooper–Shepard paradigm to demonstrate that hand binding could be tightly controlled by the experimenter. Participants had to interpret an ambiguous hand silhouette palm up or palm down, rather than left or right hand. We tested if this perceptual decision, which had no laterality judgment, would again interact with the responding "felt" hand. On each trial, participants first received an advance cue specifying the laterality of the forthcoming test stimulus. That is, subjects knew in advance if a right- or left-hand stimulus would be presented, eliminating hand judgment altogether. The left/right instruction also indicated which hand to use to indicate their palm-up/palm-down decision. In doing so, the decision making has no uncertainty in the mapping between "right" and "left" stimuli and the side of the body to be used to respond. After a short delay, a test stimulus depicting only a hand shape was presented. Participants judged whether the test stimulus depicted the palm-up or the palm-down view of the hand of known laterality with an index or ring finger button press. Despite explicit prior knowledge of the expected hand laterality, pre-attentive mechanisms involved in laterality identification were predicted to still be involved. We found that the advance preparation of the response hand induced a "selective attention" to the felt representation of the responding hand, while inhibiting inputs from the other (nonresponding) hand. Consistent with the hand-binding hypothesis, only shapes correlated with the palm-down position of the response hand led to successful binding, but not shapes corresponding to the palm-up view, even though these latter shapes are correlated with the palm-down position of the nonresponding/unattended hand. The palm-down stimuli of each hand were associated with the characteristic RT mirror asymmetry of the correct-hand effect, but not the palm-up stimuli. This systematic difference in RTs between the palm-down and palm-up stimuli supports the assumption of the hand-binding hypothesis that successful binding is the basis for recalibration and the associated illusory movement reported by many subjects. These results further argue that the mechanism causing the illusory movements is not under direct strategic control, despite the extensive voluntary control over the sensory inputs and the interpretation of the outputs. If it were a "strategy," then it would require participants to pre-identify the palm-up and for palm-down stimuli in order to apply a different strategy to each. Furthermore, since the palm-down stimuli for one hand are identical to the palm-up stimuli for the other hand, these results are inconsistent with the exclusive use of a strategy exploiting the visual position of the thumb. Additionally, if participants used "simulated" movements to either confirm or disconfirm their decisions, the RT asymmetries based on the correct-hand effect should be present on both palm-down and palm-up stimuli, contrary to the observed results (Fig. 6.6).

Automatic Multisensory Hand Binding When It Is Irrelevant We further tested if multisensory hand binding is an automatic process, unrelated to hand judgment, in a two-handed version of the laterality task. Subject's observed two ambiguous hand silhouettes positioned one above the other (Fig. 6.7a). The task was to decide as quickly as possible if the two silhouettes were rotated versions of the same shape, or different, mirror-symmetric versions of the two shapes. The main axes of the two shapes were always oriented 120° apart (Fig. 6.7b). Extensive research in perceptual matching studies of rotated objects has established that the solution to this problem is to mentally rotate one object to match the orientation of the other and the time to do this depends on the arc length or angle of the rotated object (Cooper and Shepard 1984). Because the two orientations are always 120° apart, the time should be the same irrespective of the absolute orientation of the images (as shown on the circle in Fig. 6.7c). The orientations were chosen such that subjects could not use visual symmetry as a perceptual "shortcut" for detecting two mirror shapes. Critically, if there is multisensory hand binding, then the automatic binding of either of the seen

Fig. 6.6 Binding without laterality judgment: In this task, subjects are told if the stimulus is a left or right hand and told to respond with the corresponding left or right hand and report if the stimulus corresponds to a palm-up or palm-down orientation. Thus, there is no laterality judgment and no uncertainty over the laterality of the motor response. Subjects demonstrate a correct-hand effect for palm-down hand stimuli that match the responding hand, but not for matching palm-up stimuli



hands and the observer's responding hand will lead to biomechanically constrained delays in response time and a dependency of RT as a function of where the axes are positioned (Fig. 6.7d). This RT dependency on position was found to be particularly dramatic for orientations associated with the most uncomfortable position to rotate the hands into (Fig. 6.7e). When results of this two-handed version of the laterality task are combined with the traditional single-hand judgment studies, the generality of the results as well as the automaticity of the behavior constitute strong evidence that multisensory binding is an ecologically valid process (De Gelder and Bertelson 2003).

6.5 Reinterpreting the Laterality Task

Multisensory hand binding and recalibration of body position are sufficient to explain much of the behavioral phenomenology typically found in experiments that use the laterality task or its variations. First, it is well known that conflicts between seen and felt body positions can induce a sense of motion without any overt motor command or covert motor simulation. Anyone who has experienced aftereffects of motion from a carnival ride or experienced "sea-legs" after returning to the shore can attest to this (Cohen 1996). In other words, a sense of motion by itself is insufficient evidence to conclude that a motor simulation is occurring. Second, 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. That is, our ability to mentally represent the position of our body in space (irrespective

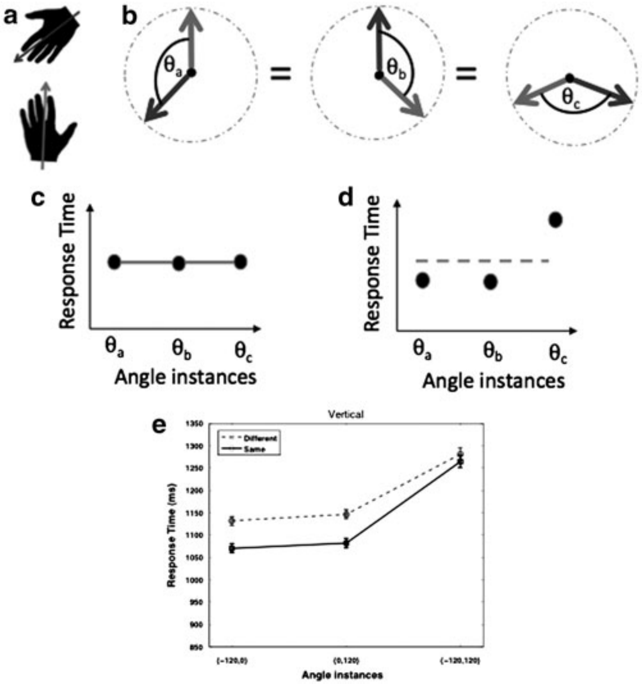


Fig. 6.7 In the two-handed matching task, two hand silhouettes with ambiguous chirality are presented, and the subject must decide if they are the same hand or a mirror (different) pair (**a**). The stimuli are presented one above the other to avoid perceptual mirror symmetries. The two hands are always presented with the primary axis rotated 120° with respect to each other (**b**). Mental rotation of one object to another would lead to response times that are invariant to the absolute angle instances (**c**). In contrast, if hand binding occurs, there will be delays in response times as a function of angle instance (**d**). Data from subjects performing this task confirm there is a strong hand-binding effect (**e**)

of our generation of motor commands) is strongly constrained by real biomechanics. Furthermore, as amplified below, any clinical disorder that disturbs the body schema (amputation, locked-in syndrome, chronic pain) could distort the internal representation of body position and influence the time needed to relate this internal schema with visual hand stimuli. Third, the sensitivity of response times to the static posture of the observer could be due to peripheral, proprioceptive influences on the internal model of the body position, irrespective of any motor involvement (Riemer et al. 2010). Fourth, experimentally distorting hand position (using methods such as vibrotactile stimulation of the biceps tendon) should influence RTs in the laterality task (McCormick et al. 2007). Fifth, the multisensory hand-binding process appears to be pre-attentive or automatic. Laterality judgment delays are resistant to explicit control such as instructions that tell the subject a stimulus is their own or another person's (Ferri et al. 2011).

6.6 Neural Mechanisms of Multisensory Binding

The multisensory hand-binding model proposes that the registration of different estimates of body position plays a dominant role in the preparation for action. Proprioceptive representations of one's hands are continuously accessible as they provide a running estimate of the position of the hands relative to the body, both when the hand is at rest and in motion, and even when the hands cannot be seen. It is known that the cross-modal comparison of the representations of a seen hand with that of the felt hand is critical for maintaining the coherence of one's body schema (Graziano and Botvinick 2001; Ehrsson et al. 2004), and essential for enhancing motor performance (Desmurget et al. 1995). Intersensory conflicts can result in a variety of body schema distortions such as the rubber hand illusion (Botvinick and Cohen 1998; Pavani et al. 2000), extracorporeal perception, and errors of agency attribution (Petkova and Ehrsson 2008; Slater et al. 2009).

The need for coherence across sensory modalities implies that there is a high level of specificity to the perceived visual stimulus, as a visually seen right hand should not be confused with a felt left hand, and vice versa. Neurons identified in Brodmann's area 5 of the superior parietal lobule (SPL) of the nonhuman primate exhibit such specificity (Graziano et al. 2000). They have a graded response depending on the angular disparity between the felt arm and a seen artificial arm. Furthermore, these neurons respond in the same manner to an inverted hand (the back of the same hand) but not when the visual cues imply that the inverted hand belongs to the opposite arm. In this latter case, the neurons responded as if there was no stimulus present at all. Similar properties are observed in dorsal premotor cortex (PMd) (Graziano 1999). These two areas form a network that transforms vision and body-centered reference frames (Caminiti et al. 1996; Crawford et al. 2011). The properties of neurons within these two areas in nonhuman primates form a compelling substrate for multisensory hand binding. That said, further studies are needed to understand the relationship between the time it takes to resolve multisensory conflict and the computational processes within SPL neurons that could be mediating this process.

While direct neuronal evidence of the hand-binding process is not available in humans, a wealth of indirect evidence using functional imaging with both positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), spanning 15 years of study in 10 experiments and over 120 subjects, demonstrate localization to the SPL and to a lesser degree PMd (Hetu et al. 2013). The SPL loci are remarkably similar in location to nonhuman primate recordings in Brodmann's area 5. The specific involvement of SPL in imaging is particularly apparent when hand judgment is contrasted with object rotation, which effectively controls for motor cortex activity related to making the motor response (Bonda et al. 1995; Kosslyn et al. 1998; de Lange et al. 2005). Using parametric event-related fMRI, SPL activity scales with biomechanical complexity during the laterality task. We propose this graded response is related to the multisensory binding, analogous to what is observed in nonhuman primate neurons rather than to a simulation (de Lange et al. 2006).

Hand binding in the laterality task appears to be a highly specialized property of the superior parietal cortex, based on a comparison with other functional determinants of body representation. In a factor analysis of patients with parietal lobe stroke, a laterality task deficit was distinct from other tests of body representation including (1) chronometric scaling while imagining moving the fingers contralateral to the lesion, (2) localization and identification of body parts, and (3) understanding the relative position of different segments of the arm (e.g., that the wrist is distal to the elbow). Furthermore, lesion overlap maps demonstrated increased involvement of the SPL for patients with laterality deficits that were different from probable lesion locations for the other body representation disorders (Schwoebel et al. 2001). The behavioral and lesion location differences of laterality judgment and imagined finger movements are quite important, as the latter is generally considered to be a prototypical example of motor simulation (Sirigu et al. 1995).

Each parietal-premotor cortex represents to a greater degree the proprioceptive state of the contralateral hand (Bernier and Grafton 2010). Thus, binding should only occur between a seen hand and the felt hand of only one hemisphere. This might be reflected in PET and fMRI experiments by greater brain activity for one hand than the other. However, most imaging studies show bilateral recruitment of SPL and PMd cortices in the laterality task, even when activity for each hand is modeled separately (de Lange et al. 2006). This might be expected, given that the hemispheres are reciprocally connected, and activation of one will co-recruit the other. Patient studies could possibly provide evidence that only one hemisphere is “bound” per trial. In stroke patients, lesions of the left hemisphere lead to slowing of judgments to either hand stimulus whereas right brain damage slows neither (Tomasino et al. 2003; Daprati et al. 2010). Irrespective of the side of the lesion, there might be mechanisms unrelated to multisensory binding influencing patient performance. The lesion location is diverse across subjects, there is an influence of hemispheric specialization for hand dominance, and patients may under go reorganization post stroke. The best evidence that the SPL is specialized to bind vision and proprioception of the opposite hand can be found in patients with a sectioning of the corpus callosum (Parsons et al. 1998). Using hemifield stimuli and the hand laterality task, it is clear from error rates that each hemisphere only matches the contralateral hand.

6.7 Is the Motor Cortex Involved in the Laterality Task?

One possible acid test of motor simulation in the laterality task would be a demonstration that the motor cortex of healthy subjects is involved during performance of the task. Motor cortex can clearly be activated in tasks explicitly cueing imagined movement (Lotze et al. 1999; Sharma et al. 2008). However, the evidence for motor cortex engagement in the laterality task is by no means apparent. Early PET imaging experiments of the laterality task using block designs reported activity of the motor cortex (Kosslyn et al. 1998). With well-balanced experimental designs and higher-resolution imaging, it became evident that motor cortex activity is not greater for hand judgment than object rotation (Bonda et al. 1995). Furthermore, motor cortex activity only appeared at the time of a response, presumably after any perceptual decision had occurred (de Lange et al. 2005). A recent meta-analysis of 75 imaging studies of motor simulation compared localization in the laterality task with other forms of motor simulation, such as kinesthetic or visual motor imagery (Hetu et al. 2013). With the laterality task, motor cortex activation is rare whereas the other forms of motor imagery task demonstrated motor cortex involvement about 25 % of the time. When single-pulse transcranial stimulation (Ganis et al. 2000) or slow, 1 Hz, repetitive transcranial magnetic stimulation (TMS; Pelgrims et al. 2011) was used to create a "virtual" lesion of motor cortex, there was a general slowing of RTs in the laterality task. However, these results did not influence the correct-hand effect and only described a generalized slowing of responses. Furthermore, in a detailed single-pulse TMS experiment in which virtual lesions of motor cortex were chronometrically manipulated and the correct-hand effect was carefully measured, there was a complete failure to disrupt hand judgment performance at any stimulation time post stimulus, establishing that there is no time window during which the motor cortex makes a contribution to mental rotation of the hand (Sauner et al. 2006). Although motor cortex may be involved in other motor simulation paradigms such as kinesthetic motor imagery, there is no compelling evidence that it is used in hand laterality judgments, undermining the argument for a motor simulation process in this task.

6.8 The Malleable Body Schema

State estimation is a computational process that has been proposed as a way to integrate sensory and motor information of position in real time (Tin and Poon 2005; Mulliken et al. 2008). Retinotopic-based reference frames appear to play a dominant role in representing space and planning action under typical experimental conditions. Vision provides a powerful and accurate map of limb position and the environment and may serve as a default reference frame for organizing body state and action (Cohen and Andersen 2002). There is growing consensus that the reference used to determine position is not absolute, but contingent on available evidence from different sensory channels (Denève and Pouget 2004; Faisal et al. 2008; McGuire and Sabes 2009). While vision-based information typically dominates, body-based reference frames can also be used under degraded vision. However, maps of the body position based on proprioception as well as tactile input are far less veridical than visual inputs (Kammers et al. 2009). They are easily distorted by illusions induced by visual–tactile (Botvinick and Cohen) or visual–proprioceptive (Burrack and Brugger 2005) mismatches and do not clearly map onto the body topology precisely (Longo and Haggard 2010). Nevertheless, the correct-hand effect of the laterality task suggests that recalibration relies on a body-centered reference frame with a "default" proprioceptive configuration: palms down and fingers pointed upwards.

Notably, the default configuration that is “bound” in the laterality task can be reshaped by additional information such as repositioning of the subject (Riemer et al. 2010). It is also influenced by the illusion of wrist flexion induced by vibrotactile stimulation to the wrist extensor tendons. In this case, RT delays were only observed when judging hand stimuli corresponding to the side of the stimulation (McCormick et al. 2007). It also appears to be overridden by biases induced by experimental context, such as constraining motor responses to one side or the other, as well as handedness (Ní Choisdealbha et al. 2011). Other contextual influences, such as ongoing observed or executed action, also influences the estimated body configuration (Conson et al. 2009). Interestingly, in young children, motor behavior is strongly shaped by a body representation that is close to the default position described in the laterality task and they are less influenced by their own body position (Saimpont et al. 2009). As they develop and acquire knowledge of the dynamics of their bodies, their body representation becomes more closely aligned with the actual physical position and this is reflected in a sensitivity of laterality judgment times to the participant’s position. It is possible then that in the face of uncertainty about limb position, adults might resort to this developmentally more primitive map of body position.

6.9 Multisensory Binding in Patients

Many patient populations have been tested with the laterality task and abnormal findings have invariably interpreted as evidence for deficits of motor simulation, even when there is no lesion of the motor system. In many cases, a more direct explanation can be drawn from multisensory binding. An illustrative case is patients who have undergone a limb amputation. It is well established that they can have a significantly distorted body schema (Ramachandran and Hirstein 1998). In the framework of multisensory binding, it is the poor alignment of a visual hand to a distorted body map that leads to the delays of laterality judgment, particularly for the hand stimulus corresponding to the distorted body schema (Reinersmann et al. 2010).

Another illustrative population who has abnormalities of laterality judgment is patients with pain disorders. For those with unilateral, chronic limb pain, there is a delay in laterality judgments to the hand stimuli corresponding to the affected side. The delay is also related to the duration of symptoms and to the pain that would be evoked by executing the movement (Moseley 2004b; Coslett et al. 2010b; Reinersmann et al. 2010). When a picture of a foot is used as the stimulus, delays in judgment are also observed for the stimuli corresponding to the painful foot, even when the subject responds with their intact hands (Coslett et al. 2010a). The fidelity of the laterality task for tracking pain severity has led to the proposal that it be used as an objective independent measure of subjective pain (Coslett et al. 2010b).

Schwoebel interpreted the response delays for stimuli corresponding to the painful limb (whether hand or foot) as evidence that there was a sensitivity of the internal representation of body position, particularly the nonvisual representation, to pain

(Schwoebel et al. 2001). The multisensory binding model draws on the same general explanation that the delay is related to a distortion of the body schema. However, with multisensory binding, there is an important new distinction worth amplifying. In most of the studies of chronic pain, including the original paper by Schwoebel, the "movement" of the body representation is assumed to be a motor simulation or emulation, where the subject volitionally manipulates a body schema to solve the laterality task. This of course reintroduces the conundrum of the correct-hand effect and is inconstant with new experimental evidence (van Elk et al. 2012). In contrast, with multisensory binding the rotation of the body schema is automatic and driven by the incongruence with the observed hand position. This actually simplifies the explanation.

It has been found that patients with chronic neuropathic pain can actually gain some relief as measured by subjective pain scales when "treated" with the laterality task. Explanations for this improvement have been uncertain, and based on recruitment of motor and premotor networks (which we now know is not an accurate account of the networks used in this task) or perhaps due to focused attention on the affected hand (which could just as readily make the pain worse) (Moseley 2004a). The multisensory binding model provides an alternative explanation: One of the consequences of chronic pain could be a distortion of the body schema, particularly for the affected limb. Normalizing this distortion either by overt motor activity or through coregistration of seen and felt limb positions in the laterality task might reduce the distortion by image and associated pain.

6.10 When Does Binding Occur?

The laterality task reveals an illusion where a seen and felt hand are perceptually bound and spatially matched. When does this illusion generalize? Evidence to date would suggest the phenomenon also occurs with foot stimuli (Parsons 1987b). However, it is not at all clear that a correct-hand effect is observed when the hand stimulus is replaced with a glove (Daprati et al. 2010) or is attached to a body (Zacks et al. 2002). In this case, RT effects are more consistent with typical object rotation tasks or spatial compatibility effects. This would suggest that there is something special about disarticulated hands and feet as sources of perceptual confusion. Binding for these stimuli appears irrespective of the 3-D orientation of the stimulus (Parsons 1987b, 1987a). This undermines an assumption in some experiments that uncomfortable positions of visual stimuli would be treated by the observer as allocentric, whereas comfortable positions would be egocentric (Brady et al. 2011).

Another important and unanswered question is whether an analogous binding mechanism might be involved in the matching of the proprioceptive felt hand to an object in the environment. Consider a primate swinging through the trees. Limb grasping would require rapid accurate matching of limb orientation with a palm-centric reference frame. This could be performed through a rotation of visual and proprioceptive reference frames, with planning time influenced by biomechanical effects including end-state comfort. As with the hand-binding model, there is no need for motor cortex "simulation" to solve this realignment problem. Of note, when subjects make perceptual decision about how their hand should be oriented to make a power grasp on a dowel, the decision times have all these properties (Johnson 2000b). Furthermore, imaging studies demonstrate that both the SPL and PMd are associated with the simulated hand rotation, in regions that are remarkably similar to those found in the laterality task (Johnson et al. 2002). Finally, patients with hemiparesis and motor cortex damage can continue to perform this grasp selection task, further undermining a motor simulation account (Johnson 2000a). We speculate that the object itself provides a visual reference frame that the felt hand can be bound to without any need for motor simulation. For more complex behavior, including the manipulation of tools, additional control mechanisms and estimates of position would certainly need to be invoked.

6.11 What Should We Call Motor Simulation?

A consequence of the hand-binding model is that the perceptual judgment of a hand does not rely on a motor simulation process. At a certain level, this is not surprising. The perceptual demands of making a hand laterality judgment are not particularly difficult when considered in the context of many other difficult perceptual problems we face every day, and where no motor simulation is required. The hand-binding model also suggests that much of the evidence that is used to make a case for motor simulation, whether it is an objective behavioral measure or subjective report of movement, is inadequate. The observation that RTs are sensitive to hand orientation, to biomechanical constraints, to body posture, to physical injury, or to a distorted body scheme are insufficient evidence on their own to conclude that a motor simulation is occurring in a task. Similarly, a sense of motion could be based purely on sensory mismatch. This does not mean we are proposing that motor simulation cannot occur. Instead, we simply argue that the range of tasks involving motor simulation may be smaller than is commonly stated. The outcome of our work with the laterality task is that a higher burden of proof is needed to conclude that a motor simulation is involved in cognitive problem solving. The most convincing experiments suggesting that a motor simulation is occurring require subjects to explicitly imagine they are achieving specific action goals, such as walking to a target, tapping fingers in a specific sequence, drawing, reaching, tracking, and making bimanual actions (Decety et al. 1989; Sirigu et al. 1995; Decety 1996; Vargas et al. 2004). In all these cases, there are chronometric links between real and imagined actions. The tasks clearly involve willful, explicit motor emulation centered on a goal, rather than on a perceptual decision.

Acknowledgments The work was supported by a grant from the James S. McDonnell Foundation and the Institute for Collaborative Biotechnologies through contract no: W911NF-09-D-0001 from the US Army Research Office.

References

Barsalou LW. 2008. Grounded cognition. Annu Rev Psychol 59:617–645.

Bernier PM, Grafton ST. 2010. Human posterior parietal cortex flexibly determines reference frames for reaching based on sensory context. Neuron 68:776.

Bonda E, Petrides M, Frey S, Evans A. 1995. Neural correlates of mental transformations of the body-in-space. Proc Natl Acad Sci U S A 92:11180–11184.

Botvinick M, Cohen J. 1998. Rubber hands 'feel' touch that eyes see. Nature 391:756.

Brady N, Maguinness C, Ní Choisdealbha A. 2011. My hand or yours? Markedly different sensitivity to egocentric and allocentric views in the hand laterality task. PLoS ONE 6:e23316.

Burrack A, Brugger P. 2005. Individual differences in susceptibility to experimentally induced phantom sensations. Body Image 2:307–313.

Caminiti R, Ferraina S, Johnson PB. 1996. The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. Cereb Cortex 6:319–328.

Cohen H. 1996. Vertigo after sailing a nineteenth century ship. J Vestib Res 6:31–35.

Cohen YE, Andersen RA. 2002. A common reference frame for movement plans in the posterior parietal cortex. Nat Rev Neurosci 3:553–562.

Conson M, Sarà M, Pistoia F, Trojano L. 2009. Action observation improves motor imagery: specific interactions between simulative processes. Exp Brain Res 199:71–81.

Cooper LA, Shepard RN. 1975. Mental transformations in the identification of left and right hands. J Exp Psychol Hum Percept Perform 104:48–56.

Cooper LA, Shepard RN. 1984. Turning something over in the mind. Sci Am 251:106–107, 110–104.

Coslett HB, Medina J, Kliot D, Burkey A. 2010a. Mental motor imagery and chronic pain: the foot laterality task. J Int Neuropsychol Soc 16:603–612.

Coslett HB, Medina J, Kliot D, Burkey AR. 2010b. Mental motor imagery indexes pain: the hand laterality task. Eur J Pain 14:1007–1013.

Crawford JD, Henriques DYP, Medendorp WP. 2011. Three-dimensional transformations for goal-directed action. Annu Rev Neurosci 34:309–331.

Daprati E, Nico D, Duval S, Lacquaniti F. 2010. Different motor imagery modes following brain damage. Cortex 46:1016–1030.

De Gelder B, Bertelson P. 2003. Multisensory integration, perception and ecological validity. Trends Cogn Sci 7:460–467.

de Lange FP, Hagoort P, Toni I. 2005. Neural topography and content of movement representations. J Cogn Neurosci 17:97–112.

de Lange FP, Helmich RC, Toni I. 2006. Posture influences motor imagery: an fMRI study. Neuroimage 33:609–617.

Decety J. 1996. Do imagined and executed actions share the same neural substrate? Brain Res Cogn Brain Res 3:87–93.

Decety J, Jeannerod M, Prablanc C. 1989. The timing of mentally represented actions. Behav Brain Res 34:35–42.

Deconinck FJA, Spitaels L, Fias W, Lenoir M. 2009. Is developmental coordination disorder a motor imagery deficit? J Clin Exp Neuropsychol 31:720–730.

Denève S, Pouget A. 2004. Bayesian multisensory integration and cross-modal spatial links. J Physiol Paris 98:249–258.

Desmurget M, Rossetti Y, Prablanc C, Stelmach GE, Jeannerod M. 1995. Representation of hand position prior to movement and motor variability. Can J Physiol Pharmacol 73:262–272.

Ehrsson HH, Spence C, Passingham RE. 2004. That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. Science 305:875–877.

Faisal AA, Selen LP, Wolpert DM. 2008. Noise in the nervous system. Nat Rev Neurosci 9:292–303.

Ferri F, Frassinetti F, Costantini M, Gallese V. 2011. Motor simulation and the bodily self. PLoS ONE 6:e17927.

Ganis G, Keenan JP, Kosslyn SM, Pascual-Leone A. 2000. Transcranial magnetic stimulation of primary motor cortex affects mental rotation. Cereb Cortex 10:175–180.

Graziano MS. 1999. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. Proc Natl Acad Sci U S A 96:10418–10421.

Graziano M, Botvinick M. 2001. How the brain represents the body: insights from neurophysiology and psychology. Common mechanisms in perception and action 19:136–157.

Graziano MS, Cooke DF, Taylor CS. 2000. Coding the location of the arm by sight. Science 290:1782–1786.

Grush R. 2004. The emulation theory of representation: motor control, imagery, and perception. Behav Brain Sciences 27:377–396; discussion 396–442.

Helmich RC, Aarts E, de Lange FP, Bloem BR, Toni I. 2009. Increased dependence of action selection on recent motor history in Parkinson's disease. J Neurosci 29:6105–6113.

Hetu S, Gregoire M, Saimpont A, Coll MP, Eugene F, Michon PE, Jackson PL. 2013. The neural network of motor imagery: an ALE meta-analysis. Neurosci Biobehav Rev 37:930–949.

Holmes PS, Collins DJ. 2001. The PETTLEP approach to motor imagery: A functional equivalence model for sport psychologists. Journal of Applied Sport Psychology 13:60–83.

Ionta S, Fourkas AD, Fiorio M, Aglioti SM. 2007. The influence of hands posture on mental rotation of hands and feet. Exp Brain Res 183:1–7.

Jeannerod M. 2001. Neural simulation of action: a unifying mechanism for motor cognition. Neuroimage 14:S103–109.

Jeannerod M, Decety J. 1995. Mental motor imagery: a window into the representational stages of action. Curr Opin Neurobiol 5:727–732.

Jeannerod M, Frak V. 1999. Mental imaging of motor activity in humans. Curr Opin Neurobiol 9:735–739.

Johnson SH. 2000a. Imagining the impossible: intact motor representations in hemiplegics. Neuroreport 11:729–732.

Johnson SH. 2000b. Thinking ahead: the case for motor imagery in prospective judgements of prehension. Cognition 74:33–70.

Johnson S, Rotte M, Grafton S, Hinrichs H, Gazzaniga M, Heinze H. 2002. Selective activation of a parietofrontal circuit during implicitly imagined prehension. Neuroimage 17:1693–1704.

Kammers MP, Longo MR, Tsakiris M, Dijkerman HC, Haggard P. 2009. Specificity and coherence of body representations. Perception 38:1804–1820.

Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM. 1998. Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 35:151–161.

Kosslyn SM, Ganis G, Thompson WL. 2001. Neural foundations of imagery. Nat Rev Neurosci 2:635–642.

Longo MR, Haggard P. 2010. An implicit body representation underlying human position sense. Proc Natl Acad Sci U S A 107:11727–11732.

Lotze M, Montoya P, Erb M, Hulsmann E, Flor H, Klose U, Birbaumer N, Grodd W. 1999. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. J Cogn Neurosci 11:491–501.

Luria AR. 1966. Higher cortical functions in man. London: Tavistock.

McCormick K, Zalucki N, Hudson M, Moseley GL. 2007. Faulty proprioceptive information disrupts motor imagery: an experimental study. Aust J Physiother 53:41–45.

McGuire LM, Sabes PN. 2009. Sensory transformations and the use of multiple reference frames for reach planning. Nat Neurosci 12:1056–1061.

Moseley GL. 2004a. Graded motor imagery is effective for long-standing complex regional pain syndrome: a randomised controlled trial. Pain 108:192–198.

Moseley GL. 2004b. Why do people with complex regional pain syndrome take longer to recognize their affected hand? Neurology 62:2182–2186.

Moulton ST, Kosslyn SM. 2009. Imagining predictions: mental imagery as mental emulation. Philos Trans R Soc Lond, B, Biol Sci 364:1273–1280.

Mulder T, Zijlstra S, Zijlstra W, Hochstenbach J. 2004. The role of motor imagery in learning a totally novel movement. Exp Brain Res 154:211–217.

Mulliken GH, Musallam S, Andersen RA. 2008. Forward estimation of movement state in posterior parietal cortex. Proc Natl Acad Sci U S A 105:8170–8177.

Ní Choisdealbha Á, Brady N, Maguinness C. 2011. Differing roles for the dominant and non-dominant hands in the hand laterality task. Exp Brain Res 211:73–85.

Parsons LM. 1987a. Imagined spatial transformation of one's body. J Exp Psychol Gen 116:172–191.

Parsons LM. 1987b. Imagined spatial transformations of one's hands and feet. Cognit Psychol 19:178–241.

Parsons LM. 1994. Temporal and kinematic properties of motor behavior reflected in mentally simulated action. J Exp Psychol Hum Percept Perform 20:709–730.

Parsons LM, Gabrieli JD, Phelps EA, Gazzaniga MS. 1998. Cerebrally lateralized mental representations of hand shape and movement. J Neurosci 18:6539–6548.

Pavani F, Spence C, Driver J. 2000. Visual capture of touch: out-of-the-body experiences with rubber gloves. Psychol Sci 11:353–359.

Pelgrims B, Michaux N, Olivier E, Andres M. 2011. Contribution of the primary motor cortex to motor imagery: a subthreshold TMS study. Hum Brain Mapp 32:1471–1482.

Petkova VI, Ehrsson HH. 2008. If I were you: perceptual illusion of body swapping. PLoS ONE 3:e3832.

Ramachandran VS, Hirstein W. 1998. The perception of phantom limbs. The D. O. Hebb lecture. Brain 121:1603–1630.

Reinersmann A, Haarmeyer GS, Blankenburg M, Frettlöh J, Krumova EK, Ocklenburg S, Maier C. 2010. Left is where the L is right. Significantly delayed reaction time in limb laterality recognition in both CRPS and phantom limb pain patients. Neurosci Lett 486:240–245.

Riemer M, Trojan J, Kleinböhl D, Hölzl R. 2010. Body posture affects tactile discrimination and identification of fingers and hands. Exp Brain Res 206:47–57.

Saimpont A, Pozzo T, Papaxanthis C. 2009. Aging affects the mental rotation of left and right hands. PLoS ONE 4:e6714.

Sauner D, Bestmann S, Siebner HR, Rothwell JC. 2006. No evidence for a substantial involvement of primary motor hand area in handedness judgements: a transcranial magnetic stimulation study. Eur J Neurosci 23:2215–2224.

Schwoebel J, Friedman R, Duda N, Coslett HB. 2001. Pain and the body schema: evidence for peripheral effects on mental representations of movement. Brain 124:2098–2104.

Sekiyama K. 1982. Kinesthetic aspects of mental representations in the identification of left and right hands. Percept Psychophys 32:89–95.

Sharma N, Jones PS, Carpenter TA, Baron JC. 2008. Mapping the involvement of BA 4a and 4p during Motor Imagery. Neuroimage 41:92–99.

Shenton JT, Schwoebel J, Coslett HB. 2004. Mental motor imagery and the body schema: evidence for proprioceptive dominance. Neurosci Lett 370:19–24.

Shepard R. 1978. The mental image. Am Psychol 33:125.

Sirigu A, Duhamel JR. 2001. Motor and visual imagery as two complementary but neurally dissociable mental processes. J Cogn Neurosci 13:910–919.

Sirigu A, Cohen L, Duhamel JR, Pillon B, Dubois B, Agid Y, Pierrot-Deseilligny C. 1995. Congruent unilateral impairments for real and imagined hand movements. Neuroreport 6:997–1001.

Slater M, Perez-Marcos D, Ehrsson HH, Sanchez-Vives MV. 2009. Inducing illusory ownership of a virtual body. Front Neurosci 3:214–220.

ter Horst AC, van Lier R, Steenbergen B. 2010. Mental rotation task of hands: differential influence number of rotational axes. Exp Brain Res 203:347–354.

Tin C, Poon CS. 2005. Internal models in sensorimotor integration: perspectives from adaptive control theory. Journal of Neural Engineering 2:S147–163.

Tomasino B, Toraldo A, Rumiati RI. 2003. Dissociation between the mental rotation of visual images and motor images in unilateral brain-damaged patients. Brain Cogn 51:368–371.

van Elk M, Viswanathan S, van Schie HT, Bekkering H, Grafton ST. 2012. Pouring or chilling a bottle of wine: an fMRI study on the prospective planning of object-directed actions. Exp Brain Res 218:189–200.

Vargas CD, Olivier E, Craighero L, Fadiga L, Duhamel JR, Sirigu A. 2004. The Influence of Hand Posture on Corticospinal Excitability during Motor Imagery: A Transcranial Magnetic Stimulation Study. Cereb Cortex 14:1200–1206.

Viswanathan S, Fritz C, Grafton ST. 2012. Telling the Right Hand From the Left Hand Multisensory Integration, Not Motor Imagery, Solves the Problem. Psychological Science 23:598–607.

Williams J, Anderson V, Reddihough DS, Reid SM, Vijayakumar N, Wilson PH. 2011. A comparison of motor imagery performance in children with spastic hemiplegia and developmental coordination disorder. J Clin Exp Neuropsychol 33:273–282.

Zacks JM, Ollinger JM, Sheridan MA, Tversky B. 2002. A parametric study of mental spatial transformations of bodies. Neuroimage 16:857–872.