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The Mirror Illusion's Effects on Body State Estimation

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Abstract

The mirror illusion uses a standard mirror to create a compelling illusion in which movements of one limb seem to be made by the other hidden limb. In this paper we adapt a motor control framework to examine which estimates of the body's configuration are affected by the illusion. We propose that the illusion primarily alters estimates related to upcoming states of the body (the desired state and the predicted state), with smaller effects on the estimate of the body state prior to movement initiation. Support for this proposal is provided both by behavioral effects of the illusion as well as neuroimaging evidence from one neural region, V6A, that is critically involved in the mirror illusion and limb state estimation more generally.

Keywords

Body state estimate; mirror illusion; mirror therapy; V6A

Skilled motor behavior requires that the brain maintains a continually updated estimate of the configuration of the body's segments, sometimes referred to as the body "state".

Researchers in the field of motor control have long puzzled over how such an estimate is derived (for thorough introductions, see Sarlegna & Sainburg, 2009, Shadmehr, Smith, & Krakauer, 2010). However, it is generally agreed that multiple body state estimates are generated over the course of movement planning and execution. These state estimates are derived from a combination of current sensory input (primarily vision and proprioception) and the anticipated sensory input that would result from a particular motor command (generated from so-called "forward models", which we will describe below).

In this paper, we will focus on how one experimental paradigm, the mirror illusion, has been used to examine the processes contributing to body state estimation. Although the technique is quite simple, it allows researchers to tease apart and explore the factors that influence the body state estimate that are otherwise intricately intertwined outside of the mirror environment. In a typical experimental setup, a mirror is aligned sagittally midway between the participant's two limbs (see Figure 1). When the limb facing the reflective surface moves, it provides mirrored visual feedback of movement that is attributed to the limb hidden behind the mirror. If the two limbs are placed asymmetrically relative to the mirror, the mirrored visual feedback about the hidden limb does not match the motor command sent to, or the proprioceptive feedback from, that limb. This dissociation is exploited to examine

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how the brain estimates the state of the hidden limb when it performs goal-directed movement.

Although it is clear that the mirror illusion alters the perceived state of the body, to date there have been few links drawn between the mirror illusion's effects and the proposals made by current models of motor control regarding body state estimation. One of the goals of the present paper is to begin to address this limitation in the literature. We will begin by reviewing the distinctions between a number of interrelated body state estimates that might evolve in the course of movement planning and execution. We adapt these distinctions from an influential framework of motor control (Wolpert & Ghahramani, 2000). Next, we attempt to link existing behavioral results from the mirror illusion literature to changes in specific estimates of the body state. Then, we review studies of the neural substrates of the mirror illusion, in particular the involvement of area V6A, as well as how other studies of V6A's role in body representation may inform our understanding of the mirror illusion. Finally, we briefly review the therapeutic use of the mirror illusion.

It is important to note that our proposed links between the effects of the mirror illusion and the various body state estimates are primarily derived from logic rather than direct experimental examination. Accordingly, they should be viewed speculatively. Nonetheless, we hope our discussion will encourage other researchers to pursue experiments that more directly test our ideas as well as those that would further expand upon them. Such experiments could have potentially important implications for both our understanding of body state estimation as well as the therapeutic application of the mirror illusion to improve the lives of individuals with sensorimotor disorders.

Multiple body state estimates during movement production cycle

According to Wolpert's theory of motor control (Wolpert & Ghahramani, 2000), the state of the body is estimated across different stages throughout the motor planning and execution process. The putative body state estimates are important inputs to, and outputs from, sensorimotor transformation modules known as internal models. An "inverse" model transforms the goal of the action and the body state at the start of the movement into a motor command that accomplishes the action's goal. In contrast, a "forward" model takes in a motor command and generates a predicted state of the body given that command, as well as the corresponding sensory feedback that would result from it.

As a concrete example of this process, when a given motor act is intended (e.g., grasping a cup of coffee), an estimate of the *initial state* of the hand is generated to capture its current position and posture (e.g., my hand is palm down on the keyboard of my laptop). In addition, a *desired state* must be developed that accomplishes the goal of the action (e.g., my hand around the coffee cup so that I can then lift it to my mouth). These two state estimates are fed into an inverse internal model that computes parameters of the motor program to transform the initial state into the desired state. The motor command is then executed, producing a change in the limbs' positions. In tandem, a copy of the program (the efference copy) is routed to the forward model, which projects out an estimate of the *predicted state* of the hand on its way to the cup given the motor command. This predicted state estimate

predicts how the hand should look and feel as the motor command is executed. Finally, incoming multisensory input is integrated during the execution of the reaching movement to estimate the *feedback state* of the body. The predicted and feedback states are then compared so that any discrepancy between them can be used to modify the inverse and forward models to make future performance more accurate, as well as inform the initial state estimate of subsequent movements. These processes are summarized in Figure 2.

The mirror illusion and the body state estimates

A number of behavioral studies show that the illusory visual representation of a limb reflected on a sagittal mirror is considered by the brain to be a reliable source for gauging the state of the limb concealed behind it. A study by Holmes, Crozier, and Spence (2004) provides a prototypical illustration of the phenomenon (see also Jax, Rosa-Leyra, & Coslett, 2015; Kunz, Creem-Regehr, & Thompson, 2010; Romano, Bottini, & Maravita, 2013). In the study the experimenter placed the left hand of participants 12 cm to the left of the reflective surface of a sagittal mirror. The participant's occluded right hand was then placed either 12, 5, or 19 cm to the right of the mirror, while its apparent visual location was always at the 12-cm spot. Across trials, participants reached forward with their hidden right index finger to a target that was always aligned to the 12 cm hand location. In trials where the proprioceptive and visual locations of the hand were mismatched, terminal reaching errors indicated a systematic bias towards the initial hand location of the visible arm, reflected by the mirror. That is, participants' fingers landed to the right of the target when their right hand started at the 19 cm location, and to the left of the target when they started at the 5 cm location. The magnitude of this directional bias was reduced threefold when the mirrored visual feedback was removed by covering the mirror.

Given these results, which body state estimates from the Wolpert model could have been altered by the mirrored visual feedback? In the following sections, we propose how at least three forms of the body state estimate (the initial, the desired, and the predicted) may have been affected.

The initial state estimate

One straightforward explanation of the reaching error in the Holmes, Crozier, and Spence (2004) setup confines the cause of the reaching errors to an altered estimate of the initial state of the right hand. In their study, Holmes and colleagues only provided mirrored feedback of the right hand *before* the start of the movement. The motor system may have assigned more weight to the mirrored visual input than the concurrent proprioceptive input in the estimate of the initial hand location. If this occurred, the subsequent motor command would be incorrect because the trajectory to the desired state would be based on the misspecified initial location. On the above parsing, then, the mirror image only alters the estimate of the initial state. This primary misspecification triggers a chain of secondary misspecifications that are carried down the planning and execution pipeline.

The desired state estimate

Primary alteration of the initial state alone could be sufficient to produce the terminal error reported by Holmes and colleagues (2004). However, the results from at least one subsequent study indicate the mirror may also have influenced the desired state estimate. Support for this hypothesis comes from a study by Snijders, Holmes, and Spence (2007). Snijders and colleagues capitalized on a prior observation that the motor system does not weigh evidence from the two primary body state relevant sensory modalities (vision and proprioception) equally under all conditions. For example, proprioception is assigned relatively more weight for movements along the radial plane (towards and away from the body) and visual information is assigned relatively more weight for movements along the azimuth (i.e., sideways; van Beers, Wolpert, & Haggard, 2002). Accordingly, Snijders and colleagues designed a study similar to Holmes and colleagues (2004) but had participants reach for targets placed along the radial plane (i.e., reaching forward) and along the azimuth (i.e., reaching to the side). Critically, in both conditions there was an equal mismatch at the start of the movement between the visual and proprioceptive hand location along the axis perpendicular to the reaching axis. What differed between conditions was simply the upcoming direction of movement. If the mirror-induced mismatch only alters the brain's initial state estimate, then the magnitude of the terminal errors should be equivalent in both conditions.

Results from the study, however, showed that systematic endpoint reaching errors along the azimuth were larger than errors along the radial axis. The fact that both conditions resulted in reaching error indicates that the initial hand location was misspecified irrespective of the intended reaching direction. However, the finding that the end position of the target affected the magnitude of the mirror's effect suggests that an additional body state estimate must have also been misspecified. If participants in the study followed the instructions to perform fast, uncorrected, movements to the target, then their movements should not have relied critically on the feedback state estimate because they were not modifying their preplanned movements. Instead, we propose that the source of the additional error pertains to the direction-specific influence of proprioception on the estimate of the desired state of the hand. When the target required movement along the azimuth, proprioception provided relatively more accurate estimate of the desired state of the hand in relation to the target. Thus, terminal error in this condition largely results from a misspecified initial-hand state. When the target required radial movement, the terminal error was a combination of the misspecified initial hand state and relatively more inaccurate specification of the desired state of the hand in relation to the target.

The predicted state estimate

Finally, there is indirect evidence that the estimate of the predicted body state may also be influenced in the mirror context. Although the mirror illusion can be induced by simply placing the limbs in the mirror context (Holmes & Spence, 2005; Holmes et al., 2006; Snijders et al 2007), other studies have required that participants perform cycles of synchronous bimanual movements prior to engaging in the main reaching task (e.g., Guerraz et al., 2012; Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005; Metral et al., 2015). One study (Holmes & Spence, 2005) showed that the magnitude of the illusion (1)

was stronger when preceded by active bimanual movement than passive viewing without movement and (2) increased incrementally as the duration of bimanual movement increased (4, 8, or 12 seconds). Thus, although mere visual exposure can induce the illusion, it is strengthened by active bimanual movement.

Consider how the afferent and efferent signals underlying these bimanual movements might work. A motor command for flexing the hidden hand is programmed, followed by an efference copy that is sent to the forward model to predict the visual and proprioceptive outcomes of the command. During execution of the flexion command, the proprioceptive feedback arising from the hidden hand confirms the predicted proprioceptive correlates of flexion. Given that the hand is occluded, the predicted visual correlates of flexion have no direct match from the hidden hand's visual feedback. Instead, the visual feedback reflected from the visible hand is received in tandem with the predicted feedback. Since the bimanual flexion is synchronous, but the hands are asymmetrically placed around the mirror, the reflected visual feedback will be consistent with almost all of the kinematic information specified by the hidden hand's command. The spatial disparity between the visual location of the hand as predicted by the command and the visual location as specified by the reflected feedback constitutes the only major mismatch. Over time, the forward model could recalibrate, in much the same way as in sensorimotor adaptation studies (Krakauer, Ghilardi, & Ghez, 1999). That is, the forward model could "learn" to generate a displaced visual prediction of the hand's location alongside the veridical proprioceptive location. This recalibration may alter the later estimate of the predicted state of the body in the subsequent reaching task. Specifically, the estimate of the predicted state of the body generated by the reaching command inherits a normalized mismatch between the proprioceptive and visual correlates of reaching. One way to directly examine this hypothesis may involve exploring if a mirror aftereffect could be detected after extensive mirror reaching in much the same way that other forms of adaptation produce aftereffects (Krakauer, Ghilardi, & Ghez, 1999).

Area V6A and the mirror illusion

Our review of the behavioral effects of the mirror illusion indicates that the initial, desired, and predicted body state estimates may be affected by the mirror illusion. In the following sections, we review how studies of area V6A may further inform our understanding of the mirror illusion's effects on the body state estimates. V6A, localized on the mesial wall of the posterior parietal lobe, is a multisensory node in a dorso-medial circuit comprising the medial intraparietal sulcus (mIPS) and the dorsal premotor cortex (PMd). V6A is thought to subserve sensorimotor integration and motor planning for the upper limbs (Gallivan, McLean, Smith, & Culham, 2011), while the lower limbs seem to be subserved by more anterior areas in the precuneus (Leone, Heed, Toni, & Medendorp, 2014). Our focus on V6A is driven by the fact that its contribution to the limb state estimate has the most converging support from both neuroimaging studies of the mirror illusion as well as from an independent body of neuroimaging literature on limb state estimation. [A thorough review of all brain areas engaged during the mirror illusion can be found in Deconinck and colleagues (2015)]. We first review the potential contribution of V6A in the mirror context before turning to evidence about V6A outside of the realm of the mirror illusion. As with the studies focusing on the behavioral effects of the illusion, few of the neuroimaging studies we

cite were specifically designed to distinguish between the putative multiple body state estimates. Thus, our discussion must again be viewed as speculative. We present our review, however, as potentially converging evidence for the behavioral data reviewed above.

Christian Dohle and his group have reported consistent activation of V6A in mirror-like sensorimotor contexts across several studies (Dohle et al., 2004; 2011; Mehnert et al., 2013; Wang et al., 2013a; 2013b). In an early study, Dohle and colleagues (2004) projected onto a screen a finger-opposition movement performed by the participant's occluded right hand so that it appeared as a left-hand movement. Participants always fixated the hand displayed on the screen. Perception of mirrored visual feedback from the (stationary) left hand was accompanied by increased activity strictly lateralized to right V6A; that is, in the hemisphere that would normally represent left hand movement. Later studies replicated the involvement of V6A contralateral to mirrored visual movement (Dohle et al., 2011; Mehnert et al., 2013). In addition, although V6A activity in the hemisphere ipsilateral to the stationary hand was lower than the corresponding activity in the contralateral hemisphere, the activity in contralateral V6A was still higher than the resting baseline level. Thus, under mirror illusion conditions, V6A regions in both hemispheres are simultaneously engaged in computation of the state of the contralateral limb.

Which of the four body state estimates might the above V6A activity reflect? Intuitively, the activation profile in the above studies is most consistent with stimulus-driven feedback processing, and therefore may most strongly implicate the feedback state estimate. V6A may be a sensory feedback hub that tracks the feedback state of the contralateral limb, while assigning more weight to visual information relative to proprioceptive information. However, results from at least one study may indicate that the V6A limb state estimate may not be strictly feedback driven (Wang et al., 2013a). In this study, when a participant passively observed another person's hand movement lateralized to the side of their stationary hand, the activity of the contralateral V6A diminished relative to when the mirrored image was produced by movement of the participant's own other hand. This indicates that visual feedback alone cannot account for the involvement of V6A in the mirror illusion. Programming and execution of relevant motor commands are essential drivers of the estimation processes in V6A.

Area V6A outside of the mirror context

Although there is clear evidence for the role that V6A plays in the mirror illusion, the neuroimaging studies cited above fail to clearly discern whether V6A primarily specifies information about the initial, desired, predicted, or feedback state estimates. Neuroimaging studies run outside of the mirror illusion context may shed light on the particular body state estimates that are computed by V6A. Given that (to our knowledge) no study has specifically been designed to address this issue, we cannot directly link V6A to a specific body state estimate. However, careful examination of several studies of V6A may allow us to logically eliminate the involvement of V6A in all but one (or more) of these state estimates. Of course, inference based on this stepwise elimination strategy is suggestive pending further direct investigation.

Ruling out the feedback state estimate

First, there is straightforward evidence corroborating our conjecture that V6A is not primarily a feedback processing node. V6A has repeatedly been found to carry action-relevant information prior to action onset. Since, by definition, the feedback state is constituted by sensory input during motor execution, the reliable pre-execution activity of V6A indicates that it is not primarily a feedback node.

One example of a study reporting V6A activity prior to movement initiation comes from Gallivan and colleagues (Gallivan, McLean, Smith, & Culham, 2011). In this study participants fixated the center of a workspace where two lateral cubes were visible and then, a few seconds later, they were instructed to plan either a saccade or right-hand movement to one of the cubes. Finally, participants were cued to perform the planned action few seconds later. Using a machine-learning approach, the spatial distributions of the blood oxygen level-dependent (BOLD) signal over V6A voxels were analyzed during both the planning phase as well as a comparison phase immediately prior to presentation of the movement instructions. Information encoded in V6A predicted whether the upcoming movement involved the eye or the hand during the planning phase. In addition, V6A activation also predicted the direction of the upcoming movement, but only in the hand trials. In fact, later studies showed that finer information could be distilled out of V6A's voxels prior to movement (Gallivan, McLean, Flanagan, & Culham, 2013; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011). For example, V6A's preparatory activity predicted whether the participant planned a right-hand or left-hand reach to a central cube, and whether the reach was intended for touching or grasping the cube. Importantly, these effects were strongly lateralized to the contralateral V6A. Information gleaned from ipsilateral V6A had no predictive value. For equivalent findings using the standard BOLD signal amplitude change, see Fiehler, Burke, Bien, Roder, & Rosler, 2009; Parkinson, Condon, & Jackson, 2010; Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, 2006.

Thus, V6A seems to carry fine-grained information about the upcoming body state well before motor execution. Thus, it seems to be more involved in estimating the state of the body during one or more of the motor planning stages than in processing sensory feedback during motor execution. But which of these states is the most plausible candidate, the initial, desired, or predicted?

Ruling out the initial state estimate

There is also logical evidence that V6A does not primarily encode the initial state of the body during action planning. This may be found in the above studies, since the differential V6A activity was obtained even though participants had their hands placed in the same initial location across trials. Additional findings from fMRI studies using a different technique further support this claim. BOLD signal repetition suppression is a method that isolates neural populations specialized for processing a given type of information by detecting reductions in the BOLD signal upon repeated exposure to a target stimulus or target feature (relative to alternating between relevant and irrelevant stimuli or features). Using this method, Monaco and colleagues had participants use their unseen right hand to plan and execute a grasp of a bar that was presented with the same or a different orientation

across a pair of trials (Monaco et al., 2011). Importantly, participants initiated the hand movement from the same position in both of the repeated-orientation and nonrepeated-orientation trial pairs. Thus, if V6A encodes the initial hand position, the amplitude of its signal should drop in the second trial of both repeated and nonrepeated trial pairs. Results indicated that reduction of V6A activity was reliable only on the repeated-orientation trials. Importantly, this transient functional efficiency was not evident when participants only looked at the bars without planning hand action. In a later study (Monaco, Sedda, Cavina-Pratesi, & Culham, 2015), participants reached for and grasped an object whose location and size were independently either repeated or changed from the previous trial. Although the initial position was the same in both trial types, V6A adapted only in the repeat size trials and the repeat location trials, but not in the nonrepeat trials.

These studies show that V6A activity is modulated during movement tasks even when the initial body state is held constant. Thus, V6A appears to code information about the potential future body state after movement initiation, implying it has importance in representing either the desired or predicted state estimate.

Could V6A encode the predicted state estimate?

The desired state of the body must be known early in the motor planning process, as it constitutes input to the inverse model which determines the motor command (see Figure 2). The predicted state, on the other hand, represents the expected motor and sensory consequences of an already determined motor command. Thus, time of activation during the planning and execution process may be one dimension that distinguishes these two body representations. It could be argued that, once exploited in the construction of the motor command, representation of the intended desired state subsides. Accordingly, it might not be vividly maintained through the execution stage of the movement. The predicted body state, on the other hand, emerges prior to movement initiation and is maintained throughout the execution phase to subserve its initial function of monitoring motor performance. It tentatively follows from the above, then, that if V6A activity bridges the planning and execution phases, then it most likely represents the predicted state of the body. Several studies do indeed show that movement-specific V6A activity can be demonstrated during the execution phase of action.

Filimon and colleagues (Filimon, Nelson, Huang, & Sereno, 2009) had participants execute either a reach or saccade to one of five horizontal targets, while their reaching hand could be directly perceived or not. Relative to baseline, the BOLD signal of V6A was higher during execution of a reach relative to a saccade. Cavina-Pratesi and colleagues (Cavina-Pratesi et al., 2010) had participants execute either a saccade, touch, or grasp to a cube placed far from their initial right-hand position, in either the left or right hemispaces. Relative to saccades, both hand actions elicited higher BOLD signal in the contralateral V6A. This suggests that this region is active during motor execution, not just planning prior to movement onset.

Further support for the conjecture that V6A is more sensitive to the predicted consequences of already programmed motor commands than to programming of the desired state comes from a study that examined the response of V6A both before and after training participants on arbitrary stimulus-response pairings (Tosoni, Galati, Romani, & Corbetta, 2008). At

baseline, V6A did not show any differential activity to centrally-fixated photos of faces and places. Participants were then trained to plan and perform a delayed saccade when a face was presented, or a delayed hand pointing when a place was presented. In both conditions, the movement was aimed at a peripheral visual target briefly presented alongside the arbitrary stimulus. The stimulus-response pairings were counterbalanced across participants. Thus, after training, there were two levels of sensory inputs driving the programming of the saccade and reach motor commands. The arbitrary stimulus drove the choice of the effector and the peripheral spatial stimulus drove the choice of the desired goal of the motor command. Results showed that V6A activity did not correlate with either of the two precursors to motor programming. Instead, V6A was only active when the programmed motor command would result in upcoming hand displacement.

Thus, the evidence that V6A is one of the information nodes involved in the estimation of the limb state during the mirror illusion suggests that it is unlikely to be a mere feedback hub. Nor does it seem to subserve the estimation of an initial state during action planning. Tentatively, V6A seems to be predominantly involved in estimating the state of the limb at one of the stages that “sandwich” the generation of the motor command (the desired or predicted state). We sided here with the possibility that V6A information encodes the predicted state of the body as the programmed motor command gets executed. More direct investigation is required to support this conjecture, however.

The mirror illusion and rehabilitation

In addition to its usefulness as a tool to understand how the brain integrates vision, proprioception, and predictions from the forward model to maintain body state estimates, the mirror illusion has also been used in the rehabilitation of sensorimotor deficits (for a review, see Ramachandran & Altschuler, 2009). In the final section, we briefly review the application of mirror therapy to two populations, individuals with phantom limb pain and individuals with post-stroke hemiparesis, both of which illustrate the role that body state estimates and V6A may play in the rehabilitation process. We do so to highlight that developing a better understanding of the perceptual-motor processes that are affected by the mirror illusion may lead to improved rehabilitation outcomes.

The mirror therapy setup for an individual with phantom limb pain entails placing the intact limb on the reflective side of the mirror and the amputated limb behind the mirror. When she attempts to move the phantom limb while viewing the mirrored visual feedback from the intact limb, the individual's pain may be reduced, sometimes almost immediately (Boesch, Bellan, Moseley, & Stanton, 2016; Ramachandran, Rogers-Ramachandran, & Cobb, 1995). A recent treatment study provides clear evidence that the body state estimates affect, and are affected by, mirror therapy (Foell, Bekrater-Bodmann, Diers, & Flor, 2014). Foell and colleagues observed a strong relationship between (1) the perceived similarity between the phantom and intact limbs and (2) reduction in pain over 4 weeks of mirror therapy. Individuals whose phantom limbs were sized similarly to the pre-amputation limb, and thus for whom the mirrored visual feedback closely matched the phantom, experienced a 51.2% decrease in phantom limb pain. In contrast, individuals whose phantom limbs were shortened so that the distal portion of the arm is perceived near the residual limb

(“telescoping”), and thus for whom the mirrored visual feedback did not match the phantom, experienced less than a 1% reduction in pain. The representation of the limb state in the latter group of individuals with telescopic phantoms was affected by mirror therapy, however. Over the course of therapy they reported an increase in their ability to “relate the movement seen in the mirror with their phantom limb” (Foell et al., 2014, p. 731). No such change was reported without a telescopic phantom. Although post-treatment ratings on this measure were lower for the telescopic group than the non-telescopic group, future studies could investigate whether a longer duration of mirror therapy may further improve the perceived match between phantom and mirror feedback in the telescopic group, which in turn may lead to reduced pain.

Mirror therapy for post-stroke hemiparesis uses a similar setup to improve functioning of the impaired contralesional limb by providing false visual feedback in which the impaired arm’s movements (made behind the mirror) appear to be made as skillfully as the unimpaired arm located on the reflective side of the mirror. Several randomized control trials have confirmed that mirror therapy improves measures of movement production (Dohle et al., 2009; Michielsen et al., 2011; Radajewska et al., 2013; Thieme et al., 2013; Wu, Huang, Chen, Lin, & Yang, 2013; Yavuzer et al., 2008; see Thieme, Mehrholz, Pohl, Behrens, and Dohle, 2013 for review). One recent mirror therapy study clearly supports our earlier suggestions about the critical role of V6A in the mirror illusion. Brunetti and colleagues (2015) tracked the improvement of post-stroke patients undergoing intensive mirror therapy in the first month following stroke. Only patients whose baseline V6A activity was successfully lateralized by the mirror illusion (i.e., increased ipsilesional V6A and decreased contralesional V6A activity) showed reliable motor function benefits from mirror therapy. Based on this result, future therapies could augment mirror therapy with concurrent noninvasive brain stimulation to potentially increase the therapeutic benefits of mirror therapy.

Conclusions

In summary, in this paper we have reviewed how the mirror illusion may affect a number of body state estimates proposed by a prominent model of motor control (Wolpert & Ghahramani, 2000). Using evidence from both behavioral studies of the mirror illusion and a range of neuroimaging studies of area V6A, an area critically involved in the mirror illusion, we propose that the mirror illusion primarily affects estimates related to upcoming states of the body (the desired state and the predicted state), with smaller effects on the estimate of the initial state of the body. We find little evidence that the mirror illusion affects the estimate of body state derived from sensory information after movement execution (the feedback state). These claims, as we have noted, remain quite speculative and future research will be required to confirm them. Such research, however, may shed further light on how the brain maintains a dynamic representation of the body state and may potentially improve the application of the mirror illusion to those suffering from sensorimotor disorders.

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Figure 1.
The mirror illusion setup.

Figure 2.

An illustration summarizing the process of movement planning and execution, including the body state estimates available at each processing stage.