

The man who executed “imagined” movements: Evidence for dissociable components of the body schema

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Abstract

We examined the nature of representations underlying motor imagery and execution in a patient (CW) with bilateral parietal lesions. When imagining hand movements, CW executed the imagined motor act but was unaware of the movements. These movements were significantly more accurate than volitional movements for the left but not right hand. CW also exhibited preserved motor imagery for the left but not right hand. Consistent with previous accounts, these findings suggest that motor imagery may normally involve the inhibition of movements. CW’s unawareness of movements during motor imagery may reflect inattention or misattribution of the unexpected sensory feedback. Furthermore, in line with current models of motor control, motor imagery may depend on the integrity of a “forward model” derived from motor outflow information to generate a prediction of the consequences of a motor command. Such predictions appear to be preserved for imagery of left but not right hand movements in CW. Action may additionally depend on precise updating of effector position derived from the comparison of predicted and actual sensory information. We propose that CW’s impaired volitional movements may be attributable to the degradation of such an updating mechanism. © 2002 Elsevier Science (USA). All rights reserved.

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1. Introduction

Converging evidence from neuroimaging and psychophysical investigations suggests that both real and imagined movements may depend on similar processes. For example, several recent positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) investigations have revealed similar patterns of neural activity involving areas underlying motor planning (i.e., dorsolateral prefrontal cortex, inferior frontal cortex, and the posterior parietal cortex) as well as motor execution (i.e., motor cortex, premotor cortex, lateral cerebellum, and basal

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ganglia) for both motor imagery and motor execution tasks (Decety et al., 1994; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Lotze et al., 1999; Parsons & Fox, 1998; Porro et al., 1996; Roth et al., 1996; Stephan et al., 1995). Further, based on extensive psychophysical investigations demonstrating strong correlations between the times required to simulate and execute movements, Parsons (e.g., 1987 and 1994) has suggested that simulated movements may depend on the same on-line representation of body movement and position that guides actual movements. Parsons and Fox (1998, p. 586) state, “In summary, motor imagery appears generally to involve the same movement representation used by the executive motor processes—a unitary representation of movements as they occur, in accordance with the physical laws underlying motor control and implementing all physiological and pathophysiological constraints.” In agreement with this account, several investigators have suggested that the mental representations underlying motor imagery and execution differ primarily in that inhibitory processes suppress motor output during imagery (e.g., Lotze et al., 1999; Decety, 1996; Jeannerod, 1994).

However, Sirigu and colleagues have observed that while normals and patients with motor cortex damage display strong correlations between the times required to imagine and execute sequential finger movements, times for patients with parietal damage are poorly correlated (Sirigu et al., 1995, 1996). These findings suggest that the parietal cortex may be an important component of the neural substrate underlying motor imagery ability and, critically, that the representations underlying motor imagery and motor execution may differ in at least some respects.

Additional evidence supporting this claim comes from several observations. For example, Sirigu, Daprati, Pradat-Diehl, Franck, and Jeannerod (1999) recently demonstrated that patients with left parietal damage are impaired relative to controls on a task that requires them to determine whether observed finger movements are being executed by themselves or by the examiner. The patients were more likely to claim that movements executed by the examiner were actually executed by themselves even when the movements made by the examiner did not precisely match the movements made at the same time (but out of sight) by the patient. For example, one patient, after a poorly executed movement, falsely attributed the well-executed movement made by the examiner to herself and exclaimed, “Tiens j’ai réussi cette fois!” (“Look, this time I succeeded!”). These findings were interpreted as indicating an impaired ability to compare an on-line representation of sensory feedback concerning finger movements with an internally generated representation of the planned finger movements (such a comparison is termed the “Sensory Comparator” and is shown in Fig. 1 and described below).

Reports of illusory movements in patients with anosognosia for hemiplegia (i.e., unawareness and explicit denial of hemiplegia) are also relevant in this context (Babinski, 1914; Feinberg, Roane, & Ali, 2000; Levine, Calvanio, & Rinn, 1991). For example, Feinberg et al. (2000) reported that after being asked to raise their plegic arms, 5 of 11 anosognosic patients reported raising their arm despite no actual movement. Further, Heilman, Barrett, and Adair (1998) observed a patient suffering from a right hemisphere stroke who claimed that when he attempted to move his contralateral arm he could feel it moving. As noted by these investigators, such confabulations concerning movements of a plegic limb suggest that some patients with anosognosia may deny their hemiplegia because they misconstrue neural activity associated with the planning of an intended movement as evidence of actual movement (in terms of the model illustrated in Fig. 1, may be a confusion between “Predicted Movement” and the “Proprioception/Sensation Feedback” resulting from actual hand movement). Thus, while the denial of hemiplegia is expressed in linguistic terms, the underlying cause of anosognosia for hemiplegia, on this account, is thought to be mediated not by language, but instead by a failure to discriminate between representations of predicted movements and representations of movement

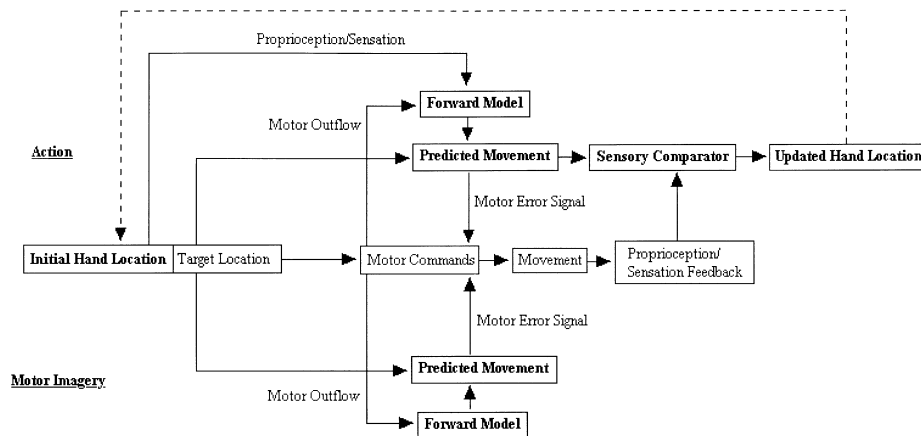


Fig. 1. A diagram illustrating the proposed model of movement control and the distinctions between processes underlying action (upper portion) and motor imagery (lower portion). CW's pattern of performance suggests a disruption of the Sensory Comparator for both left and right hand volitional movements and a disruption of the ability to generate Predicted Movements for the right but not left hand during motor imagery.

derived from sensory feedback. Consistent with this account, we recently observed a patient (JD) with left posterior parietal damage who exhibited impaired pointing accuracy (without vision) following passive movements of her arm, but a relatively preserved ability to update her pointing trajectory after active movements of her arm (Schwoebel, Coslett, & Buxbaum, 2001). For example, JD was able to point to the remembered position of a visual target after actively moving her hand to her nose, but was unable to point to the same target after the examiner moved her hand to her nose. These results suggest a possible dissociation between an on-line representation of movement derived from sensory information (i.e., Proprioception/Sensation Feedback), which appears to be impaired in JD, and an internally generated model of predicted movement (i.e., Predicted Movement), which appears to be relatively intact in JD.

In addition to evidence suggesting that predicted movements and sensory feedback from movements may be integrated (i.e., in a Sensory Comparator) in order to generate precise updates of effector location, there is also evidence suggesting that predicted hand movements are normally derived from two main sources: motor outflow/efferece copy information and initial sensory inflow information. This type of prediction is analogous to predicting whether shooting a basketball will be successful based on the motor command used to launch the ball and the initial observed trajectory of the ball. For movements, such a prediction, such as the final position of the hand when attempting to reach to a target, may be integrated with target location information in order to provide on-line corrective feedback during a reaching movement (Bard et al., 1999; Desmurget et al., 1999; Desmurget & Grafton, 2000; Van Sonderen, Gielen, & Denier, 1989; Wolpert, Ghahramani, & Jordan, 1995). For example, Bard et al. (1999) demonstrated that a deafferented patient could correct reaching trajectories, despite not being able to view her moving limb, in a double-step task in which target location was changed during the ocular saccade. Such corrections suggest the modification of initial motor commands based on forward models derived solely from motor outflow information. Importantly, the more accurate corrections made by control subjects suggest that forward models based on the integration of motor outflow and sensory inflow may normally produce better predictions of hand movement/location.

As illustrated in Fig. 1, which was adapted from Desmurget and Grafton (2000) and Wolpert et al., 1995, the above findings suggest the possibility that on-line

information about the position of the body in space—a level of representation which we (Buxbaum, Giovannetti, & Libon, 2000; Coslett, 1998; Schwoebel et al., 2001) and others (e.g., Head & Holmes, 1911–1912) have termed the “body schema”—may be composed of distinct representational modules.

Initial sensory inflow (e.g., Proprioception/Sensation) may be integrated with Motor Outflow information in a Forward Model that, in turn, generates a prediction or estimate of the dynamic and sensory consequences of a planned movement (i.e., Predicted Movement). Such a prediction may subsequently be compared with target location information in order to provide on-line corrective feedback to motor commands (i.e., Motor Error Signal). Additionally, the Predicted Movement may also be integrated (i.e., Sensory Comparator) with actual sensory information (i.e., Proprioception/Sensation Feedback) in order to generate a precise update of effector location (i.e., Updated Hand Location). We suggest that the components of this model that comprise the body schema (in bold) are the Initial Hand Location, Forward Model, Predicted Movements, Sensory Comparator, and the Updated Hand Location in that they are all critical to the accurate dynamic estimation of body position. Further, while we note that distinctions between the control of reaching and finger movements (i.e., grasping) have been proposed (Arbib, 1981), we suggest that these movements may be coordinated (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995) and may rely on body schema processes similar to those outlined above.

An important point to be noted in this context is that imagined movements differ in a critical way from executed movements in that they normally do not involve actual movement. Thus, while motor imagery and action may both be dependent on the generation of predicted movements, the forward model for action may be derived from both sensory and motor outflow information, while the forward model generated during motor imagery may depend primarily on motor outflow information. Further, only action is expected to involve the integration of predicted and actual sensory information by the sensory comparator. Indeed, as discussed further below, there is evidence suggesting that sensory information may normally be attenuated during motor imagery in order to reduce conflicting signals regarding movement (Craver-Lemley & Reeves, 1992).

We report data relevant to this account of the differences between motor imagery and motor execution. The investigations were motivated by initial observations of a patient (CW) with bilateral parietal lesions who generated movements, without awareness, while “imagining” such movements. Importantly, these movements appeared to be more fluid, precise, and effortless than movements generated with volition. First, we document our initial observations concerning CW’s failure to inhibit movements and unawareness of movements of both hands during motor imagery tasks. We also demonstrate, in two different tasks, that movements of CW’s left hand during imagery were more precise than volitional movements of the left hand. No differences were observed for right hand movements. Second, we examine the possibility that the impaired volitional left hand movements might be attributable to faulty updating of hand position due to the degradation of the Sensory Comparator.

2. Patient description

CW is a 67-year-old man who suffered a right hemisphere stroke manifested as dysarthria and mild left hemiparesis 4 years prior to the evaluation reported here. He improved substantially before suffering a second stroke 2 years later resulting in a moderately severe right hemiparesis, inability to walk, and language impairment. At the time of testing, he exhibited a mild anomic aphasia but not alexia. He correctly named 16 of the first 20 items of the Boston Naming Test. He read text aloud without error. His description of the Cookie Theft Picture of the Boston Diagnostic Aphasia

Examination (Goodglass & Kaplan, 1983) was normal. Visual fields were full to confrontation. Motor examination revealed that the right hand was moderately weak with mild pyramidal clumsiness. The left hand was strong but quite clumsy; he was

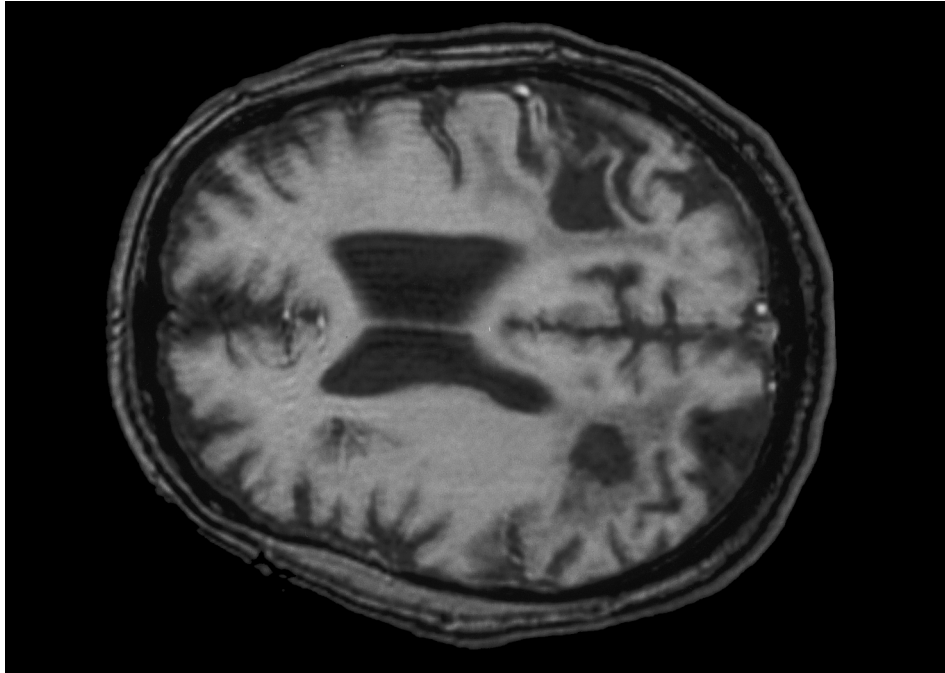


Fig. 2. A high ventricular section of a T1-weighted MRI demonstrating bilateral subcortical and cortical lesions involving posterior parietal cortex; left is greater than right.

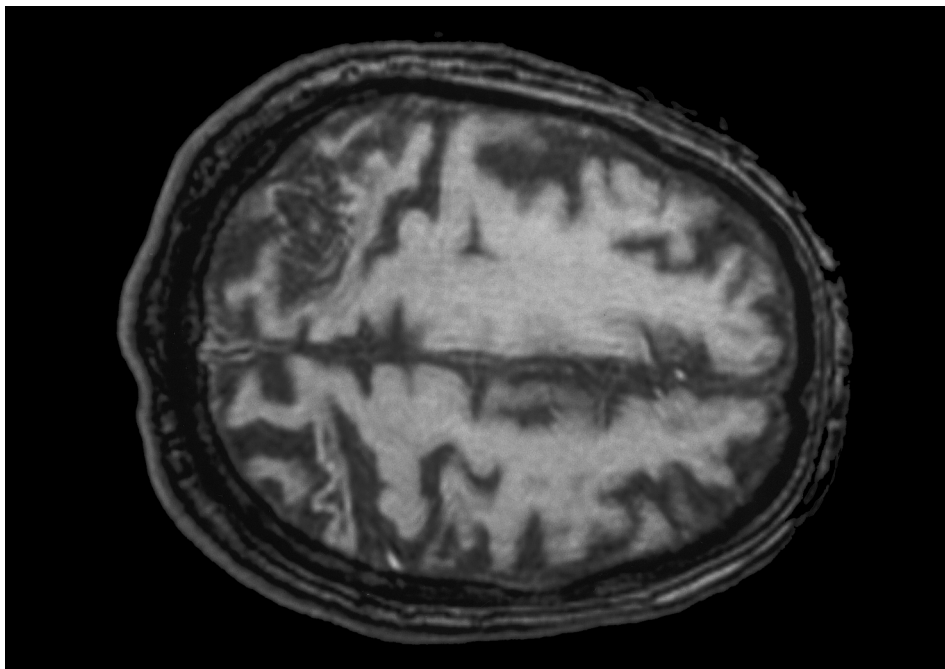


Fig. 3. Supraventricular section demonstrating encephalomalacia bilaterally and right superior parietal infarction.

unable to pick up a coin with the left hand. Sensation was reduced for all primary modalities in the right hand and arm; proprioception was impaired but he was able to correctly report the direction of finger movement for each of the fingers on the right hand. Sensation in the left hand was preserved to touch, temperature, and vibration. Proprioception was impaired at the distal interphalangeal joint but he reliably indicated the direction of small movements of the entire finger on the left hand. Proprioception was also assessed by asking the patient to touch the tips of his index fingers together with arms extended and eyes closed. He accomplished this on multiple trials without difficulty. There was no optic ataxia. Consistent with a previous report of unilateral apraxia following right superior parietal damage, CW exhibited ideomotor apraxia with the left but not the right hand (Heilman, Gonzalez-Rothi, Mack, Feinberg, & Watson, 1986). Magnetic resonance imaging (MRI) scans performed approximately 1 year after the second stroke revealed chronic infarctions involving the parietal lobes bilaterally, as shown in Figs. 2 and 3. The left hemisphere lesion appeared to involve Brodman areas 22 (posterior) as well as 39, 40, and 37. The right hemisphere lesion appeared to involve areas 1–3, 5, 39, and 40.

3. Experiments 1a and 1b

3.1. Experiment 1a

Methods. In order to confirm and extend our initial observation that CW exhibited movements of which he was unaware during motor imagery tasks, we used a task adapted from Sirigu et al. (1996) in which CW was asked to imagine and execute sequential finger movements of varying complexity. This task involved first imagining five different finger movements, each repeated five times in succession, and then executing the same movement sequences. The movements involved (1) touching the index finger and thumb, (2) raising the thumb, (3) crossing the index and middle fingers, (4) extending the index finger alone, and (5) simultaneously touching all five finger tips together. Both imagery and execution tasks were performed without vision. For both conditions, each trial began when the examiner said “go” and ended when CW completed the movement sequence. For the imagery conditions CW was instructed to say “stop” when he had completed each series of movements so that the examiner could record the time required to imagine each series. CW complied with this request and his stop signal corresponded with the completion of his actual movements observed by the examiner. Times were recorded by the examiner with a stopwatch. To assess the quality and accuracy of CW’s movements in the two conditions, six judges, who were naïve with respect to the issue under investigation, independently rated the accuracy of CW’s movements while watching a videotape of the left and right hands during both the imagery and execution conditions. Judges were instructed to watch the experimenter perform each target movement and then to watch CW perform the same movement sequence. After each movement sequence, judges indicated its accuracy on a Likert scale ranging from 1 (*unrecognizable as the target movement*) to 7 (*exact replication of the target movement*). Judges rated each of the five different movements for both the left and right hands during both the imagery and execution conditions for a total of 20 ratings.

Results. CW moved both the left and right hands during the imagery task, yet reported no awareness of the movements when questioned. The raters tended to agree on the accuracy of CW’s movements as indicated by the average correlation between ratings ($r = .85$) and the effective reliability of the ratings ($R = .97$).

As shown in Figs. 4 and 5, the movements of the left hand during the imagery task were significantly better than those produced when CW was instructed to execute left hand movements [$F(1, 29) = 58.96$, $p < .0001$]. Left hand movements were also



Fig. 4. Examples of CW's left hand movements in Experiment 1a when instructed to imagine (upper) and execute (lower) a movement which involved touching the index finger and thumb.

consistently faster during imagery ($M = 9.02$ s) than execution ($M = 11.89$ s) conditions (sign test, $p < .03$). No such advantages were observed for the right hand [accuracy: $F(1, 29) = 0.74$, $p < .40$; time: Imagery ($M = 15.93$ s) Execution ($M = 19.17$ s), sign test, $p < .31$].

3.2. Experiment 1b

Methods. In this task, CW was instructed to imagine or execute a thumb opposition movement to the site of tactile stimulation, which was delivered to the index, middle, or ring finger of the same hand. Responses were coded as correct if CW touched the same finger that was stimulated and incorrect if he touched a different

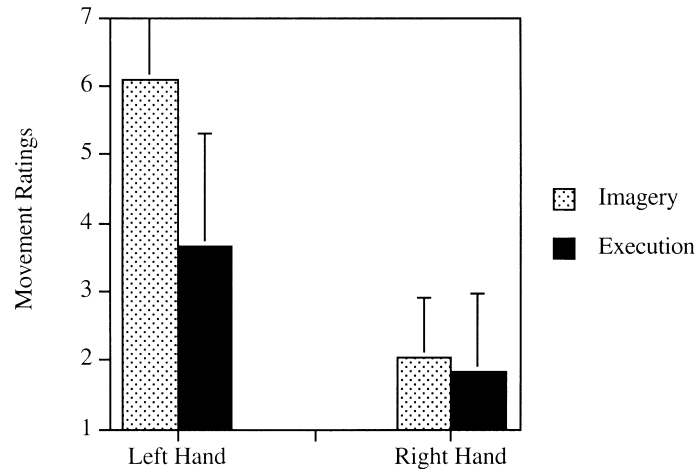


Fig. 5. Mean ratings of videotaped left and right hand finger movements during imagery and execution conditions of Experiment 1a. Ratings were made on a scale ranging from 1 (*unrecognizable as the target movement*) to 7 (*exact replication of the target movement*). Error bars indicate standard deviations.

finger. Both tasks were performed without vision. Blocks of nine trials were counterbalanced in an ABBA design (i.e., imagery, execution, execution, and imagery). There were a total of 36 trials for both the imagery and execution conditions of each hand for a total of 144 trials.

Results. Consistent with the findings of Experiment 1a, CW again produced movements during the imagery task, yet denied making such movements when questioned. Additionally, as shown in Fig. 6, greater accuracy for left hand movements was observed during motor imagery (69% correct) as compared to execution (47% correct) conditions; this advantage approached significance (Fisher's Exact $p < .09$). No such advantage was observed for right hand movements produced during imagery (42% correct) as compared to execution (39% correct) conditions (Fisher's Exact $p < .99$).

3.3. Discussion

These data from two different tasks confirm and extend our informal observations that CW (1) moved both hands during motor imagery tasks, (2) explicitly denied

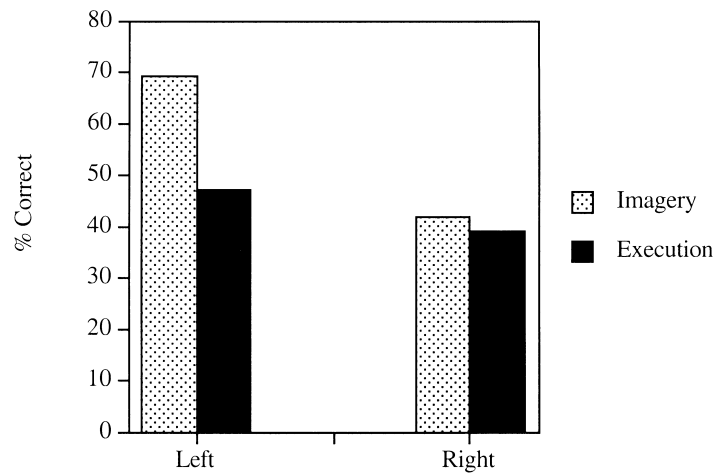


Fig. 6. Mean accuracy of left and right hand thumb opposition movements during imagery and execution conditions of Experiment 1b.

making these movements, and (3) exhibited improved movements of the left hand during imagery as compared to execution tasks. Before discussing the implications of these observations it should be noted that the movements observed during imagery conditions are not readily attributable to a misunderstanding of the instructions. CW complied with all other aspects of the experimental tasks (e.g., he performed the correct movement sequences, started on the “go” signal, and said “stop” at the completion of movements during the imagery trials).

How, then, can CW’s movements during imagery tasks be explained? One possible account is that CW was unable to inhibit movements during this task. The fact that neuroimaging investigations involving both PET (Decety et al., 1994; Grafton et al., 1996; Parsons & Fox, 1998; Stephan et al., 1995) and fMRI (Roth et al., 1996; Porro et al., 1996; Lotze et al., 1999) reveal largely overlapping patterns of activation during motor imagery and action has been interpreted by several investigators as evidence that motor imagery requires inhibition of action (e.g., Lotze et al., 1999; Decety, 1996; Jeannerod, 1994). In line with this interpretation, we suggest that CW complied with our request to imagine finger movements, yet failed to inhibit the motor consequences of this imagery. We return to this issue under General Discussion. Note that we do not suggest that CW exhibited a general impairment in inhibition. He exhibited no other behavioral or motor symptoms such as motor or speech perseveration or a tendency to vocalize when asked to read silently that would suggest that he was unable to inhibit actions in other contexts.

To explain CW’s unawareness of movements we appeal to a second important dimension on which action and motor imagery differ. Critically, sensory feedback is normally neither generated nor expected during motor imagery. We suggest, then, that there may be at least two possible accounts of CW’s unawareness of movements. First, he may have been unaware of movements during motor imagery because the unexpected sensory feedback was unattended or suppressed. We note that there is precedence for such a suggestion in the visual modality. Normal subjects perform less well on visual perceptual tasks while engaging in visual imagery (Perky, 1910; Craver-Lemley & Reeves, 1992). Second, CW may have misconstrued the unexpected sensory feedback as resulting from the predicted movements underlying motor imagery and thus denied actual movements. This possibility is consistent with accounts of anosognosia for hemiplegia (Levine et al., 1991; Feinberg et al., 2000; Heilman et al., 1998) as well as accounts of illusory movements of phantom limbs in amputee patients (Ramachandran & Hirstein, 1998), as discussed further under General Discussion.

Note that it is unlikely that a primary sensory deficit contributed substantially to CW’s deficit. While CW does have some degree of proprioceptive loss, sensory examination revealed that he was able to reliably detect movements of substantially lesser magnitude than those he exhibited during the motor imagery task. Furthermore, his ability to touch the fingers of his right and left hands with his eyes closed and his lack of impairment on activities of daily living also suggest that sensory loss alone would not be expected to result in the unawareness of movements during motor imagery.

The results from this experiment also confirm that, for the left hand, the movements generated during motor imagery are significantly more precise than those generated when attempting to move, while the movements in these two conditions were similarly impaired for the right hand. One account of CW’s better movements during the left but not right hand imagery conditions of Experiments 1a and 1b is that they reflect an intact ability to generate predicted movements and provide corrective feedback to motor commands for the left but not right hand in the context of an impaired ability to inhibit imagined actions. In contrast, the relatively impaired movements observed during execution conditions for both hands may reflect impaired updating of hand location due to degradation of the Sensory Comparator.

If the improved movements of CW's left but not right hand during imagery conditions were attributable to a relatively preserved generation of predicted movements for the left hand, then we would expect that CW would exhibit preserved motor imagery for the left but not right hand. Further, if preserved motor imagery of the left hand is observed, in conjunction with evidence for relatively intact proprioception of the left hand noted above, then impaired volitional movements of the left hand would be expected to reflect the degradation of the sensory comparator. To examine these possibilities, the integrity of CW's motor imagery was assessed in Experiments 2a and 2b. CW's hands were restrained in these experiments in order to obtain a valid assessment of his motor imagery abilities.

4. Experiments 2a and 2b

4.1. Experiment 2a

Methods. Motor imagery was assessed by asking CW to again imagine and perform sequential finger movements, as in Experiment 1a. Critically, however, in this experiment the examiner restrained CW's hand movements during the imagery conditions. The procedure was the same as in Experiment 1a except that a subset of four finger movement sequences were examined and CW's movements during the imagery condition were constrained by holding his hand flat against the table in front of him. Eighteen control participants imagined and executed each movement twice with each hand for a total of 32 trials. CW imagined and executed each movement four times with each hand for a total of 64 trials.

Results. As shown in Fig. 7, and as previously observed by Sirigu et al. (1996), reaction times for imagined and executed movements increased as a function of movement complexity for the normal controls [$F_s(3, 51) = 6.06, p < .0013$]. Imagined movement times for both the left and right hands tended to overestimate actual movement times (Left: $M = 20\%$ error, $SD = 10\%$; Right: $M = 19\%$ error, $SD = 9\%$), but there was no significant difference between the accuracy for predicting execution times for imagined movements of the left and right hands [$F(1, 17) = 0.53, p < .48$].

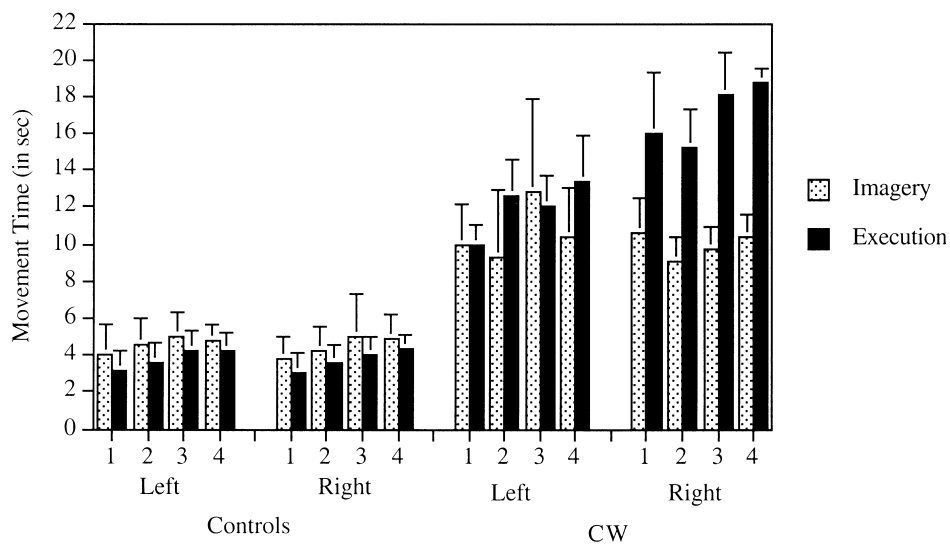


Fig. 7. Mean durations and standard deviations for imagined and executed movements of the left and right hands for both controls and CW in Experiment 2a.

In contrast, CW's ability to accurately predict actual movement times was significantly better for the left than the right hand [Left: $M = 25\%$ error, $SD = 18\%$; Right: $M = 40\%$ error, $SD = 12\%$; $F(1, 15) = 11.61$, $p < .004$]. Furthermore, whereas no significant difference was observed between CW's accuracy and the mean accuracy of the control participants for imagined movements of the left hand [$F(1, 32) = 0.68$, $p < .42$], CW was significantly less accurate than controls for the right hand [$F(1, 32) = 34.41$, $p < .0001$]. Note that while CW was able to accurately predict movement times through motor imagery of the left but not right hand, he was slower to execute movements of both the left and right hands compared to control participants [Left: $F(1, 32) = 214.01$, $p < .0001$; Right: $F(1, 32) = 433.69$, $p < .0001$].

4.2. Experiment 2b

Methods. In Experiment 2b, we attempted to replicate and extend the findings of Experiment 2a with a different motor imagery task. Parsons (1987, 1994) observed strong correlations between the time required to judge the laterality of pictured hands and the time required for participants to actually align their hands with stimuli. This suggests that participants may mentally align their hands with the pictured hands in order to make the laterality judgments. Furthermore, Parsons and colleagues have shown that, whereas split brain patients exhibit normal performance on the hand laterality task when a left or right hand is visually presented to the contralateral hemisphere (e.g., presenting a left hand to the right hemisphere), their laterality judgments are below chance when hands are presented to the ipsilateral hemisphere (Parsons, Gabrielli, Phelps, & Gazzaniga, 1998). This suggests that performance on this task may depend on lateralized forward models of left and right hand movements. Thus, this dissociation between forward models of left and right hand movements, in conjunction with the findings of Experiment 2a, further led us to expect CW to exhibit a preserved ability to imagine left hand movements despite an impaired ability to imagine right hand movements on this task. CW's movements were constrained in this task in order to examine the integrity of the body schema representations underlying his ability to identify left and right hands (i.e., predicted movements).

The examiner insured that CW's hands remained still throughout testing by holding CW's hands flat against the table in front of him. While CW's hands were constrained in this manner he was asked to discriminate right from left pictures of hands presented in varying orientations. Pictures of both left and right hands appeared either palm-up or palm-down in one of four orientations. Each hand appeared facing left (8 trials), right (8 trials), up (8 trials), or down (8 trials) for a total of 64 trials, which were presented randomly. Eighteen control participants were also tested using the same stimuli and were instructed to place their hands on the table in front of them and to not move their hands during testing.

Results. As shown in Fig. 8, while CW's performance was nonsignificantly different from the mean performance of the control participants when identifying left hand stimuli (CW: 84% correct; Controls: $M = 86\%$, $SD = 10\%$, Fisher's Exact $p > .99$) his ability to identify right hand stimuli was significantly impaired (CW: 50% correct; Controls: $M = 88\%$, $SD = 10\%$, Fisher's Exact $p < .0025$).

4.3. Discussion

The findings of Experiments 2a and 2b suggest that CW may have relatively preserved motor imagery of his left but not right hand despite an impaired ability to execute movements of both hands. As predicted, this pattern of findings is consistent with our suggestion that spared predicted movements derived from a forward model

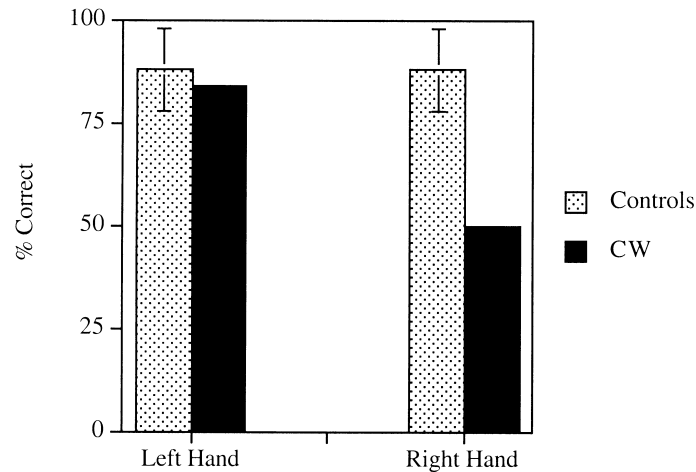


Fig. 8. Mean accuracy and standard deviations for hand laterality judgments for both controls and CW in Experiment 2b.

may underlie the improved movements of the left hand observed during imagery tasks in Experiments 1a and 1b. Furthermore, in conjunction with previous findings (Parsons et al., 1998), the present data suggest a lateralization of such forward models of movement. We have previously reported a similar asymmetry in motor imagery performance in patients with neglect (Coslett, 1998). When asked to perform the hand laterality task, patients with right hemisphere damage resulting in left neglect exhibited lower accuracy for pictures of left relative to right hands, suggesting an impaired ability to generate or monitor a forward model of left hand movements. Thus, consistent with previous findings, the present findings suggest the possibility that spared parietal areas in the right but not left hemispheres may account for the asymmetry in the accuracy of CW's motor imagery.

5. General discussion

Three major observations were reported. First, CW exhibited movements in the context of motor imagery tasks. Second, he was unaware of these movements and, in fact, explicitly denied that they occurred. Third, left hand movements produced when CW was attempting to imagine such movements were faster and more accurate than those produced when he attempted to execute left hand movements. The implications of these findings are discussed in turn.

First, while previous investigations of normal participants have demonstrated increases in electromyographic activity and motor evoked potentials limited to the muscles associated with simulated movements (Fadiga et al., 1999; Hashimoto & Rothwell, 1999; Kasai, Kawai, Kawanishi, & Yahagi, 1997; Wehner, Vogt, & Stadler, 1984), to the best of our knowledge, this is the first report of a patient who fully executes "imagined" movements. We suggest that CW complied with our request to imagine finger and hand movements, yet failed to inhibit the motor consequences of this imagery. We note that this account requires the assumption that the performance of motor imagery tasks normally entails the inhibition of action. While we are unaware of definitive experimental evidence regarding this matter, there are several lines of evidence which are consistent with this claim. A recent PET investigation contrasting imagined and executed movements demonstrated increased activity during imagery but suppressed activity during execution in the inferior frontal cortex, a brain region thought to be important to inhibitory processes (Deiber et al.,

1998). Additionally, studies using fMRI and electroencephalogram techniques to examine cortical activity associated with inhibition during Go/No-Go tasks have also implicated the inferior frontal cortex (Jackson, Jackson, & Roberts, 1999; Rubia et al., 2001). Interestingly, Rubia et al. (2001) also reported that activity in the posterior parietal region is selectively suppressed during No-Go trials requiring the inhibition of a manual response and that this modulation in activity is preceded by activity in the inferior frontal cortex. Disruption of this fronto-parietal articulation due to bilateral parietal damage may account for CW's failure to inhibit movements during motor imagery.

We suggest that CW's unawareness of movements is attributable to inattention or suppression of sensory information during motor imagery. This possibility is consistent with previous demonstrations of reduced sensitivity to visual stimuli during visual imagery (Craver-Lemley & Reeves, 1992) as well as reports of anosognosia for speech production errors in aphasic patients (Maher, Rothi, & Heilman, 1994; Shuren, Hammond, Maher, Rothi, & Heilman, 1995). An alternative, but not mutually exclusive, account of CW's unawareness of movement suggests that he may have failed to distinguish between the predicted movements generated by the forward model and actual sensory feedback from movements. A deficit at this level of representation may have led CW to misinterpret the unexpected sensory feedback as motor imagery resulting in his denial of movements during motor imagery tasks.

Consistent with the latter account of CW's unawareness of movement, previous accounts of anosognosia for hemiplegia suggest that anosognosic patients may interpret predicted movement as evidence of actual movement and thus deny their movement deficits (Levine et al., 1991; Feinberg et al., 2000; Heilman et al., 1998). Further, this suggestion is also consistent with an account of illusory volitional movements (e.g., reaching for objects and waving good-bye) of the phantom limbs of amputee patients (Ramachandran & Hirstein, 1998). That is, when speaking of motor area activity, Ramachandran & Hirstein (1998) state the following:

It is likely that these movement commands are simultaneously monitored by the parietal lobes which are concerned with body image. In a normal person, messages from the frontal lobe are sent either directly, or via the cerebellum, to the parietal lobes which monitor the commands and simultaneously receive feedback from the arm about its position and velocity of movement. There is, of course, no feedback from a phantom arm, but the monitoring of motor commands might continue to occur in the parietal lobes, and thus the patient vividly feels movements in the phantom. (p. 1620)

Last, CW exhibited improved movements of the left hand during imagery as compared to execution tasks. The findings of Experiments 2a and 2b are consistent with the suggestion that the improved movements may be attributable to a relatively spared generation of predicted movements for CW's left hand despite an impaired ability to integrate predicted movements with actual sensory feedback in order to generate precise updates of effector location. Thus, we suggest a functional dissociation between divisions of the body schema underlying motor imagery and execution; i.e., between predicted movements and the sensory comparator.

Consistent with this suggestion, a recent fMRI investigation has demonstrated different patterns of parietal area activations during motor imagery and execution (Gerardin et al., 2000). While motor imagery of sequential finger movements was associated with activity in posterior portions of superior and inferior parietal cortex (i.e., BAs 7 and 40), execution was associated with primary and secondary sensory areas (i.e., BAs 1–3 and SII and BAs 40 and 43).

Additionally, converging evidence from electrophysiological investigations in monkeys demonstrates that neurons in more anterior regions of the parietal cortex tend to begin responding after movement onset, respond to passive movements, and are suppressed by deafferentation. In contrast, neurons located in more posterior

regions tend to begin responding before movements, are not responsive to passive movements, and are unaffected by deafferentation. Thus, these findings also suggest an anterior–posterior distinction in the parietal cortex for the coding of sensory and centrally generated information (Burbaud, Doegle, Gross, & Bioulac, 1991; Kalaska, Caminiti, & Georgopoulos, 1983; Mountcastle, Lynch, Georgeopoulos, Sakata, & Acuna, 1975; Seal, Gross, & Bioulac, 1982). More recently, Desmurget et al. (1999) have also demonstrated that when transcranial magnetic stimulation (TMS) is applied over the contralateral posterior parietal cortex at the onset of a pointing movement, subjects fail to correct movement trajectories to reflect changes in target location in a double-step task, suggesting an important role for this area in generating corrective feedback from a comparison of target location and the predicted endpoint of a reaching movement. Thus, functional imaging, electrophysiological, and TMS findings indicate that posterior parietal areas may serve as the substrate for predicted movements derived from a forward model, while additional activation in more anterior parietal areas may be necessary for the comparison of the predicted movement with sensory feedback.

In sum, consistent with previous accounts (e.g., Lotze et al., 1999; Decety, 1996; Jeannerod, 1994), the present findings suggest that motor imagery may normally involve the inhibition of actual movements at some level. Further CW's uninhibited movements during motor imagery tasks suggest that the parietal areas may normally play a critical role in such inhibitory processes. Further, in line with findings reported by Sirigu and colleagues, CW's pattern of performance on motor imagery and execution tasks suggests that parietal areas may also be critically involved in the generation and guidance of imagined and actual movements (Sirigu et al., 1996, 1999). However, contrary to accounts suggesting that motor imagery and execution are dependent on a unitary representation of movement (e.g., Parsons & Fox, 1998), the present findings, in conjunction with those of Gerardin et al. (2000), suggest a functional and anatomical dissociation between cortical areas underlying motor imagery and motor execution. More specifically, we argue that a critical difference between processes underlying motor imagery and execution is that execution depends on the updating of effector location derived from the sensory comparator, while motor imagery depends solely on the generation of predicted movements derived from a forward model based on motor outflow information.

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