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Within grasp but out of reach: evidence for a double dissociation between imagined hand and arm movements in the left cerebral hemisphere

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Abstract

What roles are played by the cerebral hemispheres in planning object-oriented reaching and grasping movements? In an attempt to address this question, we compared the abilities of the left and right hemispheres of commissurotomy patient J.W. to imagine hand manipulation (i.e., grasp) or arm transportation (i.e., reach) movements. A graphically rendered manipulandum (dowel) was briefly presented to the left (LVF) or right (RVF) visual fields in a variety of different orientations. In the grasp selection task (experiment 1), J.W. was required to determine which side of a dowel his thumb would be on if he were to engage the stimulus in a power grip using either his dominant (right) or non-dominant hand. In the reach selection task (experiment 3), J.W. judged which end his elbow would be on if he treated the dowel as an armrest for his dominant or non-dominant forearm. No actual movements were allowed in either task. Movements selected in the imagery tasks were compared with those chosen during actual motor control under comparable circumstances. These comparisons revealed a left hemisphere advantage for representing grasping movements involving the right hand, and reaching movements involving the left arm. The right hemisphere, by contrast, displayed moderate accuracy when representing grasping movements with the left hand, but appeared incapable of imagining reaching movements with either arm. The double dissociation between imagery for hand and arm movements in the left cerebral hemispere is consistent with the hypothesis that grasping and reaching components of prehension involve dissociable planning mechanisms.

Keywords: Motor imaging; Motor planning; Callosotomy; Cerebral asymmetry; Prehension

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A growing body of evidence suggests that motor ideation, or imagery, involves many of the same mechanisms as motor planning and control (see reviews in [1,21,22]). Following the pioneering work of Roland and colleagues (e.g., [38]), nearly two decades of functional neuroimaging studies have consistently found that imagining movements activates areas involved in motor planning and control including: cerebellum and basal ganglia (e.g., [3,35]), supplementary and/or premotor areas (e.g., [4,28,37]), posterior parietal cortex (e.g., [28,42]), and in some cases even primary motor cortex (e.g., [17]). Studies of neurologically impaired patients suggest that these areas may contribute to different aspects of motor imagery. Patients with lesions of posterior parietal cortex often have difficulty generating accurate motor images (e.g., [41]). By comparison, patients with lesions of primary motor cortex may be capable of generating motor images, but show considerable slowing when imagining movements of afflicted muscles (e.g., [40]). Comparable slowing of actual and imagined movements has also been reported in patients with Parkinson's disease [5].

However, it is also important to acknowledge that motor imagery is dissociable from motor control. Apart from the obvious fact that imagery does not involve overt movement, paralyzed individuals may retain the ability to generate motor images and internally simulate movements (e.g., [2,9,18,27,47]). For instance, when asked to judge whether they would prefer an overhand or underhand grip to engage a dowel presented in various orientations, most left and right hemiplegic

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patients retained the ability to select responses that were highly consistent with the biomechanical constraints of their paralyzed limbs Only patients with right posterior parietal and left frontal lesions were impaired in this task [27].

Together these results are consistent with the hypothesis that motor imagery involves a subsystem of those mechanisms involved in motor planning and/or control (e.g., [21,25,26,30,42]). Precisely which components are common to both imagery and action, and how they are implemented in the brain, remains to be established. In the present study we sought to advance our understanding of this relationship by exploring how processing components involved in motor imagery are organized in the cerebral hemispheres. In particular, we explored whether the cerebral organization of motor imagery — involving grasping with the fingers and hand or reaching with the shoulder and arm — was consistent with the patterns of lateralization established for distal and proximal motor control, respectively.

2. Intra- and inter-hemispheric pathways for grasping and reaching

Extensive behavioral studies suggest that prehension involves coordinated activity of two relatively independent, yet highly coordinated, processing components: one that controls transportation of the hand to the target by movements of the shoulder and arm (i.e., reaching), and another that controls manipulation of the fingers and hand (i.e., grasping; for a comprehensive review see [20]). Neurophysiological evidence suggests that manipulation and transport components may be controlled by distinct visuomotor channels within the dorsal visual stream [23]. Specifically, directional coding of reaching movements (i.e., the transport component) involves a circuit running from the parieto-occipital extrastriate area to the dorsal premotor cortex (area PMd), either directly or via the medial intraparietal sulcus (area MIP). Grasping, by contrast, is mediated by a circuit running from the dorsal extrastriate cortex to the ventral premotor cortex (area PMv) via the anterior intraparietal area (area AIP).

There is also reason to believe that grasping and reaching may rely on partially independent mechanisms. It has long been known that the distal musculature of the fingers and hand, and the proximal musculature of the shoulder and upper arm are controlled by two relatively independent divisions of the corticospinal tract [43]. The majority of fibers of the lateral corticospinal tract originate in Brodmann Areas (BA) 4 (motor cortex) and 6 (premotor cortex), cross to the contralateral side of the spinal cord at the pyramidal decussation, and are involved in the control of distal, and to a lesser extent, proximal musculature (e.g., [15]). Conversely, the majority of fibers of the ventral corticospinal tract originate in BA 6, do not cross over at the pyramidal decussation, and are involved in controlling proximal musculature (e.g., [15]). On the basis of this anatomical evidence, one would expect that each hemisphere has the potential to exert dominant control over grasping with the contralateral hand, and reaching movements of both the contra- and ipsilateral arms. This hypothesis has received support from functional neuroimaging studies (e.g., [29]), and psychophysical studies with normals (e.g., [8,45]). Likewise, monkeys that have had both the optic chiasm *and* corpus callosum transected — so that each hemisphere receives input exclusively from the ipsilateral eye — can accurately reach toward and intercept a target when either eye is occluded. However, they remain unable to accurately grasp food with the response hand contralateral to the stimulated hemisphere (e.g., [10,11,43]). As suggested by Trevarthen and Sperry [44], one possible explanation of these findings is that the surgical manipulation caused a disconnection of cortical visuomotor mechanisms involved in the control of distal movements, while sparing a subcortical (i.e., brainstem) system used to control proximal movements.

Studies of commissurotomized (i.e., split brain) humans also suggest that the distal control needed for grasping is primarily accomplished within the hemisphere contralateral to the response hand (e.g., [13,33,46]). However, these studies also indicate an asymmetry in motor control, favoring the motor dominant left hemisphere. Gazzaniga et al. [13], for example, reported that patients accurately mimicked postures of visually presented hands when stimuli were displayed to the hemisphere contralateral to the response hand. The most accurate responses occurred when stimuli were presented to the left hemisphere, and responses were executed with the dominant right hand. When stimuli were presented to the left hemisphere, performance with the ipsilateral left hand was moderately impaired, yet substantial dyspraxia was evident when stimuli were presented to the right hemisphere and responses were made with the ipsilateral right hand.

A very different pattern emerged when commissurotomized patients were required to point toward a visually-presented Target — a task primarily involving control of proximal limb segments of the upper arm and shoulder. Under these conditions, patients performed well with the hand ipsilateral to the stimulated hemisphere: When the target was presented to the left hemisphere, reaching with the left hand was highly accurate; when the target was presented to the right hemisphere, reaching with the right arm was moderately accurate. However, it was also apparent that right hemisphere control of the right arm was not exclusive, as contradictory information presented simultaneously to the left hemisphere interfered significantly with reach accuracy [13] (p. 609). This suggests that in humans, as in monkeys, each hemisphere is capable of controlling reaching movements involving proximal musculature on the ipsilateral side.

To the extent that motor imagery shares these same processes, similar dissociations are predicted for tasks demanding motor ideation. Consistent with this prediction, two recent studies found an advantage for each hemisphere when imagining movements of the contralateral vs. the ipsilateral hand. Parsons et al. [36] reported that commissurotomy patients were more accurate at determining whether line drawings depicted left or right hands, when stimuli were presented to the hemisphere contralateral to the patients' correct hands (e.g., a right hand presented to the left hemisphere). Likewise, in a divided visual field study involving healthy subjects, Johnson [25] found that less time was required to select whether an underhand or overhand grip was more appropriate when a manipulandum was presented to the hemisphere contralateral to the designated response hand.

The present studies extend this work to include ideation of both distal grasping and proximal reaching movements in the hope of further delineating the relationship between the cerebral organization of motor imagery and action. To the extent that mechanisms involved in motor imagery are organized similar to those involved in action, we predicted a double dissociation between the two hemispheres when making decisions about reaching and grasping objects. Based on the evidence reviewed above, we reasoned that decisions involving deciding how to grasp an object — a process that would involve distal musculature of the lower arm and hand to perform, would be most accurately accomplished by the contralateral hemisphere. By contrast, we expected that decisions involving how to orient the upper arm to an object — a process that would involve proximal musculature of the shoulder and upper arm to execute — would be most accurate when controlled by the ipsilateral hemisphere.

Our strategy was to compare the accuracy of commissurotomized patient J.W.'s left and right hemispheres in using motor imagery to select movements involving the ipsi- and contralateral hands (experiment 1), or arms (experiment 3). Similar to Johnson [25], stimuli consisted of a graphically rendered dowel presented briefly to the left (LVF) or right visual field (RVF) in a variety of different orientations, and J.W. was asked to choose which of two response options would be most natural for performing the designated action with a specified response hand or arm. No actual reaching or grasping movements were allowed. Instead, J.W. merely pressed one of two response keys to indicate his preference.

In experiment 1, J.W. was required to choose whether an underhand or overhand grip would be most natural for grasping the dowel in the center using a power grip (i.e., as one would grip a hammer). It was reasoned that this task would involve imagining movements of the distal musculature (forearm and hand) required to orient the hand correctly; a key aspect of the hand manipulation (i.e., grasping) component of prehension (e.g., [34]). In experiment 3, J.W. determined how he would orient his forearm to match the orientation of the dowel (i.e., to treat the stimulus as an armrest). We expected this task to involve imagining movements of the proximal musculature (shoulder and upper-arm) involved in the arm transportation (i.e., reaching) component of prehension in the absence of hand manipulation. Experiment 2 was a perceptual-motor control task designed to establish that each hemisphere was capable of accurately perceiving the stimulus' orientation and issuing a button-press response.

To evaluate their accuracy, we compared results from the two imagery judgment tasks (experiments 1a and 3a) with movements selected when J.W. actually engaged a 3-D dowel presented in the same orientations within free view (experiments 1b and 3b). No hemispheric differences were expected in these motor control conditions because the stimulus information and visual feedback during the movement were available to each hemisphere. Of primary interest was the extent to which imagined and actual movement selection were similarly affected by changes in stimulus orientation within the four response hand by visual field conditions. In order to achieve a high correlation with actual movement selection, imagery must be sensitive to the biomechanical constraints unique to the given hand or arm [25–27]. We reasoned that strong correlations between response preferences in imagery and actual movements in a particular condition would therefore be evidence that the given hemisphere is capable of representing veridically grasping or reaching movements involving the designated hand or arm. Conversely, weak or nonexistent relationships between preferences in imagery and action would suggest an inability of the isolated hemisphere to accurately represent such movements. This latter pattern could be interpreted either as evidence that the necessary imagery processes are lateralized to the opposite hemisphere, or that they are organized bilaterally and have been disconnected by sectioning the corpus callosum.

3. General method

3.1. Subject

J.W. is a 46-year-old, right-handed, male who underwent a two-stage commissurotomy that spared the anterior commissures in 1979. The surgery was undertaken to treat pharmacologically intractable epilepsy that began after a closed head injury at age 13. J.W's. right hemisphere understands simple verbal commands [39], and his case has been characterized extensively in previous reports (e.g., [7,14,24,39]). Briefly, J.W. is the result of a normal, full-term, delivery, and achieved all of the normal sensori-motor milestones during development. There is no history of neurological disease in his family. Following his accident, J.W. began experiencing "infrequent episodes of absence spells" [39] (p. 325). Due to lack of tonic/clonic movements, or other abnormal behaviors, these spells were not treated. He graduated from high school at age 18, and experienced his first major motor seizure during the following year. Attempts to manage his condition with antiepileptic medications were largely unsuccessful, and he continued to have major motor seizures during the next 7 years. His "EEGs revealed irregular polyspike, and spike and wave with occasional 3-cps activity bilateral and anterior" [39] (p. 325). Patient J.W. experienced episodes of grand mal and many daily petit mal seizures during 1997–79, at which point he underwent neurosurgery at Dartmouth-Hitchcock Medical Center. Eight months after the second stage of his surgery, J.W.'s neurological exam was unremarkable with the exception of typical split-brain phenomena resulting from lack of interhemispheric transfer [12]. Two decades post-surgery, J.W.'s epilepsy is well controlled. On tasks that do not require callosal transfer, J.W.'s sensory and motor abilities continue to be normal: He is a licensed automobile operator, and constructs and paints elaborate, miniature, models in his spare time.

3.2. Stimuli and apparatus

For purposes of exposition, we describe the motor control tasks before the imagery conditions. However, during testing. imagery conditions always preceded motor control in order to prevent J.W. from basing his responses on memory of previous reaches.

3.2.1. Motor control tasks

The stimulus was a 1-in. diameter wooden dowel measuring 6 in. in length. The dowel subtended approximately 2.6° by 10.8° of visual angle when viewed from 50 cm. Half of the dowel was colored pink, and the other half was colored tan. The dowel was suspended in the center of a black wooden box. The front side of the box was open so as not to obstruct reaching movements, and measured 24 in. by 24 in.

The stimulus was attached to an axle at both ends. The rear of the axle protruded through the back wall of the box, allowing the experimenter to accurately determine the orientation of the stimulus in the picture plane — i.e., from the subject's perspective — by observing the relationship between a pointer attached to the axle, and a compass. To the subject, only the stimulus and edges of the surrounding box were visible.

The subject was seated in front of the apparatus with his hands resting palms down on designated locations on the table surface. At the beginning of each trial, the experimenter instructed the subject to perform the specified action, and then recorded the response preference. The experimenter then rotated the dowel into orientation for the next trial. Within each block, stimuli were presented in random order.

Details unique to each experiment are discussed in the specific method sections below.

3.2.2. Imagery and orientation judgment tasks

Stimuli consisted of a graphically rendered dowel subtending approximately 2.6° by 10.8° of visual angle when viewed from 50 cm, and appearing in a variety of orientations within the picture plane. Shading and reflectance were used to create the illusion of being three-dimensional (3-D). Half of the dowel was colored pink and the other half was colored tan. The innermost edge of the dowel was never closer than 2° to the central fixation point. Stimuli were presented, and responses recorded, with a Macintosh Power PC™ microcomputer and SuperLab™ software. Details of the specific experiments are presented in the respective method sections below.

At the beginning of each session, the experimenter described the particular task and — in the motor imagery tasks — demonstrated the type of movement that would be required using a model dowel. It was emphasized that J.W. should respond as soon as he had made his decision, and should not move his hands other than to press the correct response key. To ensure compliance with the instructions not to move, the position of the subject's hands was closely monitored by the experimenter throughout the study. References to "imagining movements" in order to solve these tasks were avoided.

J.W. responded by manually depressing one of two keys on the keyboard. The "b" key was labeled "pink", and the "n" key was labeled "tan". Counterbalancing is described separately for each experiment below. Each task consisted of 16 blocks: eight using the middle and index fingers of the left hand to press the response keys, and eight using the index and middle fingers of the right hand to depress the response keys. Given the crossed organization of distal motor control [15], only trials on which J.W. pressed response buttons with the hand contralateral to the stimulated hemisphere were included in the analyses. There was a self-timed rest break between the eighth and ninth blocks.

Each trial began with a 1000 ms "Ready!" signal, which was immediately replaced by a central fixation point lasting for 500 ms. The stimulus dowel appeared immediately after the offset of the fixation point — in either the LVF or RVF — and remained visible for 150 ms. A blank interstimulus interval (ISI) followed for 1500 ms. Both visual field and stimulus orientation varied randomly within each block of trials. The response timer was initiated when the stimulus became visible, and was terminated when the subject depressed a response key. The computer recorded both response time and response preference.

4. Experiment 1: grasp selection

In our initial set of experiments, we evaluated the ability of the left and right hemispheres to use motor imagery to select whether an overhand or underhand grip would be most appropriate for engaging a dowel in a power grip. In task 1a, the dowel was presented in free view, and J.W. actually grasped it using his left or right hand. Results were then compared with those of task 1b, in which stimuli were briefly presented to the LVF or RVF, and J.W. judged which grip would be preferred if he were to grasp the dowel using his left or right hand. Of primary interest was the extent to which grips selected by the isolated left and right hemispheres in the motor imagery condition (task 1b) were consistent with those chosen in the motor control condition (task 1a). The strength of this relationship was considered to reflect the accuracy of imagined movements.

4.1. Method

4.1.1. Task 1a. Motor control: grip selection

J.W. participated in eight blocks of trials using his right hand, and eight blocks using his left hand. The order of the blocks (left vs. right hand) was counterbalanced. As shown in Fig. 1(A), dowels appeared randomly in eight different orientations within each block (45° increments). The first block was treated as practice and was not analyzed.

As depicted in 1(B), J.W. was instructed to use the designated response hand to grasp the dowel in the center using a power grip, and was free to choose either an overhand or underhand grip, as demonstrated by the experimenter. Grip preference was operationalized by noting which end of the stimulus the subject's thumb was toward, pink or tan. J.W. was encouraged to respond by just "reaching out and grasping the dowel in the most natural manner".

4.1.2. Task 1b. Motor imagery: grip selection

Dowels were again presented at each of eight different orientations (see 1(A)). J.W. was now asked to indicate which end of the dowel his thumb would be on if he were to grasp it in the center using a power grip (1(B)). It was again emphasized that for each dowel orientation he should select the grip that would be most natural. On alternating blocks, J.W. based his judgments on his left and right hands.

Practice blocks consisted of a subset of the stimuli (0, 90, 180, 270°). In the first two practice blocks, stimuli were presented centrally, and remained visible until a response was made. Judgments were based on the left and right hands, respectively. In the third and fourth practice blocks, stimuli appeared for 150 ms in the center of the screen. Both the hand on which grip preferences were based, and the hand used to press the response buttons, were completely counterbalanced across the 16 test blocks. Throughout each block J.W. was verbally reminded which hand to base his grip decisions on after approximately every third trial.

4.2. Results and discussion

The probability of selecting the thumb toward the pink end (i.e., the "pink grip") was calculated separately for each hand and each stimulus orientation. As expected, J.W.'s grip preferences in the motor control task (1a) were highly correlated with means from a group of healthy subjects reported in an earlier study [24], $R = 0.81$, $F(1,46) = 90.35$, $P = < 0.0001$, $\mathrm{MSE} = 0.082$. The fact that this correlation was not perfect reflects typical variance in response preferences shown by individual subjects at stimulus orientations where either grip is comparably awkward [26]. As shown in Fig. 2, when the stimulus is vertical with the pink end at the top (0°), neutral postures were adopted by placing the thumbs of both hands toward the pink end. As the stimulus was rotated in the clockwise direction the right hand was supinating, and J.W. switched to an overhand (pronated) grip by placing his thumb toward the tan end. This grip was preferred through 180°. At 225° this grip would have become supinated, and J.W. instead switched to a pronated posture by placing the thumb toward the pink end. The pattern for the left hand is similarly shaped, but approximately 180° out of phase because it obeys joint constraints that are inversely related to those of the right hand (e.g., [25–27,32]). As the stimulus was rotated clockwise, the left hand was pronating, and J.W. continued to adopt the pink grip until he reached 180°. This was possible because the range of motion for forearm rotation — the primary biomechanical constraint in this task — is approximately twice as large for pronation as for supination. At 225°, J.W. switched to a supinated grip with the left hand by placing the thumb toward the tan end.

In order for response preferences in motor imagery (task 1b) and motor control (task 1a) conditions to correlate, motor ideation must respect the biomechanical constraints unique to the respective movements. In the present situation, this involves obeying limitations on forearm pronation and supination.

As depicted in Fig. 3, J.W. selected grips highly consistent with his actual grip preferences when stimuli were presented to the RVF (left hemisphere) and responses were based on the contralateral right hand, $R=0.95$, $F(1,6)=57.96$, $P<0.0001$, $\mathrm{MSE}=0.028$. Accuracy dropped considerably when stimuli were presented to the RVF and responses were based on the ipsilateral left hand, $R=0.42$, $F(1,6)=1.3$, $P=0.30$, $\mathrm{MSE}=0.103$. Accuracy approached conventional levels of significance, when stimuli were presented to the LVF (right hemisphere) and responses were based on the contralateral left hand, $R=0.62$, $F(1,6)=3.72$, $P=0.10$, $\mathrm{MSE}=0.048$. By contrast, the relationship between performances in imagery and motor control tasks was virtually nonexistent when stimuli were presented to the LVF and responses were based on the ipsilateral right hand, $R=0.08$, $F<1.0$.

Fig. 4 shows that RTs for stimuli presented to the RVF (left hemisphere) were faster when decisions involved the contralateral right hand. Therefore, the contralateral hand advantage in accuracy does not appear attributable to a speed accuracy tradeoff. For stimuli presented to the LVF (right hemisphere), responses based on the ipsilateral right hand tended to be faster and less accurate than those based on the left hand. This raises the possibility that the right hemisphere sacrificed accuracy in favor of speed. It seems likely that this tradeoff may be responsible for the fact that accuracy of decisions based on the left hand narrowly missed attaining significance.

To summarize, our findings from motor imagery are highly consistent with earlier studies of motor control in the commissurotomized brain (e.g., [13,33]) as well as

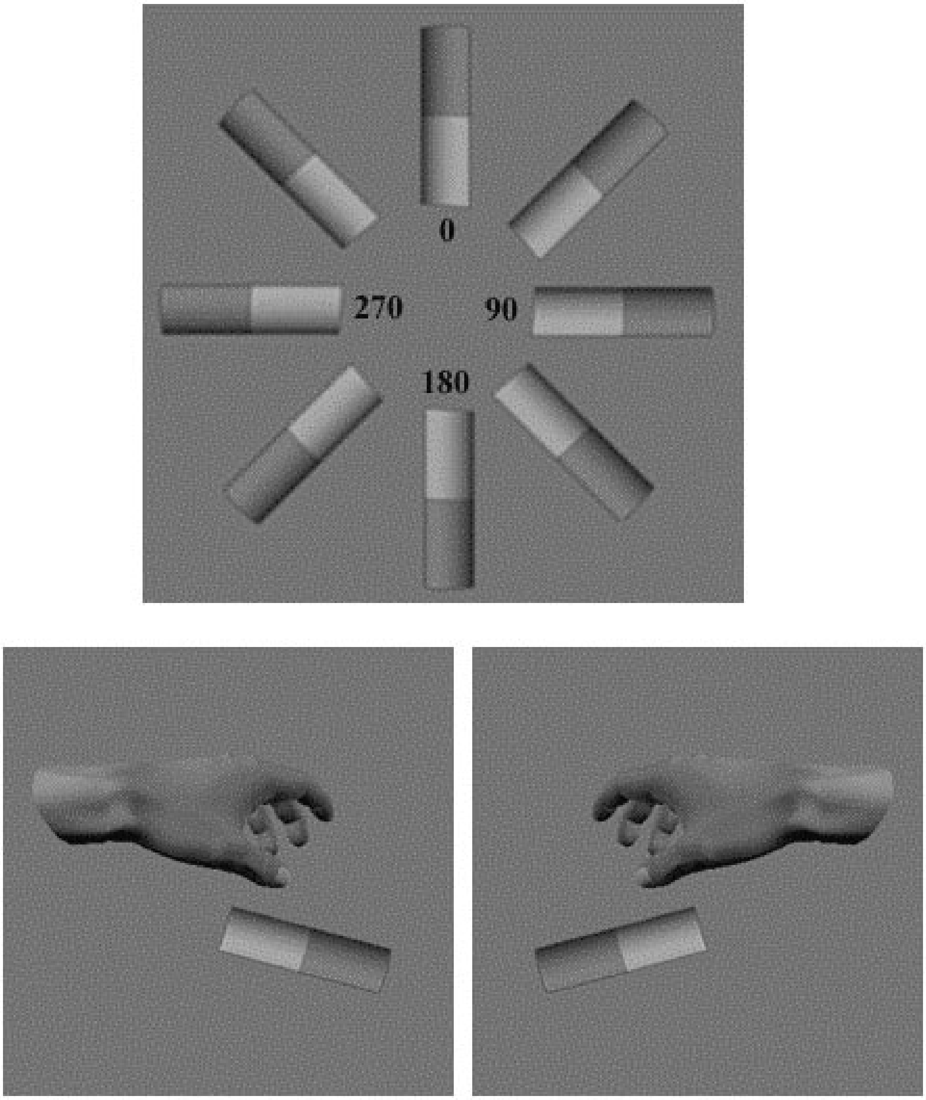

Fig. 1. (A) The eight stimulus orientations tested in experiment 1. In the actual stimuli dark gray ends were colored pink, and light gray ends were colored tan. (B) Depiction of the grasping movements executed in task 1a, and imagined in task 1b.

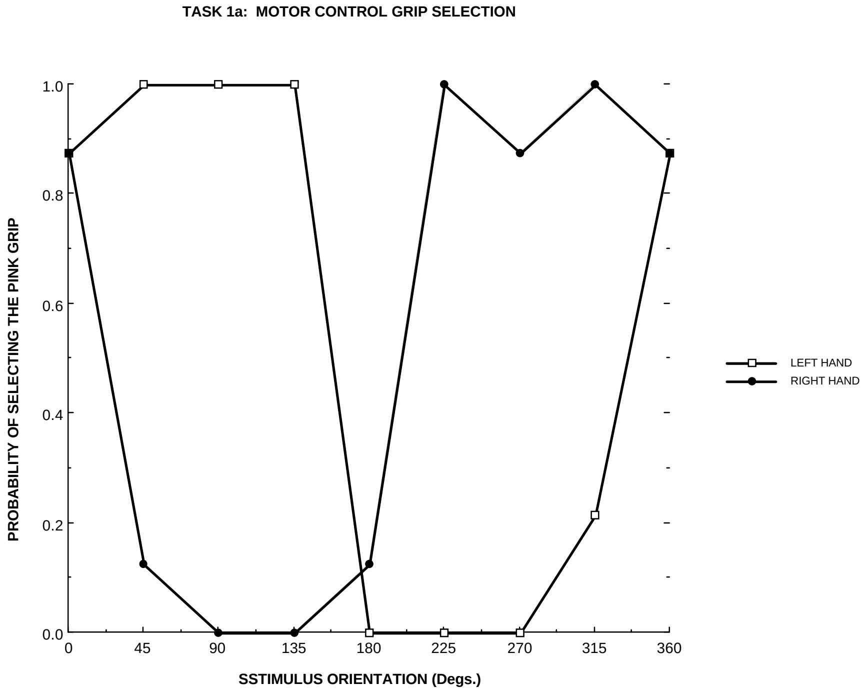

Fig. 2. Stimulus orientation had different effects on whether J.W. selected grips that placed his thumb toward the pink or tan end of the stimulus, depending on the biomechanical constraints unique to each limb; in this task pronation and supination of the forearms. The functions for the left and right hands are out of phase due to the opposing joint constraints, in this case pronation and supination of the forearms.

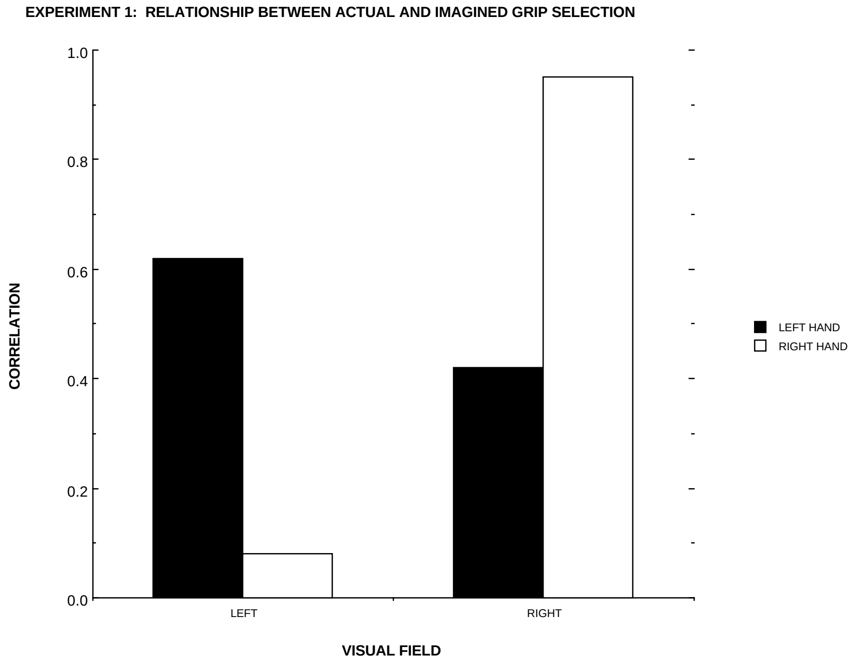

Fig. 3. Performance in the imagery task (task 1b) was more highly related to performance in the motor control task (task 1a), when grip selection was based on the contralateral hand. The left hemisphere (RVF) also shows some ability to accurately represent movements of the ipsilateral left hand.

more recent studies of motor imagery in commissurotomized [36] and healthy subjects [25]. Together these studies suggest that each hemisphere is specialized for accurately representing distal movements of the contralateral hand. Furthermore, we also observed an asymmetry in this ability; namely, the motor dominant left hemisphere appears to represent movements of the contralateral right hand with a high degree of accuracy, and those involving the ipsilateral left hand with modest success. By comparison, the right hemisphere is capable of representing movements of the contralateral left hand with moderate accuracy, but appears unable to represent movements of the ipsilateral right hand.

5. Experiment 2: orientation perception

It is possible that the RVF (left hemisphere) advantage in accuracy for grip selection involving both contralateral and ipsilateral hands might be attributed to hemispheric differences in perceptual abilities. For instance, perhaps the right hemisphere is less accurate at determining the orientation of the stimulus or localizing its pink or tan ends. This alternative seems unlikely for two reasons. First, a large body of work involving patients and normals indicates a right hemisphere advantage for many visual perception tasks (for a comprehensive review see [19]). Second, this hypothesis does not explain why J.W.'s left hemisphere was consistently more accurate in selecting grips based on his right vs. left hand. If this advantage was perceptual in nature, then one would expect judgments to be equally veridical regardless of the hand on which they were based. Nevertheless, we sought to address directly this alternative possibility through an orientation perception task that employed the same stimuli, and a procedure similar to that used in the motor imagery tasks.

5.1. Method

Dowels appearing in six different orientations (60° increments) were presented to the LVF and RVF, and J.W. was asked to decide whether the pink or tan end was higher. As in the previous tasks, responses were made by pressing either the "pink" or "tan" key, and response hands were counterbalanced across blocks.

The experiment consisted of two practice blocks and 10 experimental blocks. Each block consisted of 12 trials: six stimulus orientations presented to the LVF and RVF.

5.2. Results

As depicted in Fig. 5, error rates were quite low, and did not differ significantly between the two hemispheres, $T(35) = -1.0$, $P = 0.324$. Contrary to the hypothesis of a left hemisphere (RVF) perceptual advantage, there was a tendency to commit slightly more errors in this condition. Fig. 6 shows that the left hemisphere (RVF) did tend to respond somewhat faster than the right (LVF), and therefore the slight advantage displayed by the right hemisphere may be attributable to a speed–accuracy tradeoff.

In short, both hemispheres display comparable levels of accuracy in perceiving the orientation of the stimuli, localizing the relative positions of the colored ends, and executing button press responses. Therefore, differences between the left and right hemispheres in the accuracy of imagined grip selection (task 1a) seem not to be

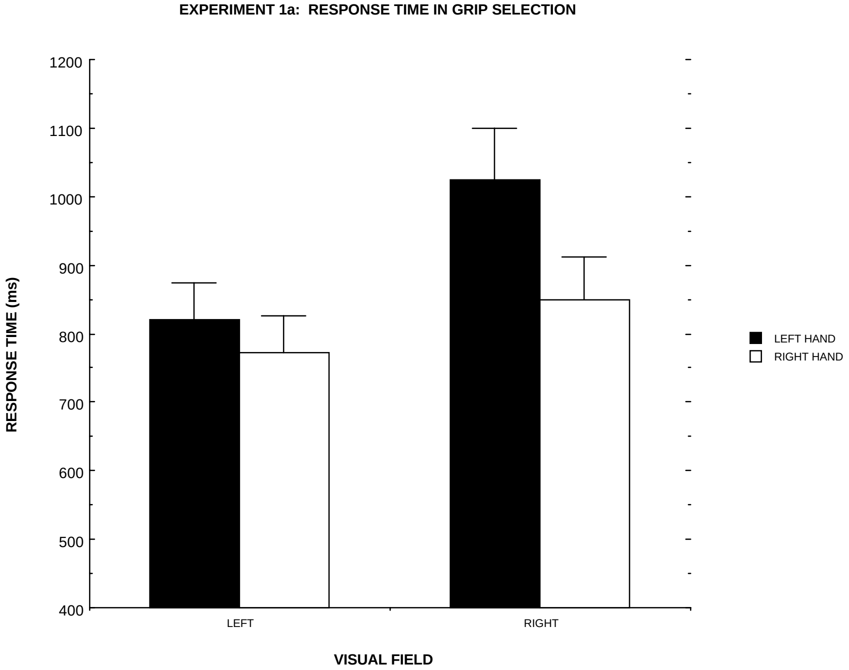

Fig. 4. Response times for trials based on the contralateral hands were not consistently slower than those based on the ipsilateral hands. Thus, the advantage for representing grasping movements of the contralateral hands does not appear to be attributable to a speed–accuracy tradeoff.

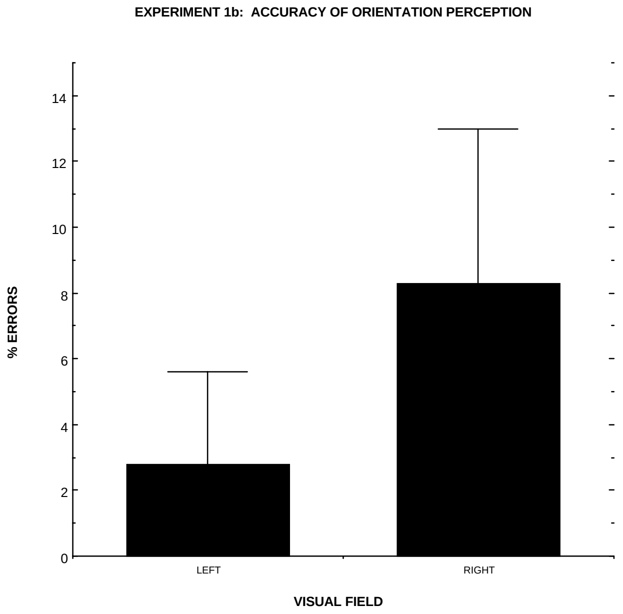

Fig. 5. There was a non-significant tendency for the left hemisphere (RVF) to commit more errors than the right hemisphere in orientation perception (task 2).

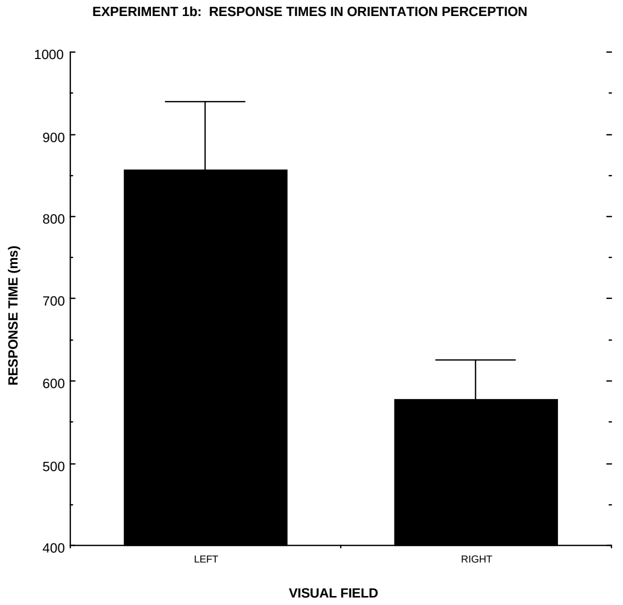

Fig. 6. The left hemisphere was slower in the orientation perception task (task 2), suggesting that the tendency to commit more errors was not attributable to a speed–accuracy tradeoff.

attributable to differences in perceptual or response-related factors.

6. Experiment 3: reach selection

The results of experiment 1 suggest that each hemisphere is specialized for representing grasping movements involving the contralateral hand. This pattern is consistent with what is known about the cerebral organization of motor control, and thus supports the hypothesis that imagery and action involve shared mechanisms. Experiment 3 sought to determine the roles played by the cerebral hemispheres in selecting movements involving proximal musculature of the shoulder and upper arm. Our objective was to dissociate the system that controls transportation of the hand to the location of the target object during reaching, from hand manipulation. This was accomplished by having J.W. determine whether his elbow would be toward the pink or tan end of the stimulus if he were to treat it as an armrest for his left and right forearms. Because proximal musculature receives efferent input via the uncrossed ventral division of the corticospinal tract, we reasoned that these tasks may involve mechanisms within the ipsilateral cerebral hemisphere. As discussed above, results from studies of motor control in split brain patients (e.g.,[13]) and monkeys (e.g., [10,11,43]) are consistent with this prediction. If this organization extends to motor imagery of proximal arm movements, then we expected to observe a double dissociation between the results of experiments 1 and 3 with judgments in the present task being more accurate when based on the ipsilateral arm. This pattern would also be consistent with the existence of a circuit dedicated to the control of grasping that is separate from those involved in other non-prehensile arm movements (e.g., [16,23]).

6.1. Method

6.1.1. Task 3a. Motor control: arm selection

The stimuli, apparatus and procedure were nearly identical to those described above in task 1a. However, as depicted in Fig. 7(B), J.W. was now asked to align the forearm of his designated response arm with the dowel as if it were an armrest. The experimenter then recorded whether J.W's. elbow was toward the pink or tan end of the stimulus. As shown in 7(A), dowels appeared in six different orientations (60° increments around a full circle).

6.1.2. Task 3a. Motor imagery: arm selection

The stimuli, apparatus, and procedure were similar to those described in task 1b. As in task 3a, however, J.W. was asked to determine whether the elbow of his designated response arm would be toward the pink or tan end of the dowel (7(B)). Likewise, the dowel appeared in six different orientations (7(A)).

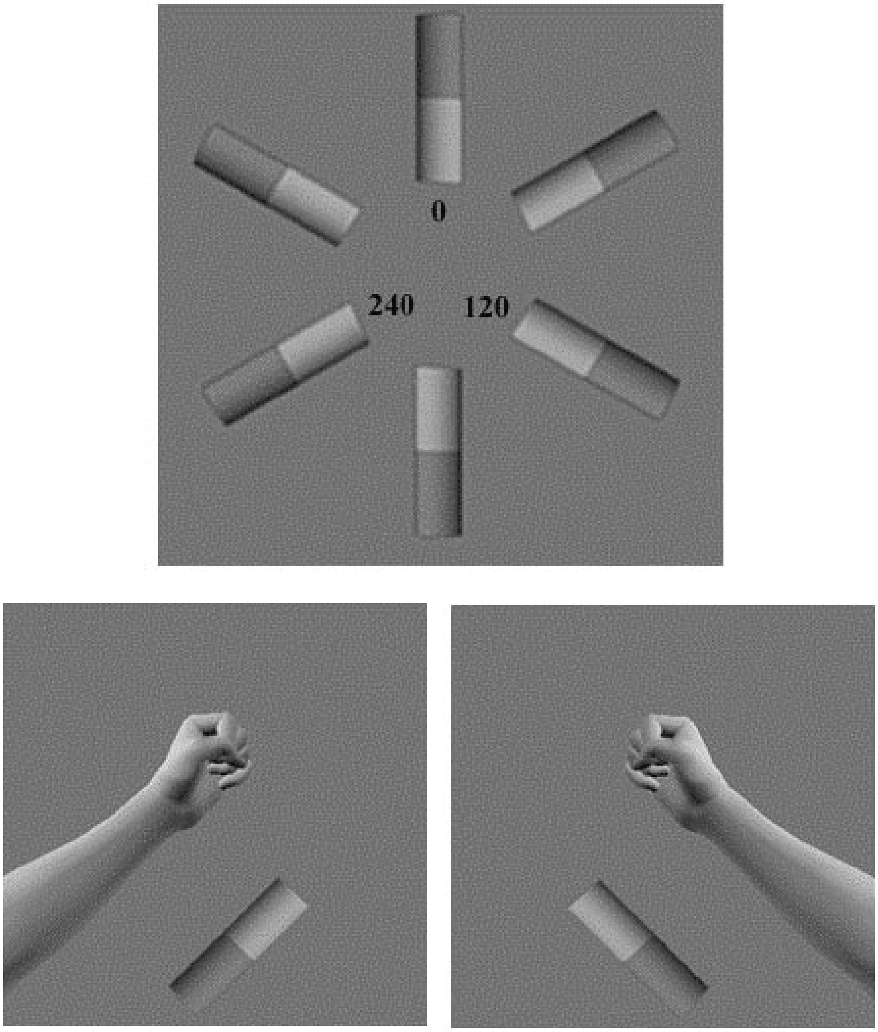

Fig. 7. (A) The six stimulus orientations tested in experiments 2 and 3. In the actual stimuli dark gray ends were colored pink, and light gray ends were colored tan. (B) Depiction of the forearm movements executed in task 1a, and imagined in task 1b. The subject was instructed to determine whether his elbow would be on the pink or tan end of the dowel if he treated it as an armrest for his forearm.

7. Results and discussion

Similar to experiment 1, the probability of selecting the elbow toward the pink end was calculated separately for each arm and each stimulus orientation. As shown in Fig. 8, when the stimulus was oriented vertically with the pink end at the top (0°), J.W. placed his elbows toward the tan end, adopting a neutral posture that aligns the primary axis of both forearms with the body's midline. As the stimulus was rotated in the clockwise direction, J.W.'s left arm was moving away from the midline of the body (abduction), while his right arm was moving toward the midline (adduction). As measured from the neutral posture, the range of motion for shoulder adduction is considerably less than that of abduction. For this reason, J.W. switched to an abducted posture with the right arm by placing his elbow on the pink end when the stimulus was posi-

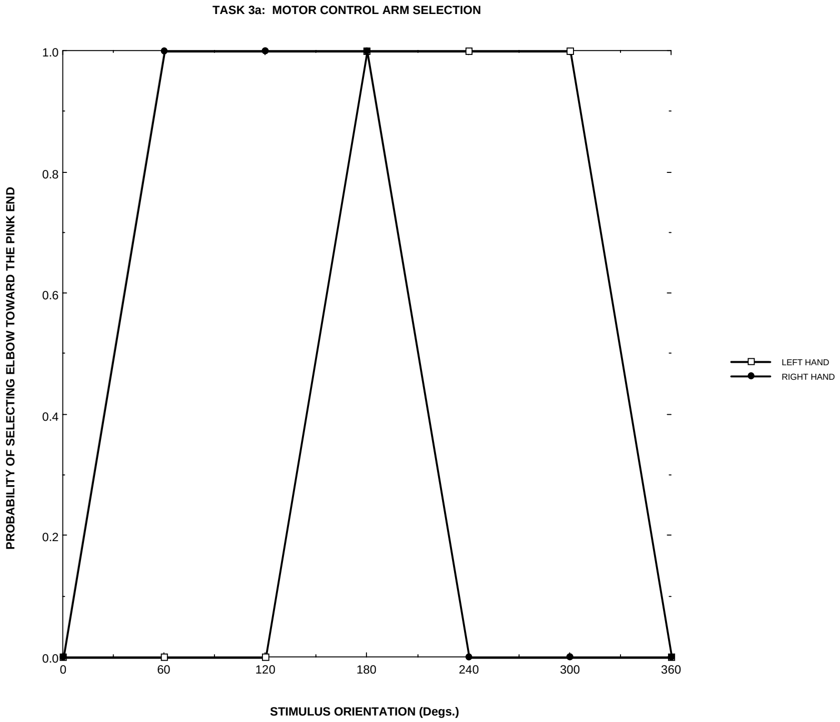

Fig. 8. Stimulus orientation had distinct effects on whether patient J.W. placed his elbow toward the pink or tan end of the dowel when treating it as an armrest, depending on the biomechanical constraints unique to each limb. The functions for the left and right arms are out of phase due to their opposing joint constraints: in this task abduction and adduction of the shoulders.

tioned at 60° (7(A)). He returned to the neutral posture at 180°, now with the elbow toward the pink end. As he had for 60°, J.W. then switched back to an abducted posture with the right arm at 240°, placing his elbow toward the tan end (Fig. 8). Because the left arm obeys joint constraints that are inversely related to those of the right arm (e.g., [30]), its function is similarly shaped but approximately 180° out of phase. More precisely, the left arm is abducting as the stimulus rotates from 0 to 120°, and the elbow is placed toward the tan end. At 180°, J.W. switched back to a neutral posture, placing his elbow on the pink end. Note that for each arm, J.W. avoids adopting awkward, if not impossible, postures by never crossing the body's midline.

It is important to recognize that the relationship between stimulus orientation and movement selection in this task differs markedly from that observed in the grip selection task of experiment 1 (cf. Figs. 2 and 8). Therefore, in order for response preferences in motor imagery and motor control conditions to correlate, motor ideation must respect the biomechanical constraints unique to the respective movements. In the present task, this involves obeying limitations on abduction and adduction of the shoulder.

As predicted, imagined arm selection was more accurate when decisions were based on the ipsilateral vs. contralateral limbs, but only when stimuli were presented to the RVF (left hemisphere). As depicted in Fig. 9, there was a perfect relationship between real and imagined performance when stimuli were presented to the RVF and responses were based on the ipsilateral left hand, $R = 1.0$. Accuracy approached, but did not reach, conventional levels of significance when stimuli were presented to the RVF and responses were based on the contralateral right hand, $R = 0.62$, $F(1,4) = 6.4$, $P = 0.07$, $\text{MSE} = 0.104$. By contrast, performance of the right hemisphere in the reaching task was quite poor for both the ipsilateral ($R = 0.20$) and contralateral ($R = 0.15$) hands, $F < 1.0$ in both cases. As summarized in Fig. 10, the accuracy advantage for RVF presentations does not appear to be attributable to a speed–accuracy tradeoff, as RTs for judgments based on both hands were slower for LVF (right hemisphere) presentations.

In short, the left hemisphere shows highly accurate, in fact perfect, performance when representing upper limb movements involving the ipsilateral arm. Indeed, the left hemisphere displays reasonable accuracy when planning movements of the contralateral right arm as well. Conversely, the right hemisphere appears unable to accurately represent movements involving either the ipsilateral or contralateral arms. This asymmetry suggests that the left hemisphere may be specialized for the selection of upper limb movements involved in reaching.

By and large these findings are quite compatible with those reported for motor control in commissurotomized humans (e.g., [13,33]). As discussed above, these patients were accurate when stimuli were presented to the left hemisphere (RVF) and pointing responses were made with the left arm. Likewise, the left hemisphere also showed moderate accuracy when controlling pointing movements with the right hand. When stimuli were

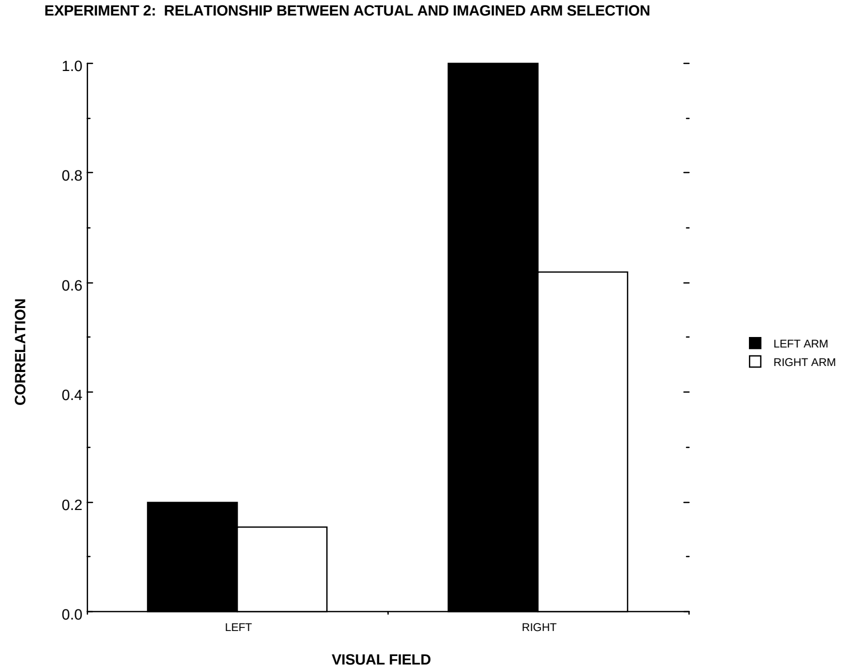

Fig. 9. Performance in the arm selection imagery task (task 2b) was highly related to motor control (task 2a) when stimuli were presented to the left hemisphere (RVF) and responses were based on the ipsilateral left arm. The left hemisphere also displayed modest accuracy for imagery based on the contralateral right arm. By contrast, the right hemisphere (LVF) appeared unable to accurately represent movements of either the left or right arms.

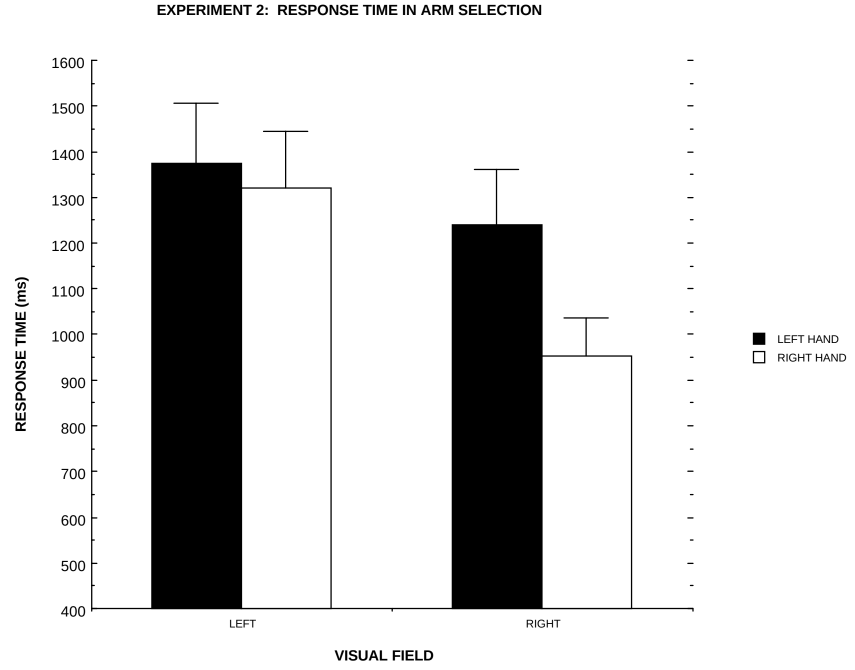

Fig. 10. As evidenced by the tendency for faster RTs to RVF presentations, the left hemisphere advantage for representing upper limb movements does not appear to be attributable to a speed–accuracy tradeoff.

presented to the right hemisphere (LVF) and responses were based on the left hand, both studies found very poor accuracy. Contrary to the present results, however, this earlier work did find modest accuracy for right hand pointing when stimuli were presented to the right hemisphere (LVF). To the extent that motor imagery and motor planning involve the same mechanisms, this discrepancy may suggest that while each hemisphere can control proximal movements involving the right arm [13], processes needed to select such movements are lateralized to the left hemisphere. When a commissurotomized patient reaches with the right arm, pre-motor plans may be computed in the left hemisphere and then communicated to control mechanisms in the right hemisphere via intact subcortical pathways. This model would be consistent with the observation that proximal, as opposed to distal, arm movements may involve a more diffuse cortico-subcortical (brainstem) pathway [43,44].

8. Summary and conclusions

8.1. Limitations of the present studies

As an initial attempt to investigate motor imagery and planning processes in the divided brain, the present work has certain limitations that deserve consideration. One drawback is the fact that in control conditions involving actual reaching, 3-D objects (experiments 1a and 3a) were presented centrally and were within view throughout the movement, as was the subject's own limb. By contrast, in the motor imagery and orientation judgment conditions, objects were 2-D images presented tachistoscopically to the LVF or RVF. It is certainly possible that these differences in stimulus presentation may have contributed to any main effects observed when comparing control and imagery conditions. However, it is not clear how these differences can account for the interactions between task (motor control vs. imagery) and visual field (LVF vs. RVF), which are the backbone of our argument. Nevertheless, if movement selection in motor imagery and planning do involve similar mechanisms (e.g., [21,26]), then were we to test J.W.'s motor abilities with brief, lateralized, presentations of 3-D objects we might observe a similar dissociation between grasp and reach selection in the left hemisphere.

A second issue concerns the nature of the demands involved in grip (experiment 1) vs. reach selection (experiment 3) tasks. Because the grip selection task requires subjects to choose between overhand vs. underhand versions of the same hand configuration — a power grip, it can be argued that there are no demands placed on components involved in grip planning. Instead, subjects only need to decide how to orient the hand via pronation or supination of the forearm. There are several reasons why we disagree with this statement. First, although not the only ingredient, correct hand orientation is an essential part of grasp formation, but is largely irrelevant to reaching. Indeed, a task similar to our own — that involves inserting ones' hand or a card through a slot placed in various orientations — has been used widely to evaluate disorders of grasping in patients with optic ataxia (see review in [34]). Second, in order to determine which end of the stimulus their thumb would be on, it was not enough just to imagine supinating or pronating the forearm. Subjects instead were required to evaluate the consequences of this decision for the orientation of their grasping hand. Finally, recent functional magnetic resonance imaging (fMRI) work using a version of the grip selection task, indicates that using motor imagery to choose between an overhand vs. underhand power-grip involves areas in the posterior parietal and premotor cortex that may be homologues of those that mediate prehension in monkeys [28]. As mentioned earlier, patients with right posterior parietal or left frontal lesions also have difficulties with this grip selection task [27]. Nevertheless, in order to increase demands on grip selection processes, future studies might include objects that demand a variety of different hand configurations.

Lastly, our results are based on a case study of a patient who has a history of severe epilepsy, and subsequent sectioning of the corpus callosum that left the anterior commissure intact [14]. Although J.W. is a highly functional and well-controlled epileptic, with no outstanding neurological impairments on tasks that do not involve interhemispheric information transfer, some caution must be exercised when generalizing these results to healthy populations.

With these limitations in mind, there are several tentative conclusions that can be drawn from these experiments, which will serve as the basis for future investigations. The present findings suggest that processes involved in motor imagery are organized within the cerebral hemispheres in a manner similar — but not identical — to those involved in motor control (e.g., [21,25,26,30,42]). Consistent with previous studies of motor control [13] and motor imagery [25,35], each hemisphere is capable of accurately representing grasping movements involving the distal musculature of the contralateral hand. Likewise, motor imagery abilities are asymmetrically organized. The left hemisphere displays some ability to represent grasping movements involving the ipsilateral hand, which the right hemisphere lacks. The most pronounced differences between the left and right hemispheres emerged when imagining movements that would be controlled by the proximal musculature of the upper arm and shoulder. Under these conditions, the left hemisphere displays remarkable accuracy for representing movements of the ipsilateral left arm, and performs with modest accuracy when ideation involves the contralateral right arm. By contrast, the right hemisphere appears incapable of accurately representing proximal movements involving either arm. This laterality effect was not anticipated based on findings of previous studies involving motor control in the divided brain [13,33,46], and suggests that motor imagery — and perhaps planning — and motor control of upper arm movements may be organized differently in the left and right cerebral hemispheres.

The double dissociation between imagery of grasping vs. reaching movements within the left cerebral hemisphere suggests that these components may be functionally independent in motor ideation as well as in action. As discussed above, there are reasons to believe that hand manipulation and arm transportation components of prehension involve separate mechanisms (e.g., [20,23]). As evidenced by the left hemisphere advantage for imagining grasping movements with the right hand and upper limb movements with the left arm, the same appears to hold for motor imagery. Given our use of a single subject with a history of neurological disease, the generality of this dissociation may be disputed. Nevertheless, this finding does establish that separate cortical circuits for imagining, and perhaps planning, hand manipulation and arm transportation components of prehension are possible.

It is worth noting that these results differ from those obtained from studies of visual imagery in J.W. and other commissurotomized patients [6,31]. These studies suggest a left hemisphere advantage for the generation of detailed visual images. By contrast, our findings suggest that both the left and right hemispheres display unique motor imagery abilities; abilities predicted on the basis of known motor system organization. Consequently, our findings are consistent with the hypothesis that motor and visual imagery are distinct representational mediums [21,26].

Further work is needed to fully understand the functional relationship between motor imagery and motor behavior. One possibility is that motor imagery arises whenever tasks evoke the generation of a motor plan that is then inhibited from execution [21]. Another possibility, consistent with the present findings, is that motor imagery is regularly used to solve the problem of movement selection during motor planning. According to the Prospective Action Model (PAM, [26]), analog simulations of internal movements are used to evaluate the biomechanical costs associated with candidate response options during motor preparation. To the extent that motor imagery and planning do overlap, the present results may reflect an important organizational feature of the motor system; that is a tendency to minimize the need for interhemispheric communication by having motor planning mechanisms reside within the same cerebral hemisphere as related motor control functions.

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