

Research Report

CEREBRAL ORGANIZATION OF MOTOR IMAGERY: Contralateral Control of Grip Selection in Mentally Represented Prehension

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Abstract—*The principle of contralateral organization of the visual and motor systems was exploited to investigate contributions of the cerebral hemispheres to the mental representation of prehension in healthy, right-handed human subjects. Graphically rendered dowels were presented to either the left or right visual field in a variety of different orientations, and times to determine whether an underhand or overhand grip would be preferred for engaging these stimuli were measured. Although no actual reaching movements were performed, a significant advantage in grip-selection time was found when information was presented to the cerebral hemisphere contralateral to the designated response hand. Results are consistent with the position that motor imagery recruits neurocognitive mechanisms involved in movement planning. More precisely, these findings indicate that processes within each cerebral hemisphere participate in mentally representing object-oriented actions of the contralateral hand.*

An important contribution to resolving the long-standing debate over the relationship between imagery and perception has been made by numerous studies indicating that the two categories of behavior involve common neural substrates (for comprehensive reviews, see Farah, 1988; Kosslyn, 1994). Disorders of visual perception following brain injury are often accompanied by corresponding changes in imagery abilities (e.g., Bisiach & Luzzatti, 1978; Farah, 1988). Likewise, functional brain-imaging studies have revealed activity in many visual (e.g., Kosslyn et al., 1993; Roland & Friberg, 1985) and auditory (e.g., McGuire et al., 1996) processing areas during the performance of like-modality imagery tasks. As a result of this evidence, the so-called imagery debate is no longer focused on whether imagery and perception involve common structures, but instead on articulating the details of this relationship. For instance, recent observations of intact imagery in an associative agnostic patient have led to the proposal that visual imagery and perception may involve separate routes of access to a common system of representations (Behrmann, Winocur, & Moscovitch, 1992). In addition, although some functional neuroimaging studies of imagery have found patterns of activation that include the primary visual cortex (e.g., Kosslyn et al., 1993), others have failed to detect such involvement (e.g., Roland & Gulyas, 1994a, 1994b). In short, evidence from cognitive neuroscience suggests that imagery and perception involve many, but perhaps not all, of the same neurocognitive mechanisms.

The involvement of common mechanisms in imagery and behavior appears not to be restricted to the perceptual domain. Despite having received considerably less attention, a growing body of evidence suggests that motor imagery and action also involve common neural substrates (for a comprehensive review, see Jeannerod, 1994). For example, studies of patients with Parkinson's disease (e.g., Dominey,

Decety, Broussolle, Chazot, & Jeannerod, 1995) and focal brain lesions (Sirigu et al., 1995, 1996) indicate that impairments in motor behavior are often accompanied by comparable deficits in motor imagery. Beginning with the work of Roland, Skinhoj, Lassen, and Larsen (1980), several functional neuroimaging studies have confirmed that motor imagery involves numerous cortical and subcortical regions known to be involved in motor planning, control, or both (e.g., Parsons et al., 1995). As is the case with perceptual imagery, precise areas activated by motor imagery appear to vary as a function of task demands (Jeannerod, 1995). For instance, the supplementary motor area (SMA) seems to be activated when subjects engage in imagery tasks demanding the representation of movements that are not constrained by the geometry of external target objects (e.g., finger tapping; Roland et al., 1980). Tasks that involve imagining object-oriented movements (i.e., prehension), however, do not appear to activate the SMA (Decety et al., 1994). Similarly, although most studies have failed to detect activity in the primary motor cortex during imagined movements (e.g., Decety et al., 1994; Parsons et al., 1995), others have found such involvement (e.g., Hallett, Fieldman, Cohen, Sadato, & Pascual-Leone, 1994).

Together, these findings support the hypothesis that motor imagery and motor planning involve common neurocognitive processes (Jeannerod, 1994, 1995). The objective of the present study was to evaluate this proposal by exploiting the well-known contralateral organization of the visual and motor systems. To accomplish this goal, the study employed a divided-visual-field task that required subjects to determine whether they would use an underhand or overhand grip if they were to reach for a dowel-shaped object, briefly presented to either the left visual field (LVF) or the right visual field (RVF). The dowel appeared in a variety of different orientations, and no overt hand movements were allowed during performance of the task. On alternating blocks, subjects based their grip decisions on the left or right hand.

SPECIFIC HYPOTHESES

The long-established observation that distal grasping movements are controlled by the contralateral cerebral hemisphere (e.g., Lawrence & Kuypers, 1969; Trevarthen, 1965) suggests that if mentally represented prehension does indeed involve mechanisms utilized in actual reaching, then decisions about how one would reach for an object should also show evidence of contralateral control.

Specific hypotheses regarding performance of this task were predicated on the assumption that response times in divided-visual-field studies are sensitive to the temporal demands of interhemispheric transfer (e.g., Helige, 1983). Accordingly, it was expected that less time would be required for those conditions demanding visual-perceptual and motor-imagery processes that reside in the same cerebral hemisphere than in those conditions in which motor-imagery processes would have to access information from perceptual processes residing in the opposite hemisphere. If mentally represented prehension involves neurocognitive mechanisms utilized in motor planning, then two possible outcomes were anticipated. Behavioral observations of

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normal populations (e.g., Goodale, 1988, 1990) and brain-injured populations (e.g., Kimura & Archibald, 1982) and neuroimaging data (e.g., Kim et al., 1993) suggest that the left cerebral hemisphere may play a dominant role in some aspects of movement planning. To the extent that such left-lateralized processes are involved in imagined prehension, response times would be expected to be faster whenever the dowel was presented to the RVF (left cerebral hemisphere), regardless of whether grip judgments were based on the left or right hand. Alternatively, if each cerebral hemisphere is specialized for mentally representing actions of the contralateral hand, then because of the crossed organization of distal motor control processes, presenting visual information to the RVF (left hemisphere) would be expected to lead to faster responses when grip decisions were based on the right hand than when decisions were based on the left hand. Conversely, presenting visual information to the LVF (right cerebral hemisphere) would be expected to lead to faster responses when grip decisions were based on the left hand than when decisions were based on the right hand.

Additionally, it was predicted that if subjects in this task were taking into consideration the biomechanical demands of actual prehension, then grip preferences would be similar to those observed in earlier experiments in which subjects actually reached for a dowel presented in similar orientations (Johnson, 1997; Johnson, Hawley, Tokowicz, & Rosenbaum, 1996). These experiments showed that subjects consistently selected grips that minimized perceived awkwardness by avoiding extremes of forearm pronation or supination.

METHOD

Thirty-one right-handed college students (16 female and 15 male) were presented on each trial with a graphically rendered dowel, half of which was colored pink and half of which was colored tan. As depicted in Figure 1, the dowel appeared in one of six different orientations within the picture plane (60° increments around the line-of-sight axis). Stimuli subtended approximately $2^\circ \times 8^\circ$ of visual angle when viewed from a distance of 50 cm, and the innermost edge was never closer than 3.5° from the fixation point.

The key to this procedure was that the dowels were presented very briefly (150 ms) to either the left or right of a central fixation point. Because it takes approximately 200 ms to initiate a saccadic eye movement, this procedure made it possible to project the dowel to either the LVF or the RVF. Because of the contralateral organization of the visual system, stimuli presented to the LVF are processed in the right cerebral hemisphere, and stimuli presented to the RVF are processed in the left cerebral hemisphere.

Subjects were instructed to determine whether the thumb side of their hand would be on the pink or tan end if they were to reach out and grasp the dowel in the center using a power grip (e.g., as one would grasp the handle of a tennis racket). This decision revealed whether an underhand or overhand grip was preferred for engaging the dowel in each orientation. While these judgments were made, each subject's head was stabilized on a chin rest, and his or her designated response hand rested palm down on a marked location in front of the display. The other hand rested comfortably at the subject's side. Throughout testing, the subject was closely monitored to ensure that he or she did not engage in any overt movements with the response hand. Response times were recorded by computer from the onset of the dowel until the subject said either "pink" or "tan" into a voice-activated key. Grip preferences were entered into the keyboard manually by the experimenter.

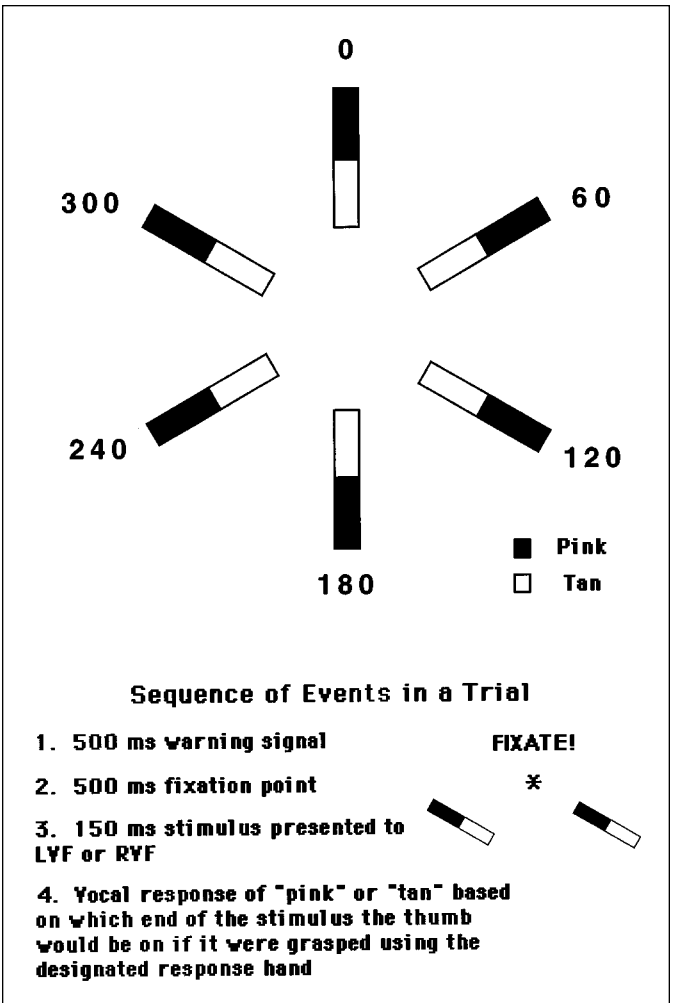


Fig. 1. The six stimuli presented and the sequence of events experienced on a given trial of the experiment. Note that in the actual experiment, stimuli appeared one at a time, and the orientation and visual field in which the dowel appeared varied randomly across trials. LVF = left visual field; RVF = right visual field.

There were 10 blocks, each consisting of 12 trials: six different dowel orientations presented to each of the two visual fields. The orientation of the stimulus and the visual field in which it appeared varied randomly from trial to trial. On half the blocks, subjects based their judgments on the left hand, and on the remaining half, judgments were based on the right hand. For each subject, order of response hand alternated across blocks, and the initial response hand was counterbalanced across subjects.

RESULTS AND DISCUSSION

Response Times

Forty-three trials were eliminated prior to the analysis because subjects were judged by the experimenter not to have their eyes fixated when the stimulus was displayed. In addition, 167 (4.5%) of the

remaining data points were defined as outliers, and eliminated prior to the analysis. These responses were either anticipatory (less than 300 ms) or inflated (greater than 2,000 ms).

Contrary to what would be expected if mentally representing prehensile movements demanded processes lateralized to the left hemisphere, mean response times did not differ significantly between LVF and RVF presentations (801.6 ms vs. 802.7 ms, respectively), $F < 1.0$. However, as predicted by the hypothesis that each cerebral hemisphere plays a dominant role in representing movements of the contralateral hand, there was a highly significant two-way interaction between response hand and visual field, $F(1, 29) = 27.89$, $p < .001$, $MSE = 13,565.25$. As shown in Figure 2, response times were considerably faster when visual information was presented to the cerebral hemisphere contralateral to the designated response hand.

Grip Preferences

Despite the absence of any overt hand movements, data were consistent with the hypothesis that grip selection in the present experiment was based on accurately anticipating the demands of actual prehension. As in experiments involving actual prehension (Johnson, 1997; Johnson et al., 1996), stimulus orientation had a significant main effect on grip selection, $F(5, 145) = 26.81$, $p < .001$, $MSE = 0.193$. As depicted in Figure 3,

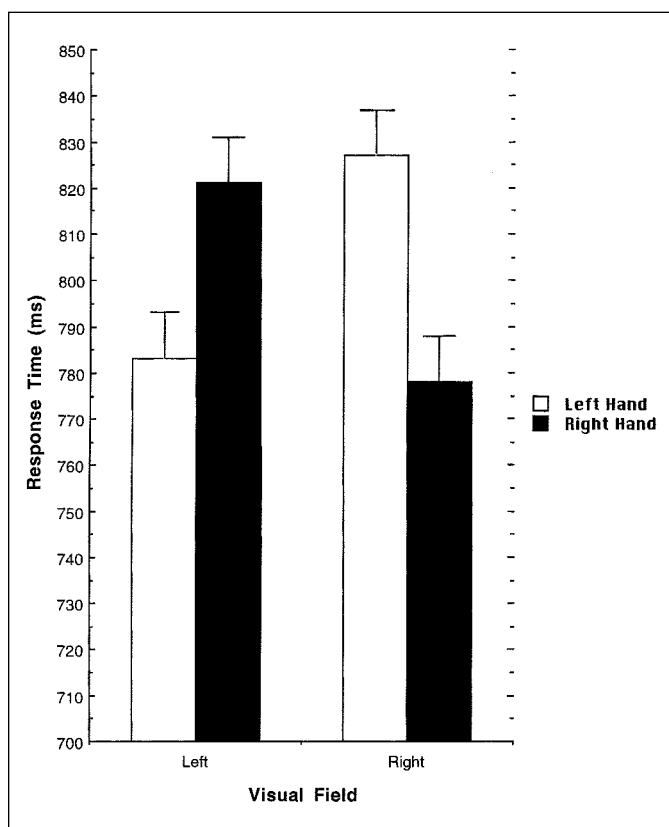


Fig. 2. Response time as a function of the visual field in which the dowel appeared and the designated response hand.

this effect was qualified by a significant interaction between stimulus orientation and designated response hand, $F(5, 145) = 164.62$, $p < .001$, $MSE = 0.084$.

Regression analysis revealed that a full 96% of the variance in grip preferences in the divided-visual-field imagery task was accounted for by preferences exhibited in the earlier prehension task, $R = .98$, $F(1, 10) = 221.98$, $p < .001$, $MSE = 0.007$. Likewise, the probability of selecting the pink grip in the present task was highly negatively correlated with previously obtained ratings of the biomechanical awkwardness of actually adopting such grips for dowels in these orientations, $R = -.85$, $F(1, 10) = 23.26$, $p < .001$, $MSE = 0.042$.

Taken together, these findings suggest that each cerebral hemisphere is capable of using motor imagery to select movements of the contralateral hand that are consistent with both the perceived orientation of the target object and the biomechanical constraints of the effector.

CONCLUSIONS

The present results are consistent with a growing body of evidence suggesting that motor imagery is supported by mechanisms involved in motor planning, control, or both (e.g., Jeannerod, 1994). Results of this divided-visual-field study suggest that, like actual grasping movements, mentally represented prehension involves contralaterally organized mechanisms in the cerebral cortex (Parsons et al., 1995). To the extent that this interpretation is correct, the present results also shed light on the cerebral organization of processes involved in solving one of the fundamental problems in motor control, that of movement selection (e.g., Rosenbaum, 1991).

It has long been realized that the problem of selecting an object-oriented movement is ill-posed because there are typically more degrees of freedom in the effector than in the description of the task to be solved (Bernstein, 1967). Consequently, the motor system is faced with the dilemma of choosing one particular movement option (i.e., set of postures) from among a very large number of alternatives that could also achieve the desired goal. In order to account for the efficiency with which the human motor system typically solves this degrees-of-freedom problem, researchers have proposed a variety of different constraints on the number of candidate movements that must be evaluated (reviewed in Rosenbaum, 1991). One class of putative constraints involves using perceptual information to construct internal premotor representations in order to anticipate the demands of forthcoming tasks (e.g., Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1990; Stelmach, Castiello, & Jeannerod, 1994). The present results suggest that each cerebral hemisphere may participate in solving the degrees-of-freedom problem by anticipating demands associated with movements of the contralateral hand.

Acknowledgments—The author wishes to acknowledge the help of Bob D'Agostino and students in the Perception Lab for their contributions to the design and implementation of this research, and to thank James E. Cutting for helpful comments on an earlier version of this manuscript. Portions of this work were presented at the 38th Annual Meeting of the Psychonomic Society, Philadelphia, November 1996.

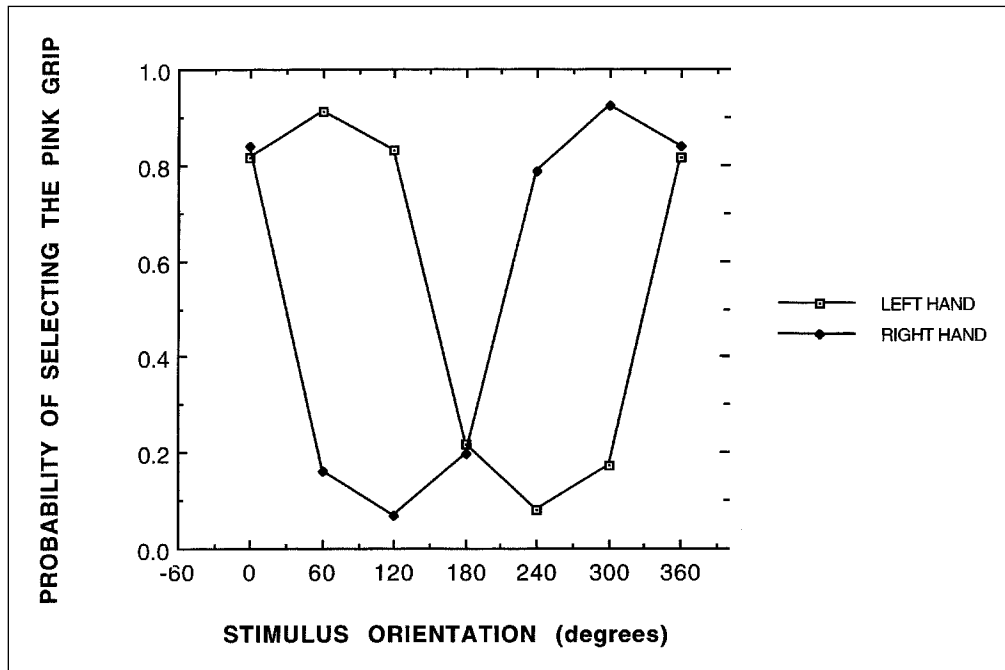


Fig. 3. Grip preference as a function of response hand and stimulus orientation. Note that data from 0° were replotted at 360° to emphasize symmetry.

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(RECEIVED 6/13/97; ACCEPTED 10/30/97)