

Hemispheric asymmetry of movement

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Studies in brain-damaged patients indicate that the left hemisphere in right-handers is specialized for controlling cognitive-motor tasks in both arms. Recent functional imaging data support this conclusion, with the finding that ipsilateral, as well as contralateral, movements activate the left, but not the right, motor cortex or association areas of either hemisphere. Future studies must aspire to identify the mechanisms for this asymmetry.

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Current Opinion in Neurobiology 1996, 6:796–800

© Current Biology Ltd ISSN 0959-4388

Introduction

The complex skilled movements we perform every day depend on primary motor characteristics, such as strength and speed, but they also depend on higher-level cognitive abilities, which are necessary to plan, self-monitor, and modify movements. Neuroanatomical, neurophysiological, neurobehavioral, and neuroimaging studies have shown that these skills depend on the interaction of neural systems, which include areas in the cerebral cortex, as well as subcortical structures [1,2,3].

Investigations of interhemispheric differences in the control of complex movements, which is the focus of this review, have primarily been conducted in brain-damaged patients with unilateral hemispheric damage (see [4••] for a review). Most experiments have demonstrated left-hemisphere dominance for complex motor skills when the limb ipsilateral to the damage is tested. These findings have been attributed to the cognitive-motor requirements of the task and the primary role of cortical association areas within the left hemisphere in controlling these processes.

More recently, functional imaging studies (see [1,5] for reviews) have begun to address these issues to provide converging methods in neurologically intact individuals that avoid the problems associated with inferring the normal functions of the brain from brain-damaged patients [6]. These approaches have considerable promise in improving our understanding of hemispheric asymmetry of movement when they are coupled with whole-brain imaging and with tasks in which systematic variations in cognitive-motor requirements are quantified by behavioral measures [7].

Here, we review the patterns of hemispheric asymmetry related to movement, with a focus on those tasks in which movements are differentially controlled by the left hemisphere. The two most plausible explanations for ipsilateral motor control—differential activation of association areas in the right and left hemispheres associated with the cognitive aspects of the movement and activation of the ipsilateral corticospinal pathways—will also be examined. Functional imaging studies that have examined hemispheric asymmetry of motor control will be reviewed as well.

Ipsilateral motor control from the right or left hemisphere

Hemispheric control of each hand is strongly influenced by the primary motor system's contralateral organization, especially for the distal muscles. Although there is no question that deficits contralateral to hemispheric damage are greater than those ipsilateral to lesion, many studies in right-handed patients with unilateral hemispheric damage have demonstrated deficits in the ipsilateral limb as well (see [4••,8] for reviews). The different patterns of ipsilateral motor impairment appear to depend on the cognitive requirements of the movement.

Most studies have found contralateral, but not ipsilateral, deficits for 'simple' tasks (e.g. unpaced rapid index finger tapping and grip strength) in which the cognitive-motor requirements appear minimal (see [4••]). Equivalent ipsilateral deficits after right- or left-hemisphere damage, implying dependence on both hemispheres, have been reported for tasks that appear to be more complex from a cognitive or sensory-motor integration standpoint (e.g. peg insertion task). Greater ipsilateral deficits after right but not left-hemisphere damage are less common but have been reported for slow-paced tapping and initiation of aiming movements. However, ipsilateral motor deficits after left-hemisphere damage (e.g. externally paced fast tapping, limb apraxia, ballistic movements, planning sequences) are more commonly found, which suggests that the left hemisphere is more dominant for controlling most cognitive aspects of movement, at least in right-handers [4••].

The left hemisphere has been associated with the computation of many cognitive-motor processes, including the construction and storage of motor programs [9,10,11••,12•], the utilization of sensory feedback to monitor and modify movements [13], the selection and retrieval of motor programs for sequential movements [14], serial ordering [15], and rapid sequential processing [16]. On the other hand, some studies [12•,17], but not all [9,10,13], have

suggested the right hemisphere plays a special role in closed-loop control, in which processing is carried out on-line to modify the trajectory or accuracy of an aiming movement.

Ipsilateral deficits in movement have been attributed to the cognitive-motor requirements of the tasks being performed, which probably require the cortical association areas, rather than to the damage incurred to the ipsilateral segment of the corticospinal pathway [4••,9,10,14,15]. The former explanation is favored because ipsilateral deficits are more common with left- than right-hemisphere damage, and they increase as the cognitive demands of the motor task increases. However, lesion studies have not methodically examined the association between intrahemispheric lesion location and cognitive-motor performance.

Hemispheric control of arm reaching

The left hemisphere appears to be more specialized than the right hemisphere for controlling arm reaching movements, but there is disagreement about the mechanism(s) for this discrepancy. Some researchers have suggested that left-hemisphere damage impairs open-loop processing, in which movements are programmed and executed without the aid of feedback mechanisms. Closed-loop processing, which is dependent on sensory feedback, appears to be intact after damage to the left hemisphere [9,10,12•]. However, others have disputed this claim [13]. These disagreements are probably attributable to many factors, including differences among studies in the cognitive-motor requirements of the task (e.g. single versus sequential aiming or target size), in subject characteristics (e.g. intrahemispheric lesion location and volume), and in the definition of open- and closed-loop processing.

Recent work suggests that the open-loop concept may not be useful in accounting for left-hemisphere dominance. In a kinematic analysis [11••], left-hemisphere damage was associated with problems in selecting and implementing an optimal movement velocity as movement amplitude increased. This finding was not affected by the availability of visual feedback, which is inconsistent with an open-loop explanation. The performance of larger amplitude movements may be compromised because greater forces are required to maintain spatial accuracy, which increases the cognitive-motor complexity.

Hemispheric control of ideomotor limb apraxia

Ideomotor limb apraxia is characterized by spatiotemporal deficits in the performance of familiar gestures, which cannot be accounted for by weakness, ataxia, sensory loss, aphasia, or other cognitive deficits. It is measured clinically by gestural performance (e.g. brushing teeth) [11••] and is more common after left- than right-hemisphere damage. Recently, these deficits have been described by elegant

kinematic studies of limb apraxic patients with parietal lobe damage as they perform a slicing gesture [18,19]. When compared to control subjects, the apraxic patients' ability to 'slice bread' was characterized by abnormalities in the plane of the motion, such that a slicing gesture was converted to a chopping motion. In addition, the relationship of velocity and trajectory shape and the coordination of movement across the different joints involved in the movement were distorted. Spatiotemporal disruptions in the movement have been attributed to degradation of the motor plan and/or in the processes necessary to retrieve and organize various aspects of the plan.

In order to ensure that these deficits are specific to apraxia, kinematic analyses will need to be done in non-apraxic left-hemisphere-damaged patients. The importance of this control has been stressed in a study of hand-posture sequencing. Here, left-hemisphere-damaged patients who were not apraxic demonstrated some of the same deficits as apraxics in controlling sequential movements [20].

Hemispheric control of sequencing

Unilateral brain damage

Abnormalities in sequencing movements have also been reported more commonly after left- than right-hemisphere damage ([10,14,15]; see [4••] for a review), although multiple mechanisms are probably involved. One study [20] examined the ability of apraxic and non-apraxic patients with left-hemisphere damage to sequence a series of hand postures to determine if previously reported sequencing deficits in left-hemisphere, but not right-hemisphere, damage [21] were specific to limb apraxia or more general to the role of the left hemisphere. Apraxic and non-apraxic patients showed normal advance preparation of repeated hand-posture sequences. Only the apraxic patients showed abnormal preparation of sequences that contained different hand postures. The pattern of the reaction time findings suggested that the apraxic group did not demonstrate the ability to utilize properties of the sequences (e.g. spatial, motor) to parse or chunk them into higher-level response groupings. Importantly, these deficits in advance planning affected the execution of the sequences.

Despite the spatial requirements of this sequencing task, performance was normal in patients with right-hemisphere damage who showed visuospatial deficits on neuropsychological tests. It appears that the preparation of movement sequences may involve processes that are largely dependent upon representations of the motor system and, therefore, left-hemisphere processing. Some, but not all, of these processes are specifically impaired in ideomotor apraxia.

Functional imaging

Several functional imaging studies have compared the relative degree of activation between the two hemispheres

for ipsilateral movements [22–24,25••,26]. All but one study [26] reported greater left- than right-hemisphere activation with ipsilateral movement. Two of these studies [24,25••] examined hemispheric asymmetry of sequential finger-thumb oppositions and found greater ipsilateral activation in the left than right hemisphere, but only in right-handers. Although one study examined only the motor cortex [24] and the other included whole-brain imaging [25•], both studies found that ipsilateral movements activated the left motor cortex more than the right motor cortex, and whole-brain imaging did not show asymmetries in other areas.

Even though these results are consistent with data from brain-damaged patients, an implicit assumption has been that left-hemisphere dominance is related to an asymmetry in the cortical association areas rather than in the motor cortex. The fact that the asymmetry for the finger-thumb opposition task appears to be localized to the left motor cortex and not to motor association areas suggests the left motor cortex may play a more important role in this relatively simple task than previously envisioned. This may be attributable to its role in regulating the parameters of movement (e.g. force) [27], the simultaneous activation of two muscles, or the order of recruitment of synergist muscles [28]. This contrasts with more complex sequences, which place greater demands on processes involved in the selection and organization of the sequence components. These types of movement sequences activate the supplementary motor cortex bilaterally, which the sequential finger-thumb opposition tasks do not [1].

The hemispheric differences in ipsilateral activation could also be attributed to differences in performing the motor task in the right (dominant) and left (non-dominant) hand. One study [29•], through use of electromyograms, found a higher incidence of covert mirror movements in the right hand when subjects performed a task with their left hand, and this was associated with bilateral motor cortex activation. Therefore, greater ipsilateral activation in the left hemisphere may reflect the mirror movements of the right hand rather than hemispheric dominance. This is a potentially important confounding factor in analyses of hemispheric asymmetry that must be controlled.

Is ipsilateral control attributable to ipsilateral output from the motor cortex?

The influence of ipsilateral motor projections through the corticospinal system must be considered, especially when similar ipsilateral deficits are seen after damage to the right or left hemisphere, or when the asymmetry of activation in functional imaging studies is localized to motor cortex. However, this explanation is a less likely one for hemispheric asymmetry because patients

who demonstrate ipsilateral deficits on complex tasks frequently do not show them on simpler tasks. In addition, pathological analyses of the human spinal cord have found asymmetry in the corticospinal pathway (with the ipsilateral projection being greater from the right than the left hemisphere in the majority of patients [30]), which is the opposite finding of the behavioral data.

Even though 10% to 15% of the corticospinal tract projects to the ipsilateral spinal cord [31], these projections affect proximal more than distal muscles [27,32,33], though one neuroanatomical study (KD Hutchins, PL Strick, *Soc Neurosci Abstr* 1987, 13:72.8) has emphasized substantial ipsilateral corticospinal tract projections to distal musculature. Nonetheless, in a behavioural study that showed some distal control, it was much less significant than the proximal control [34•]. These findings would predict greater hemispheric asymmetry for ipsilateral distal than proximal movements. However, lesion studies in humans have shown ipsilateral effects with tasks that require movement of the distal, as well as proximal, musculature. Functional imaging studies have also shown that with recovery from hemiplegia, greater activation is seen in the undamaged hemisphere when the recovered limb is moved [6].

These results suggest that the ipsilateral cerebral cortex and efferent motor pathways are sufficient to support the recovery. Unfortunately, this study did not examine whether there were differences in the ability of the left or the right hemisphere to support recovery. Whether or how these pathways contribute to normal motor functioning is not clear, although a recent functional magnetic resonance imaging study [35] has suggested that ipsilateral pathways from motor cortex play a relatively minor role. The role of ipsilateral pathways from pre-motor areas has not been established.

Conclusions

Recent functional imaging studies have demonstrated greater activation in the left than the right hemisphere during the performance of ipsilateral movements. Future studies must examine whether this hemispheric asymmetry is associated with the cognitive requirements of the action, as studies with brain-damaged patients suggest. It will also be important to determine which areas within each hemisphere are responsible for the asymmetry and their relationship to the specific cognitive-motor requirements of the task.

Acknowledgements

This work was supported, in part, by grants to KY Haaland and DL Harrington from Medical Research and from Rehabilitation Research and Development of the Department of Veterans Affairs.

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