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Neural control of hand movement

Leonardo was probably the first, both to appreciate and record its wondrous complexity. Through painstaking drawings of the dissected human hand the da Vinci eye revealed, with striking accuracy, its intricate beauty. Sadly, his anatomical drawings were not published and made widely available until much later, in the early 19th century. Instead, the depictions of Vesalius, from the 16th century, and later the cross-sections drawn by Pirogov in the 19th century have taken centre stage in our images of the hand.[1]

With deeper understanding of its functional anatomy came the startling realization that the human hand has a remarkable 27 degrees of freedom, permitting a myriad of configurations and a huge repertoire of actions,[2] including its ability to perform 'active touch'[3] and, perhaps most importantly, to use and develop a wide range of tools.[4] From an evolutionary perspective, therefore, many have argued that the hand deserves special attention. It allowed human culture to develop in spectacular fashion.

The biases of neuroscientists might, however, lead some to point out that the hand would be nowhere without the brain. The hand succeeded because the brain succeeded! Perhaps a more nuanced argument would be that brains which invested in the hand, devoting more resources to its control—both cortical space and computational power—were the ones that succeeded in evolution. That this might be so became manifestly credible with the pioneering electrical stimulation studies of human cortex led by Penfield. However, while we have learnt much about the cortical representation of hand movements in primary and secondary motor cortical regions,[5] we know far less about the wider network of brain regions that contribute to control of the human hand.

Some key insights have arisen from studies of limb apraxia, a syndrome curiously most often associated with left hemisphere pathology, including two seminal papers published in *Brain* in 2014. In the first, Buxbaum and her colleagues provided evidence of important dissociations between the left inferior parietal lobe and left middle/inferior temporal lobe.[6] In their lesion analysis of chronic stroke patients, they found that deficits of shaping the hand correctly for imitation—regardless of whether it was for copying meaningless gestures or for imitating tool-use gestures—were associated with left parietal damage. In contrast, lesions involving the left middle/inferior temporal region led to deficits of tool-related actions, irrespective of whether this was imitation or self-generated actions when shown specific tools. More fine-grained analysis revealed that it was the postural components of tool-related actions that was affected by the temporal lesions, whereas parietal damage led to deficits in the kinematics of imitative actions. These investigators also found evidence for left frontal involvement, including associations between primary and premotor cortical damage and deficits on imitation tasks.

The second paper, by Weiller's team, focused on similar issues, again in left hemisphere stroke patients, but this time in the acute setting.[7] In this population, their work revealed that more superior regions of the parietal lobe and the intraparietal sulcus were more strongly associated with imitation deficits, whereas more ventral lesions affecting the anterior inferior parietal lobe and posterior middle temporal gyrus led to deficits in pantomiming tool use. Difficulties in the ability to produce the correct action for a particular tool—so called content errors—were particularly associated with temporal lobe lesions, consistent with a role of this region in action semantics.

Although there were distinct differences between the two studies, both in terms of the chronicity of stroke and scoring systems, they provide a rich insight into two dissociable brain systems. One appears to be crucial for transforming visual information about hand posture (as for example shown by an examiner) into the motor commands required to achieve that configuration, a task we find effortlessly easy but which would tax any robot with an effector that has 27 degrees of freedom! The other appears far more linked to using concepts about tool use in order to generate the hand posture required to use it. This is a system closely tied to semantic representations of tools and objects—knowledge about what they are or do and how they are used.

Now, in this issue of *Brain*, a new study reports on the consequences of direct electrical stimulation on awake patients undergoing surgery for frontal tumour excision.[8] This investigation combines behavioural measures with EMG and brain imaging to elucidate the role of the white matter tracts underlying dorsal and ventral premotor regions in left and right hemisphere cases. Patients performed a hand manipulation task which involved shaping the hand to grasp an object and rotate it. Stimulation of the white matter below the dorsal premotor region led to arrest of hand movement when attempting to manipulate the object. In contrast, a clumsy pattern of hand movements, with slowing or uncoordinated finger movements, occurred with stimulation of the white matter underneath ventral premotor cortex. These effects were observed with stimulation of either left or right cerebral hemispheres.

Sophisticated imaging analysis suggested that it was stimulation of short U-fibres connecting parts of premotor cortex that led to movement arrest. The clumsy pattern of movement was evoked by excitation of fibres in inferior frontostriatal white matter connections and the third branch of the superior longitudinal fasciculus. Intriguingly, only resections that involved the dorsal white matter region near the supplementary motor area were associated with a functional hand movement deficit postoperatively, albeit transiently.

This kind of mapping takes our understanding of the networks underpinning neural control of hand movement one step further.

It opens up a far more precise way to map the white matter connections of posterior brain regions—as implicated in the studies on stroke patients with apraxia—to frontal premotor areas that are more closely linked to action execution. Electrical stimulation during awake surgery while patients perform imitation tasks or pantomime tool use might in the future also help to unravel the special contributions of the left hemisphere to praxis and tool use in humans.

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