How are visual areas of the brain connected to motor areas for the sensory guidance of movement?

Mitchell Glickstein

Visual areas of the brain must be connected to motor areas for the sensory guidance of movement. The first step in the pathway from the primary visual cortex is by way of the dorsal stream of visual areas in the parietal lobe. The fact that monkeys can still guide their limbs visually after cortico–cortical fibres have been severed suggests that there are subcortical routes that link visual and motor areas of the brain. The pathway that runs from the pons and cerebellum is the largest of these. Pontine cells that receive inputs from visual cortical areas or the superior colliculus respond vigorously to appropriate visual stimuli and project widely on the cerebellar cortex. A challenge for future research is to elucidate the role of these cerebellar target areas in visuo–motor control.

Mitchell Glickstein is at the Dept of Anatomy, University College London, Gower Street, London, UK WC1E 6BT.
representation of the mapping of the visual fields on the human striate cortex, which has been repeatedly confirmed since that time.

Identification of the motor area of the cerebral cortex also began with animal experiments. Fritsch and Hitzig9 showed that weak electrical stimulation of a specific region of the dog’s frontal cerebral cortex could elicit movement of the face or limb on the contralateral side of the body. If electrical stimulation of a given point elicited limb movement, ablation of the cortex at that point hindered the use of that limb. Shortly thereafter, Betz20 described the characteristic large pyramidal cells in layer V of cortex that are associated with the motor area. The interpretation of these experiments as indicating a motor-control area in the cerebral cortex was initially controversial because some authors insisted that the stimulation must have caused a sensation, and it was that sensation which led to movement. Nevertheless, by 1900 the identity and location of the primary sensory and motor cortical areas were widely accepted.

Although the evidence for localization of visual and motor functions was clear, surprisingly few questions were asked regarding how sensory areas might be linked to motor areas for the sensory guidance of movement. Most authors assumed that there must be a series of cortico-cortical connections that arise in the visual cortex and end in the motor cortex. Figure 1 reflects this generally accepted view.

Although the current terminology is more sophisticated, the assumption that a series of cortico-cortical fibres links sensory areas to motor areas of the cortex still prevails. There are no direct anatomical projections from primary visual cortex (Area 17) to the motor and premotor areas (Areas 4 and 6). Instead, cortico-cortical links between the primary visual and motor areas are indirect and the pathway is typically thought to involve a series of cortico-cortical links that originate in Area 17 and end in Areas 4, 6 or 8 for the visual guidance of the fingers, limbs or eyes. The corpus callosum is thought to mediate tasks in which the visual cortex on one side had to be linked to the motor cortex on the opposite hemisphere.

The dorsal stream of extrastriate visual areas

In 1982, Ungerleider and Mishkin proposed12 that the extrastriate visual areas could be broadly segregated into two streams on the basis of anatomical and behavioural evidence: one dorsal stream, coding the location of visual objects (‘where is it?’) and the other ventral stream, identifying the nature of the object (‘what is it?’). In the same year, Jack May and I13 proposed that a similar dichotomy exists between dorsal and ventral extrastriate cortical visual areas on the basis of the differential projections of these two areas to the pontine nuclei. The dorsal, parietal areas project heavily to the cerebellum by way of the pontine nuclei, whereas the ventral stream has little or no such projection. We suggested that an important function of the parietal lobe visual areas might be in the visual control of movement, based on its anatomical connections to the cerebellum (Fig. 2).

Although visually guided movement of the wrist and fingers of monkeys is impaired following parietal lobe lesions, control lesions of the temporal lobe or peri-arcuate cortex produce little or no impairment. The evidence is now clear that the first step in the pathway that links visual to motor cortical areas is by way of the dorsal stream of extrastriate visual areas, because lesions of these areas in monkeys profoundly impair visual guidance of movement14. By contrast, lesions of cortical areas in the ventral stream can impair form, colour or face recognition, but do not affect visuo-motor coordination15. Indeed lesions of the dorsal stream visual areas are so severe in their effects on visual control of movement that Ferrier16,17 initially misinterpreted these effects in monkeys as blindness (Fig. 3). Almost identical deficits in visually guided movement are present in humans after lesions of analogous extrastriate cortical visual areas18,19.

Connections of the dorsal stream visual areas

How do the dorsal stream visual areas connect to cortical and subcortical brain areas that control movement? Although there are indirect cortico-cortical routes from these areas to Areas 4 and 6, monkeys can still execute rapid and accurate visually guided arm movements after the white matter between the parietal lobe visual areas and the frontal lobe has been cut20. Haaxma and Kuypers21 later showed that such fibre lesions could produce deficits in the visual guidance of wrist and fingers. However, all but two of the fibre lesions were placed caudally,
that are involved in the control of eye and limb movements. In addition, Strick et al.\textsuperscript{3} have studied in detail the interconnections and output of several motor cortical areas within the frontal lobes. Far less is known about the links between visual and motor areas of the cerebral cortex, but it is clear that cortico–cortical links between the primary visual and motor areas are complex and involve a series of cortico–cortical links. Nevertheless, cortico–cortical circuits cannot account for all examples of sensory-guided movement. Therefore, there must be other, subcortical routes whereby sensory information can access motor structures. Two prominent subcortical pathways could, in principle, function in the sensory guidance of movement. One possibility would be a pathway via the basal ganglia. However, although there are visual inputs to the caudate nucleus and claustrum\textsuperscript{22}, there is a much larger route through the pontine nuclei to the cerebellum\textsuperscript{24}.

**Pontine nuclei are the major brainstem target of efferent fibres from the cerebral cortex**

Nearly all of the descending projections from the cerebral cortex to the midbrain and below are carried in the massive Crura cerebri, the large-fibre system at the base of the cerebral peduncles. A small percentage of these fibres travel past the pons and medulla to become cortico–spinale fibres (Fig. 4). Estimates based on light microscopy suggest that there are 20 million fibres in the peduncles and only one million fibres in the cortico–spinale tracts\textsuperscript{25}. The great majority of peduncle fibres end in the pontine nuclei. The possibility that cortico–spinale and cortico–bulbar fibres also give off collaterals to pontine cells as they pass through the pons\textsuperscript{16,27}, suggests that every fibre in the cerebral peduncles has a pontine target. Pontine nuclei, cerebellar hemispheres and lateral cerebellar nuclei are especially prominent, in humans and the higher primates\textsuperscript{28}. One of the major circuits through the human brain is a route that originates in the cerebral cortex and connects to the cerebellum by way of the pontine nuclei.

**Dorsal stream visual areas project to the pontine nuclei**

The dorsal stream visual areas are connected to the cerebellum by way of a relay in the pontine nuclei. Degeneration staining and the study of orthogradely labelled fibres following a tracer injection into the cerebral cortex have revealed a massive connection between the dorsal stream visual areas

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**Fig. 2. Performance of monkeys before and after cortical lesions on a visuo–motor task devised by Haaxma and Kuypers\textsuperscript{21}.** The lesions are represented in dark grey on the figure. The animals are required to reach out to a disc containing slots at various orientations for a food reward. To perform the task successfully the animal must orient its wrist and fingers to conform to the orientation of the slot. The data from five animals are presented. (a) Two monkeys (p1, solid circles and p2, open circles) had lesions that destroyed most of the dorsal stream of visual processing areas. (b) Two monkeys (a1, solid circles and a2, open circles) had sequential lesions restricted to the cerebral cortex on the rostral bank of the arcuate sulcus and the cortex just rostral to it. (c) One monkey had a large bilateral lesion of inferotemporal cortex. The two animals in which the dorsal extrastriate visual areas had been removed were profoundly impaired in guiding the orientation of their wrists and fingers. The three control animals (b and c) were mildly impaired or unaffected by the lesion. Reproduced, with permission, from Ref. 13.
and the pontine nuclei\textsuperscript{29}. Results of studies using retrograde tracers are consistent with this observation. If the pontine nuclei are filled with a retrograde tracer and labelled cells in the cortex are mapped, a massive input from the dorsal stream parietal lobe visual areas to the pontine nuclei is visible. By contrast, there are few or no projections from cortical areas in the ventral stream\textsuperscript{29}. Although the exact pattern of termination within the pontine nuclei varies among mammals, in all species that have been studied\textsuperscript{10–32} there is a rich connection between cortical visual areas and the pontine nuclei. In addition to cortical visual areas, thepons also receives an input from the superior colliculus and pretectum, which provide additional sources of mossy fibre visual information to the cerebellum\textsuperscript{33,34}.

**Pontine cells respond to appropriate visual targets**

Cells in the pontine nuclei of cats\textsuperscript{35,36}, and monkeys\textsuperscript{37,38} that receive their input from cortical visual areas or the superior colliculus\textsuperscript{39} rapidly respond to appropriate visual stimuli. The optimal stimuli for activating pontine visual cells are targets that move in a preferred direction. The receptive fields of pontine visual cells are relatively insensitive to the orientation of visual targets. The properties of pontine receptive fields are consistent with their role in providing a major link in the circuit that controls the visual guidance of movement.

**Pontine nuclei project widely on the cerebellar cortex**

If wheat germ agglutinin horseradish peroxidase (WGA–HRP) is injected among visually activated cells in the pontine nuclei, the input from the dorsal stream of extrastriate visual areas can be confirmed by mapping the location of retrogradely labelled cortical cells. The projections of these pontine visual cells can be followed by mapping labelled axon terminals on the cerebellar cortex. Such studies have revealed that visual ponto–cerebellar fibres terminate widely on the caudal cerebellum. The densest target in monkeys\textsuperscript{40}, cats\textsuperscript{41} and rats\textsuperscript{42} is the paraflocculus, although the electrophysiological and behavioural properties of the dorsal paraflocculus, a region of cerebellar cortex, have not been explored extensively. There are also projections to the uvula, paramedian lobule and Crus I and II of the cerebellar hemispheres and to lobule VII of the vermis.

**Cerebellum projections to nuclei controlling descending motor systems**

The output of the cerebellar cortex is from Purkinje cells that project to the cerebellar nuclei. The cerebellar nuclei, in turn, project directly or indirectly to the cells from which the major descending motor tracts originate. Here, we emphasize the link to the motor cortex, which is mediated by a relay in the ventral thalamus. There are also cerebellar projections to the red nucleus, the superior colliculus and brainstem areas that give rise to the descending reticulo–spinal and vestibulo–spinal tracts.

**Evidence for a role for the cortico–ponto cerebellar pathway in the visual guidance of movement**

Although the effects of lesions of the dorsal stream of extrastriate visual areas often resemble the visuo–motor deficits produced by cerebellar lesions, much of the evidence for the role of the cortico–ponto–cerebellar pathway in the visual control of movement remains indirect. One source of evidence is the fact that skilled bi-manual coordination can survive section of the forebrain commissures. In a study of intermanual transfer\textsuperscript{43}, it was found that although section of the corpus callosum blocked the normally strong transfer of somatosen-sory information between the two hands, the motor habits of testing two unseen objects showed immediate transfer when the second, untrained hand was tested first. We concluded that there must be a surviving subcortical pathway linking the two sides of the brain. Damage to efferent fibres from the parietal lobe to the pontine nuclei can also produce visuo–motor deficits. For example, a lesion in the caudal limb of the internal capsule that interrupted connections from parietal lobe visual areas to the pontine nuclei produced symptoms that resembled those caused by parietal lobe or cerebellar damage\textsuperscript{44}. Monkeys in which vision is restricted to one hemisphere and in which the forebrain commissures have been cut still use the blinded hemisphere to control rapid visually guided use of the limb. Autoradiographic evidence suggests that the link from the seeing hemisphere to the opposite motor cortex is by way of the cerebellum\textsuperscript{45}. Savaki\textsuperscript{46} trained monkeys, in which the optic tract and forebrain commissures had previously been sectioned, to perform a rapidly executed visuo–motor task, using the arm that was ipsilateral to the severed optic tract. She studied the distribution of labelled cortical cells in these animals that had been injected before testing with 2-deoxyglucose as a cell-activity marker. Although no cortico–cortical visual connections to the contralateral motor cortex in these animals remained, the ‘blinded’ motor cortex proved to be active during performance of the task.
Localization of function in the cerebellum

One of the challenges for future research is to learn the function of each part of the cerebellum. Since the 19th century, lesions of the cerebellum have been known to produce deficits in movement. The cerebellum plays a major role not only in the sensory guidance of movement, but also in reflex modification and motor learning. In addition, it has been suggested that the cerebellum is involved in cognitive functions. However, the complex folding of the cerebellar cortex makes the study of localization difficult, but fMRI studies often state that the cerebellum ‘lights up’ in subjects that are performing a given task. The challenge for the future will be to clarify the broad range of cerebellar functions and to identify the locations and the pathways that are involved.

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