

Separate neural pathways for the visual analysis of object shape in perception and prehension

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Background: Earlier work with neurological patients has shown that the visual perception of object size and orientation depends on visual pathways in the cerebral cortex that are separate from those mediating the use of these same object properties in the control of goal-directed grasping. We present evidence suggesting that the same dissociation between perception and action is evident in the visual processing of object shape. In other words, discrimination between objects on the basis of their shape appears to be mediated by visual mechanisms that are functionally and neurally distinct from those controlling the pre-shaping of the hand during grasping movements directed at those same objects.

Results: We studied two patients with lesions in different parts of the cerebral visual pathways. One patient (RV), who had sustained bilateral lesions of the occipitoparietal cortex, was unable to use visual information to place her fingers correctly on the circumference of irregularly

shaped objects when asked to pick them up, even though she had no difficulty in visually discriminating one such object from another. Conversely, a second patient (DF), who had bilateral damage in the ventrolateral occipital region, had no difficulty in placing her fingers on appropriate opposition points during grasping, even though she was unable to discriminate visually amongst such objects.

Conclusions: This double dissociation lends strong support to the idea that the visual mechanisms mediating the perception of objects are functionally and neurally distinct from those mediating the control of skilled actions directed at those objects. It also supports the recent proposal of Goodale and Milner that visual perception depends on a ventral stream of projections from the primary visual cortex to the inferotemporal cortex, whereas the visual control of skilled actions depends on a dorsal stream from the primary visual cortex to the posterior parietal cortex.

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Background

Humans are capable of reaching and grasping objects with great dexterity, and vision plays an important role in the control of this fundamental skill. Thus, when we reach out to pick up an unfamiliar object, the opening of our fingers and the orientation of our hand reflect the size of the object and its orientation in egocentric space well before we make contact with it [1,2]. Recent neuropsychological studies suggest that the visual mechanisms responsible for controlling this skill are largely independent of those that support the visual perception of object size and orientation.

Thus, for example, Goodale *et al.* [3] have reported remarkably intact visuomotor performance in DF, a 34-year-old woman who developed visual-form agnosia following anoxia from carbon monoxide poisoning. So profound is DF's visual-form agnosia that she is unable to identify or recognize familiar faces, line drawings of common objects or even simple geometric shapes. Her elementary visual abilities, however, are still relatively intact and she shows only moderate deficits in contrast sensitivity and only a slight shrinkage of her visual fields [4]. Magnetic resonance imaging (MRI), carried out 13

months after the accident, revealed evidence of damage in ventrolateral regions of DF's occipital lobe, although her primary visual cortex appeared to be spared (for details of the lesion, see [4]). Nevertheless, despite the fact that DF was unable to discriminate, in perceptual tasks, between objects that differed in size and orientation, the pre-shaping and orientation of her hand during the execution of grasping movements accurately reflected those same object attributes.

Complementary dissociations have been reported in patients with bilateral lesions of the posterior parietal cortex [5,6]. Such patients are often unable to calibrate their grasp or orient their hand appropriately when reaching out towards target objects, even though they have no difficulty in reporting the size and orientation of those same objects, or in discriminating between them. Thus, damage to one part of the cortical visual pathways, the ventrolateral region of the occipital lobe, results in perceptual deficits with preserved visuomotor abilities, whereas damage to another part, the occipitoparietal region, results in visuomotor deficits with preserved perceptual abilities.

These neuropsychological observations, together with evidence from electrophysiological and behavioural

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studies in the monkey, have led Goodale and Milner [7,8] to propose a new interpretation of the division of labour between the two streams of visual pathways that leave the primary visual cortex and project to distinct regions of the primate cerebral cortex. These two streams, which were identified in the macaque monkey over ten years ago by Ungerleider and Mishkin [9], consist of a ventral stream and a dorsal stream. The ventral stream leaves the primary visual cortex and projects via a series of cortico-cortical projections to the inferotemporal cortex; the dorsal stream projects from the primary visual cortex to the posterior parietal cortex (see inset in Fig. 1). Although one must always be cautious when drawing homologies between monkey and human neuroanatomy [10], it seems likely that the visual projections from the primary visual cortex to the temporal and parietal lobes in the human brain may involve a separation into ventral and dorsal streams similar to that seen in the macaque brain. Ungerleider and Mishkin [9] originally proposed that the ventral stream plays a special role in the identification of objects, whereas the dorsal stream is responsible for localizing objects in visual space.

Goodale and Milner's [7,8] re-interpretation of this story places less emphasis on the differences in the visual information that is received by the two streams (object features versus spatial location) than it does on the differences in the transformations that the streams perform upon that information. According to Goodale and Milner's hypothesis, both streams process information about object features and about their spatial relations, but each stream uses this visual information in different ways. In the ventral stream, the transformations focus on the enduring characteristics of objects and their relations,

and permit the formation of long-term perceptual representations that are used to identify and recognize objects. In the dorsal stream, the transformations use the instantaneous and egocentric coordinates of objects, and mediate the visual control of skilled actions — such as manual prehension — that are directed at those objects. This division of labour in the cortical visual pathways can comfortably account for the dissociations between the perception of object size and orientation, and the use of these object features in the control of prehension that were both described earlier.

Object size and orientation are not the only object features that control the parameters of grasping movements. A remarkable sensitivity to the shape of an object is also evident from merely casual observation of grasping. Is the visual analysis of object shape, in order to control a grasping movement, also dependent on neural mechanisms that are relatively independent of those underlying the perceptual identification of objects, in the same way as the related analysis of object size and orientation? To answer this question, we compared the ability of the patient DF to discriminate objects of different shape with her ability to position her fingers correctly on the boundaries of the same objects when she was asked to pick them up.

We also contrasted DF's performance with that of another patient, RV, a 55-year-old woman who had developed optic ataxia after strokes that left her with large bilateral lesions of the occipitoparietal cortex. The extent of these lesions can be seen in Figure 2. The optic ataxia, which was evident clinically as a difficulty in directing grasping or pointing movements towards objects presented in different parts of the visual field,

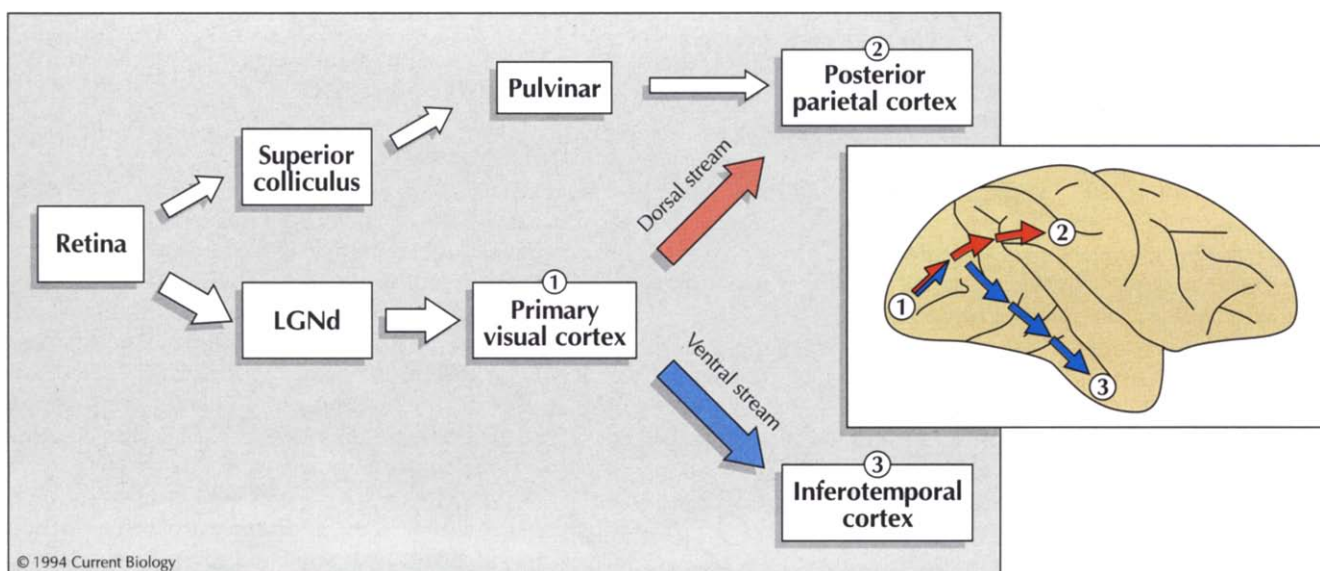


Fig. 1. Schematic diagram of the main routes whereby retinal inputs reach the dorsal and ventral streams. The larger arrows along the LGNd route to the cortex reflect the fact that these inputs are more numerous than those that arrive via the superior colliculus and pulvinar. The diagram of the macaque brain (right hemisphere) on the right of the figure shows the approximate routes of the dorsal and ventral streams of cortico-cortical projections from the primary visual cortex to the posterior parietal and inferotemporal cortex, respectively. LGNd, dorsal lateral geniculate nucleus.

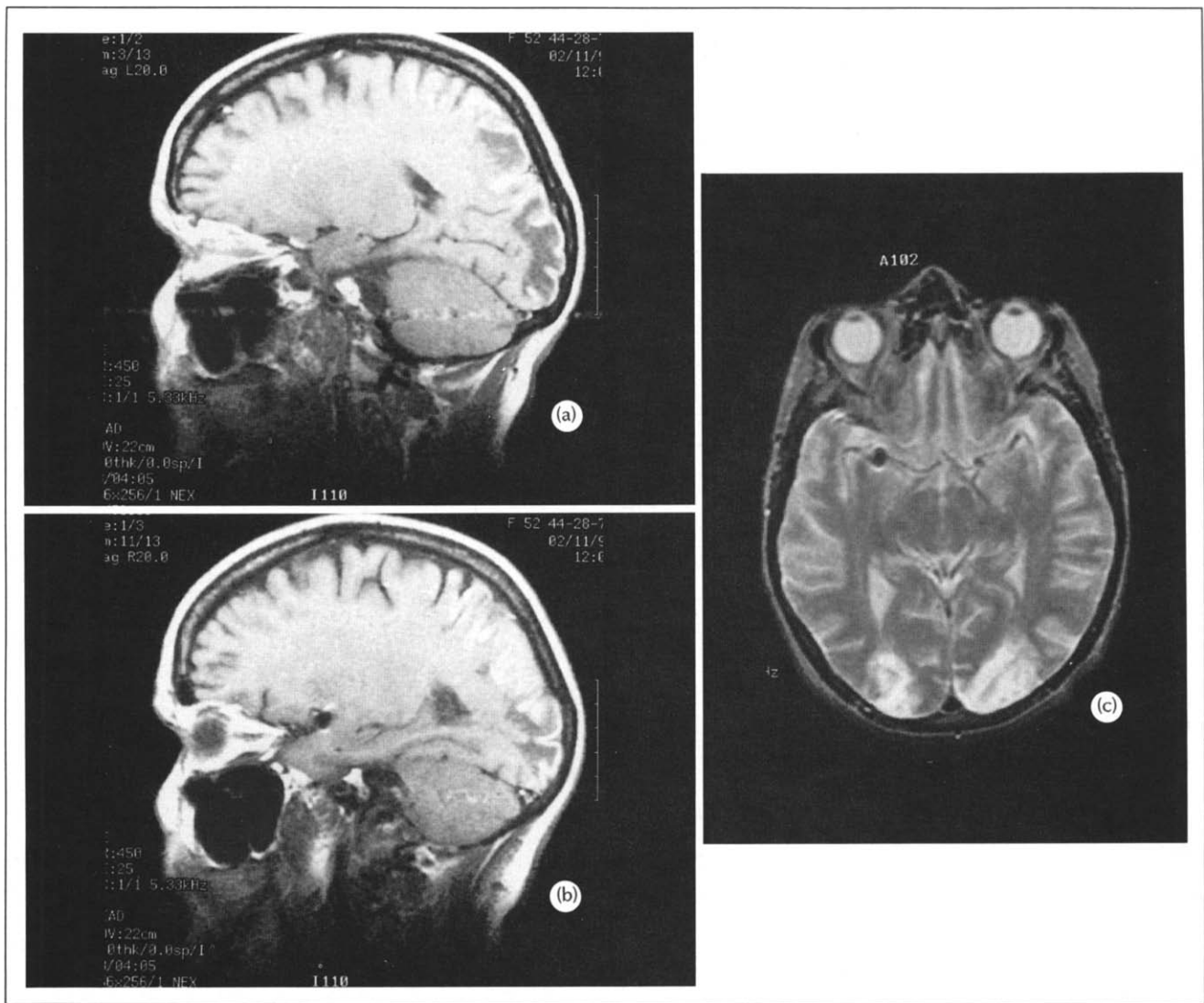


Fig. 2. Magnetic resonance images of the bilateral occipitoparietal lesion in patient RV. (a) Left and (b) right parasagittal (T1-weighted) sections. Note the extensive damage to cortex and underlying white matter in posterior parietal and occipital lobes. Damage is more extensive on the left than on the right. (c) An axial (T2-weighted) section in which the bilateral occipital infarcts can be seen. (Following the usual convention, the left side of the brain is on the right side of the photograph.) Note calcarine involvement on the left but not the right.

had resolved to some extent before we saw RV, although it was still clear that she had visuomotor problems. Nevertheless, despite her visuomotor deficits, RV's resolution acuity was in the normal range, she was not apraxic (that is, she could follow simple commands such as "show me how you would eat soup with a spoon"), and her hand strength and finger-tapping abilities were normal. She also achieved a perfect score on a 20-item test of object recognition in which she was asked to identify line drawings of common objects; DF could identify only two items correctly on this same test.

Results

Twelve different shapes (two of each) were used to compare DF's and RV's ability to discriminate between shapes and to use shape information to control grasping

(see Fig. 3). The shapes were constructed out of wood 0.6 cm thick, were painted enamel white and were presented on a flat black background. The shapes were based on the templates used by Blake [11] to develop algorithms for the control of grasping in two-fingered robots working in novel environments. These shapes have smoothly bounded contours and lack clear symmetry; the determination of stable grasp points therefore requires an analysis of the entire contour envelope of the shape.

When DF and RV were presented with pairs of these shapes in which the two shapes in any pair were either the same or different, they showed very different discrimination abilities. DF was unable to determine whether the two shapes were the same or different (see Fig. 4). Moreover, this failure was evident regardless of whether the two shapes on 'same' trials had the same

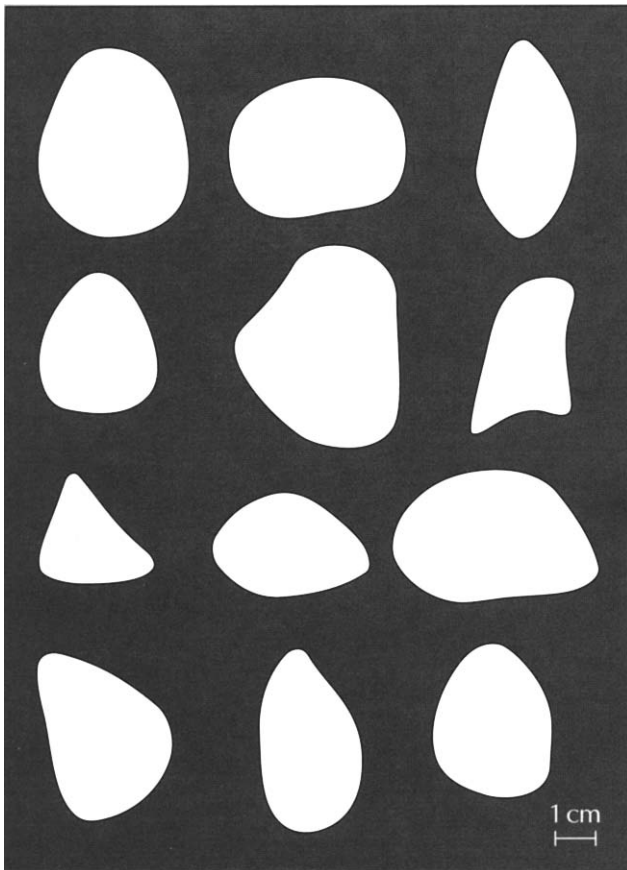


Fig. 3. The twelve different shapes used in both the same/different visual discrimination tasks and in the grasping task.

relative orientation or different orientations. In contrast, RV achieved a score of 90% correct for this same/different discrimination task when the relative orientation of the two shapes on 'same' trials was identical, falling to 80% correct when the relative orientation of the twin shapes was varied from trial to trial. In other words, whereas DF apparently failed to perceive whether two objects had the same or different outline shapes, RV had relatively little difficulty in making such a discrimination.

Quite the opposite pattern was observed when DF and RV were asked to pick up these objects using their index finger and thumb in a 'precision grip'. Even though DF failed to discriminate between these different objects, she had no difficulty in placing her finger and thumb on stable grasp points on the circumference of the object. The grasp points she selected were remarkably similar to those chosen by a neurologically intact control subject (see Fig. 5). In addition, DF showed the same systematic shift in the selection of grasp points as the control subject when the egocentric orientation of the object was changed. Moreover, the following observations, regarding both DF and the control subject, were made. Firstly, the line joining the two grasp points tended to pass through the centre of mass of the object. Secondly, these 'grasp lines' often corresponded to the axes of minimum or maximum diameter of the object. Finally,

the grasp points were often located on regions of the object boundary that would be expected to yield the most stable grip [11,12] — regions of maximum convexity or concavity.

RV's performance was very different (see Fig. 5). In contrast to both DF and the control subject, she often chose very unstable grasp points, and she stabilized her grasp only after her finger and thumb had made contact with the object. Thus, despite her apparent ability to perceive the shape of an object, RV was unable to use visual information about object shape to control the placement of her finger and thumb as she attempted to pick up that object. Once she had made contact with the object, however, her manipulation of it appeared essentially normal.

In order to quantify the differences in the performance of the three subjects, we measured the shortest distance between the grasp line (connecting opposing grasp points) on each trial and the object's centre of mass. Although this measure was similar for DF and the control subject, they both differed significantly from RV ($p < 0.001$; see Fig. 6).

Discussion

Despite DF's visual form agnosia, which made it impossible for her to distinguish one object from another on the basis of their shape, she had no difficulty using shape information to guide the placement of her finger and thumb as she reached out to pick up those objects. In fact, her grasping movements were quite normal. This

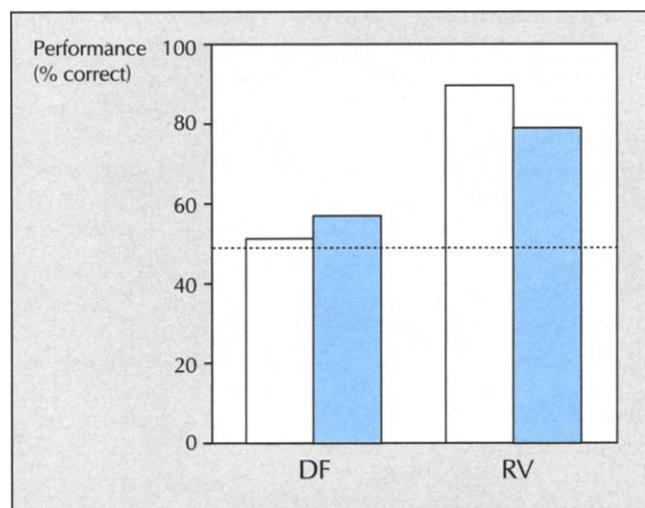


Fig. 4. Performance of DF and RV on the same/different discrimination tests. The open bars show performance on the task in which the relative orientation of the two shapes on the 'same' trial was identical; the blue bars show performance on the task in which the relative orientation of the twin shapes varied between 'same' trials. The control subject scored perfectly on both tests, although she took longer to respond when the two shapes on same trials were presented at different orientations. The dotted line indicates chance performance.

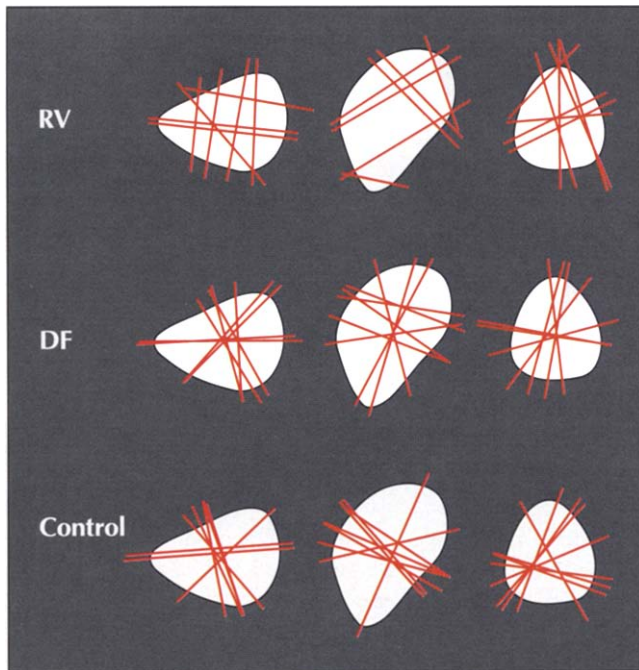


Fig. 5. The 'grasp lines' (joining points where the thumb and index finger first made contact with the shape) that were selected by the optic ataxic patient (RV), the visual agnostic patient (DF), and the control subject when picking up three of the twelve shapes. The four different orientations in which each shape was presented have been rotated so that they are aligned.

result suggests that some part of DF's remaining visual system was able to analyse the outline shape of the object and deliver the appropriate coordinates to the visuomotor networks that control the movements of the hand and fingers. This dissociation between profoundly disturbed perception and intact visuomotor control parallels the earlier observations about DF [3,4], which concentrated on object size and orientation rather than object shape.

In summary then, the brain damage that DF suffered as a consequence of anoxia appears to have interrupted the normal flow of shape and contour information into her perceptual systems without affecting the processing

of shape and contour information by her visuomotor control systems. Where is the damage in DF's brain? If, as was discussed earlier, the perception of objects and events is mediated by the ventral stream of visual projections to the human equivalent of the monkey inferotemporal cortex, then DF should show evidence for damage relatively early in this pathway. Certainly, the pattern of damage revealed by the MRI/ is consistent with this interpretation; the major focus of cortical damage is in the ventrolateral region of the occipital cortex, an area that is thought to be part of the human homologue of the ventral stream. At the same time, her primary visual cortex, which provides input for both the dorsal and ventral streams, appears to be largely intact. In addition, the dorsal stream, unlike the ventral stream, also receives input from the superior colliculus via the pulvinar, a nucleus in the thalamus (see Fig. 1). Thus, input from both these routes to the dorsal stream could continue to mediate the production of well-formed visuomotor responses in DF.

One must be cautious, however, about drawing strong conclusions about anatomy and processing pathways from patients like DF. Her deficits arose, not from a discrete lesion, but from anoxia. As a consequence, the brain damage in DF, while localized to some extent, is much more diffuse than it would be in a patient with a stroke or tumour. Thus, although the striking dissociation between DF's perceptual and visuomotor abilities can be mapped onto the functional distinction between the ventral and dorsal streams proposed by Goodale and Milner [7,8], that mapping can be only tentative. Observations in patients such as RV, whose pattern of deficits is complementary to DF's and whose brain damage can be localized to the dorsal stream with confidence, have, however, strengthened the support for Goodale and Milner's proposal.

RV, who had no difficulty discriminating between the different shapes used in this experiment, could not use information about object shape to guide the placement of her fingers. Yet, as soon as her hand made contact with the object, she corrected the position of her fingers

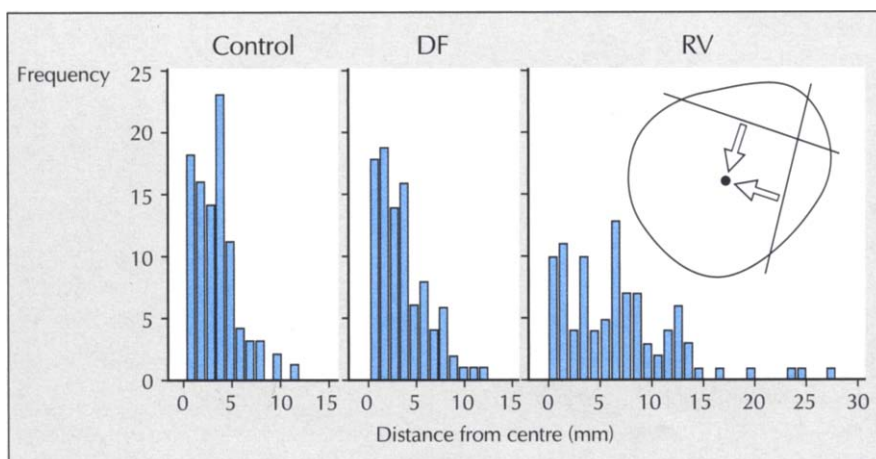


Fig. 6. The frequency distributions of the distances between the grasp lines and the centre of mass of the shape for DF, RV and the control subject for all twelve shapes. The inset shows how those distances were calculated for two different grasp lines.

before picking up the object. This suggests that, despite RV's problems in visuomotor control, she was able to use tactile and haptic information to control the placement of her fingers. As the MRI shows, the damage in RV's brain is largely confined to the occipitoparietal region (see Fig. 2), an area which is thought to be homologous to the dorsal stream in monkeys. RV's inability to use shape information to guide her precision grip is probably due to damage to these dorsal stream pathways; her ability to discriminate between different shapes (and to recognize line drawings) can be attributed to the fact that the ventral stream was spared.

The dissociation between visual perception and the visual control of skilled actions that was observed in these neurological patients (and the mapping of this distinction onto the ventral and dorsal streams) is supported by work in the macaque monkey. Thus, monkeys that show profound deficits in object recognition following inferotemporal lesions are nevertheless as capable as normal animals at picking up small food objects [13], at catching flying insects [14] and at orienting their fingers in a precision grip to grasp morsels of food embedded in small oriented slots (S. Buchbinder, B. Dixon, Y-W. Hyang, J.G. May, M. Glickstein, *Soc Neurosci Abstr* 1980, 6:675). In short, these animals behave in much the same way as DF: they are unable to discriminate between objects on the basis of visual features that they can clearly use to direct their grasping movements. Moreover, there is a long history of electrophysiological studies showing that cells in the inferotemporal cortex are tuned to specific objects or object features, and that the activity of these cells is not affected by the motor behaviour of the animal (for reviews, see [7,8,15]).

Conversely, ever since the pioneering work of Hyvärinen and Poranen [16] and Mountcastle and colleagues [17], we have known that visually sensitive cells in the posterior parietal cortex, which is the major recipient zone for dorsal stream projections in the monkey, are modulated by the concurrent motor behaviour of the animal. Thus, the activity of some visually driven cells in this region has been shown to be linked to saccadic eye movements; the activity of others to whether or not the animal is fixating a stimulus; and the activity of other cells to whether or not the animal is engaged in visual pursuit or is making goal-directed reaching movements. Of most interest, however, in the present context, is that some cells in the posterior parietal area that fire when monkeys reach out to pick up objects are selective not for the spatially directed movement of the arm, but for the movements of the wrist, hand, and fingers that are made prior to and during the act of grasping the target [16,17]. Furthermore, it has been shown recently that many of these cells are visually selective and are tuned for objects of a particular shape and/or orientation [18,19]. These manipulation neurons in the posterior parietal area thus appear to be tied to the properties of the goal object as well as to the distal movements that are required for grasping that object.

Conclusions

The pattern of visual deficits and spared visual abilities in RV and DF lends further support to the functional distinction that Goodale and Milner [7,8] have made between the two streams of visual processing in the primate cerebral cortex. According to their hypothesis, the ventral stream mediates the visual perception of objects whereas the dorsal stream plays the major role in the visual control of motor acts, such as manual prehension, directed at those objects. Both streams, it would appear, have access to visual information about the shape of objects but each stream uses this information for different purposes.

Materials and methods

Discrimination tests

For the same/different discrimination tasks, two complete sets of the twelve shapes were used. In the first discrimination task, the relative orientation of the two shapes on a 'same' trial was identical; in the second task, the relative orientation of the two shapes varied from trial to trial, with the principal axis of one shape being rotated 90°, 180° or 270° with respect to the other. For both tasks, the subject was seated at a table covered with a black cloth, and the pairs of shapes were placed in front of her, two at a time and 11 cm apart, 30 cm from the edge of the table. The order of testing was quasi-randomized: the number of same and different trials was counterbalanced but all other factors (shape, orientation, left-right position) were completely randomized. For each task, there were three practice trials and 56 test trials.

Grasping tasks

For the grasping task, subjects wore rubber thimbles, one on the thumb and one on the index finger, that were inked with different colours. Each shape was placed, one at a time, at one of the four orientations used for the same/different discrimination (0°, 90°, 180°, and 270°) 30 cm from the edge of the table in front of the subject, or 20 cm to the left or right of this midline position. Each shape was presented four times at these different orientations and positions according to a quasi-random schedule for a total of 96 trials. Between trials, subjects were asked to close their eyes and then, with the instruction 'open your eyes', to reach out naturally and pick up the shape in front of them with a 'precision grip'. The centres of the two marks on the object boundary where the thumb and index finger first contacted the shape were then recorded on prepared templates. The ink marks were then removed from the shapes with alcohol.

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