

Neurobiology

# Look but don't touch, or vice versa

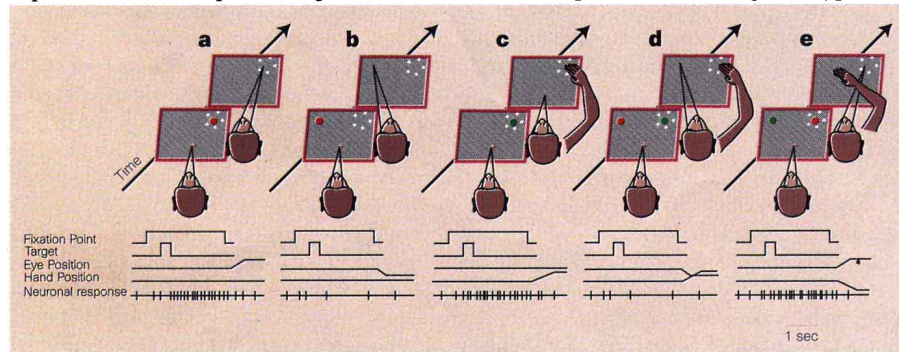
Michael Shadlen

Nowhere in the brain is the connection between body and mind so conspicuous as in the parietal lobes: damage to the parietal cortex disrupts awareness of one's body and the space that it inhabits<sup>1,2</sup>. Experiments in monkeys indicate that the neural circuits responsible for spatial perception comprise a pathway — the 'where' pathway — which leads to the posterior parietal cortex (PPC)<sup>3</sup>. However, the PPC also makes connections with the motor structures that are involved in planning and executing movements of the hands and eyes<sup>4-8</sup>. So do neurons in the parietal lobe mainly act to represent the spatial whereabouts of objects, or do they guide parts of the body to the location that these objects occupy? The former view has led to the idea that the PPC mediates attention to locations in personal and extrapersonal space. But on

page 167 of this issue, Snyder, Batista and Andersen<sup>9</sup> suggest that neurons in the PPC are instead concerned with specific motor functions. Rather than directing attention to objects and locations, Snyder *et al.* propose that the PPC signals an *intention* to do something.

In monkeys, neurons around the intraparietal sulcus respond to visual targets in an intriguing manner. They are activated by objects that appear within a restricted region of the visual field, but they do not seem to be too fussy about the nature of the object — any colour or pattern will do, as long as it falls in the right location. Moreover, the neural response can persist for several seconds after the target has disappeared, but only if the location of the target retains its significance for behaviour.

The response shown in Fig. 1a is typical of



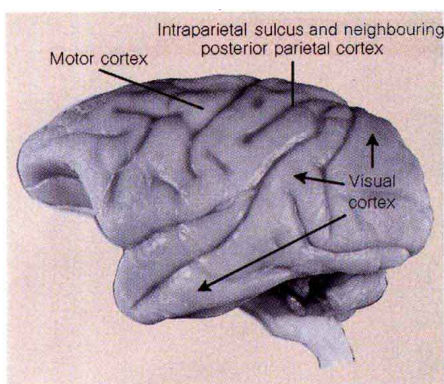
**Figure 1** Simulated response of a neuron in the posterior parietal cortex (PPC) of a monkey to oculomotor and reaching tasks, as studied by Snyder *et al.*<sup>9</sup>. The response pattern would be typical of neurons located laterally in the PPC. Upper cartoons are snapshots of the task as viewed by the monkey; lower traces show the time course of the fixation point, eccentric target(s), idealized eye and hand positions, and response of the neuron. The dotted circular region represents the visual receptive field (or movement field) of the neuron — the circle is not visible to the monkey. a, The neuron responds when the monkey plans an eye movement to the location cued by the target: the 'go' signal is the extinction of the fixation point. b, There is no response when the target and eye movement are outside the appropriate location. c, Many parietal neurons also respond when the monkey plans a reaching movement to the cued location but, according to Snyder *et al.*, this is because the monkey covertly plans an eye movement. d, e, The monkey reaches for the location cued by the green target, and simultaneously shifts its gaze to the location cued by the red target. The neuron responds only when the monkey plans an eye movement to the upper right. In medial regions of the PPC, the opposite pattern of results is obtained.

this. If a target appears briefly in a region of the visual field outlined by the dashed circle, the neuron responds with a volley of activity that persists until the monkey shifts its gaze to the cued location. The same neuron does not respond when the target appears in a different location, or if the monkey is instructed to shift its gaze elsewhere (Fig. 1b). The response is therefore said to be spatially selective, and linked in some way to the behavioural contingencies of the task. Beyond this it is difficult to interpret the response; for example, whether the neuron codes for a location in space, or a plan to move the eyes there.

About fifteen years ago, Goldberg and colleagues<sup>10</sup> examined this question by training monkeys to reach for a target in some trials and to shift their gaze to the target in others. They found many neurons that discharged when a monkey reached for a target, as shown in Fig. 1c. Interestingly, many neurons responded similarly to the cued location, whether the monkey made an eye movement or a hand movement there, supporting the hypothesis that the PPC encodes the location of objects or the focus of visual attention.

Snyder *et al.*<sup>9</sup> added a new twist to this gaze-versus-reach task, with surprising results. They trained monkeys either to reach for, or to shift their gaze towards, a cued location, but they ensured that only one or the other action was done. In some trials, the monkey touched a button while holding its gaze fixed; in others, the monkey looked towards the target while holding its hand still. Under these conditions, most neurons in the lateral region of the PPC discharged before eye movements, but not before reaches. In a more medial region, the authors found neurons that responded when the monkey reached, but not when it made eye movements. They also found many neurons that responded to the cued location regardless of which action was solicited. They then taught the monkey a 'dissociation' task — to move its eyes to one location while reaching for another (Fig. 1d and e). Not surprisingly, those neurons that responded only before eye movements did so on this task as well, responding when the monkey planned an eye movement to the appropriate part of the visual field. Reach-selective neurons also responded predictably on this task.

So, what about the neurons that responded on either action? Most of these neurons were either of the 'gaze' or the 'reach' variety. Those in the more medial regions — in the vicinity of reach neurons — no longer fired when the monkey made an eye movement to the cued location, because a hand movement was planned elsewhere: these neurons only responded when the monkey planned to reach to the appropriate location. Neu-



**Figure 2** The brain of a rhesus monkey viewed from its left surface. The neurons studied by Snyder *et al.*<sup>9</sup> are in the posterior parietal cortex, and this area is thought to be essential for coordinating spatial vision, attention and visually guided behaviour such as reaching.

rons in the more lateral region, where eye-movement-related neurons predominate, fired only when the monkey planned eye movements. This response pattern is shown in Fig. 1d and e.

Snyder *et al.*<sup>9</sup> conclude that neurons in the PPC reflect the monkey's intention to do something in particular: they do not represent the location of objects in a manner that is detached from what the animal intends to do about it. Although this conclusion is tantalizing, it must be viewed with some caution. For instance, specificity for motor intention may be less evident in the early phase of the response, just after the monkey sees the visual target (see Fig. 1, page 167). Moreover, when the monkey was not required to dissociate reach and gaze, one-third of the neurons responded to the visual target, irrespective of whether the monkey planned to reach for or look towards its location. Snyder *et al.* interpret this lack of selectivity as a covert plan to perform either action — a strategy that is only precluded through the dissociation task. The idea is that the brain naturally queues up several motor plans, only a subset of which come to be executed. But is this really distinct from the concept of attention? After all, what is meant by attention to a location if not the possibility of directing one's gaze or hand there<sup>11</sup>?

The study raises several other questions. Could the preponderance of neurons with specific allegiances to motor systems have emerged because of training on the dissociation task? Suppose the monkey had been trained to coordinate hand and eye movements to the same location: would the PPC contain more neurons that respond to both modes of behaviour? Perhaps a new class of neurons would emerge which respond selectively only when gaze and reach are coordinated; such neurons are present in the supplementary eye fields of the frontal lobe<sup>12</sup>.

More fundamental questions concern the mechanism that underlies the parietal response; for example, how visual activation gives rise to a sustained response reflecting intention. Such conversion of visual sensation to a behavioural plan seems to be at the heart of cognition<sup>13</sup>. Where in the brain do spatial targets and instructions interact to produce a plan to look, reach, or look and reach? How do these intention-related signals ultimately affect the motor structures that execute the plan? And what happens to these neural signals when a covert plan is aborted?

It is intriguing that the 'where' pathway for vision should culminate in neural structures that are linked to specific body movements. This observation indicates that the brain organizes its information in a framework that is defined by its repertoire of motor functions (Fig. 2). So, for the brain, spatial location is not a mathematical abstraction or a property of a map, but it involves the issue of how the body navigates its hand or gaze<sup>14,15</sup>. If the parietal lobe is indeed responsible for our appreciation of space — be it the position of objects or the arrangement of their parts —

then it is fascinating that this organization should reflect motor intention. □

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