

Eye–hand coordination: **Eye to hand or hand to eye?**

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Single-unit recording has revealed both hand and eye movement-related activity in the parietal cortex of the macaque monkey. These experiments, as well as neuropsychological studies, are unravelling the complex nature of how the eye and the hand work together in the control of visually guided movements.

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A defining characteristic of primate species is their ability to make rapid and accurate movements using their extremely dextrous hands. Of course, many of these dexterous movements depend on visual information about target attributes, such as position, size and orientation, as well as somatosensory information about where the arms, eyes and head are at any given time. Much of the oculomotor machinery in the primate nervous system is designed to move the eyes so that targets fall on — and stay on — the fovea. Foveation is usually thought of as crucial for identifying targets at high resolution. But recent neurophysiological results suggest that eye movements may also play a more direct role in the control of hand actions *after* targets have been identified.

Studies of the parietal cortex in non-human primates have identified subdivisions related to movements of the eyes and hands. More recently, researchers are turning to how these systems are coordinated with one another. Richard Andersen and his colleagues [1] have played a major role in describing systems in the parietal lobe which are active when monkeys make eye and hand movements. These researchers have compared and contrasted single unit activity in areas apparently specialised for the control of saccadic eye movements, such as the lateral intraparietal area (LIP), or for the control of arm movements, such as the parietal reach region (PRR) (see also [2,3]). These and other visual and visuomotor regions of the macaque cerebral cortex are depicted in Figure 1.

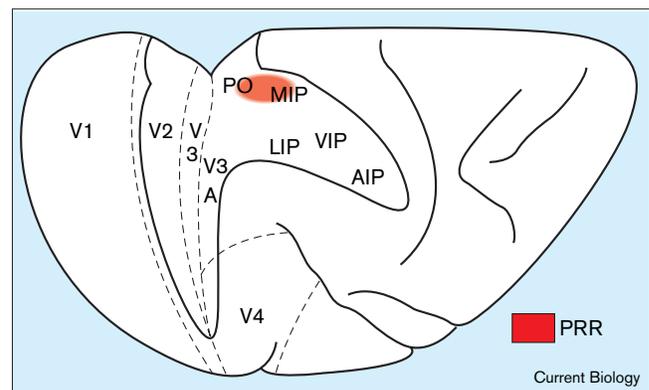
Although early studies emphasised relatively independent coding of eye and hand movement properties in these two regions — and in single cells within the PRR and LIP — more recent accounts have uncovered the importance of eye movement-related and eye position-related activity, even in so-called ‘reaching’ cells of the PRR. For example,

Batista and colleagues [4] have found that the responses of such reaching cells, despite their name, were modulated by the initial position of eyes prior to the arm movement. Changes in the initial position of the arm had no effect on the subsequent arm movement-related activity.

The same group has more recently discovered [5] that initial eye position is not the only eye-related property that influences the activity of cells supposedly restricted to coding arm movements. Snyder *et al.* [5] report that, despite a clear relationship between arm movements and firing patterns of PRR cells, 29% of 206 cells tested were influenced by saccadic eye movements in a task where no arm movement was required. The neurons were tuned for the same preferred directions for both delayed saccades made without reaches, and delayed reaches made without saccades. A fascinating property of these cells is that the activity was not related to preparing a saccade *per se*. In their delayed saccade task, monkeys were required to make saccadic eye movements to targets after a delay period; therefore activity related to preparing the saccade should have been elicited during the delay. Contrary to this possibility, Snyder *et al.* [5] found that most arm movement neurons in the PRR increased firing during or immediately after the saccade, and not during the delay period.

Snyder *et al.* [5] offer several different interpretations of their data. First, they acknowledge (and favour) the idea

Figure 1



Regions of the macaque parietal cortex implicated in eye and hand movement control. The lunate and intraparietal sulci have been opened to expose areas located in their depths. AIP, anterior intraparietal area; MIP, medial intraparietal area; PO, parieto-occipital area; LIP, lateral intraparietal area. The putative location of the parietal reach region is indicated by red shading. (Modified from [14] based on descriptions from [4].)

that the potential targets of reaching movements are represented in oculomotor, rather than arm-centred, coordinates. As they say, an oculomotor scheme used for several classes of target representation “may be a fairly general way of representing space and integrating different modalities within a particular spatial representation” [1]. A second, somewhat distinct explanation for the saccadic activity of PRR reach neurons is that, whenever a saccade is executed to a visual target, a “plan is formed in PRR that would carry the arm to the same target” [5]. Of course, in fairly contrived laboratory conditions macaque monkeys can be trained to dissociate eye and limb movements (as can University undergraduates), but in natural environments the two systems are often ‘aimed’ at the same target. The question is, which system drives the other? Perhaps Snyder *et al.*’s [5] suggestion should be modified to “whenever a potential target for an arm movement appears, move the eyes to it first”.

Experiments performed almost 20 years ago by John Fisk and Mel Goodale [6] provided an early yet elegant example of the ‘yoking’ of eye and hand movements. In this work, eye and arm movement latencies for reaches to targets on the same side of fixation as the reaching limb (‘ipsilateral’) were contrasted with reaches to targets across the body midline (‘contralateral’). Fisk and Goodale [6] found that contralateral arm movements were about 40–50 milliseconds slower to get started than ipsilateral arm movements. The eye movement latencies were, of course, much shorter than the arm movement latencies, probably because lower inertial forces act on the low-mass eyeballs. Eye movements are not ‘ipsilateral’ or ‘contralateral’ either — the required eye movement to a right-sided target is the same whether or not the right or the left hand is subsequently reaching. The crucial finding was that eye movements associated with contralateral arm movements were initiated about 40–50 milliseconds slower than those associated with ipsilateral arm movements, suggesting to Fisk and Goodale [6] that a common control mechanism links the two effectors. This study suggests that eye movements are ‘yoked’ to movements of the hand, even though the eyes begin and complete their movements more rapidly than the hand.

Recent experiments by Neggers and Bekkering [7] have elegantly demonstrated eye–hand ‘symbiosis’ in a completely novel way. Participants in their experiments were required to make rapid aiming movements to suddenly appearing visual targets. The authors took advantage of the fact that saccadic eye movements to visual stimuli are usually completed while the moving hand is still approaching the target. In a control condition, the ‘static trigger’ trials, when the hand had landed on the visual target, a second target was illuminated. The participants were required to look at the second target while keeping their hand on the first. In the experimental condition, the

‘dynamic trigger’ trials, the second target was illuminated before the hand landed on the target but after the saccade to the first target was completed (Figure 2). Both of these conditions were compared to eye movement-only trials, matched for first and second target onset times from the two pointing conditions just described.

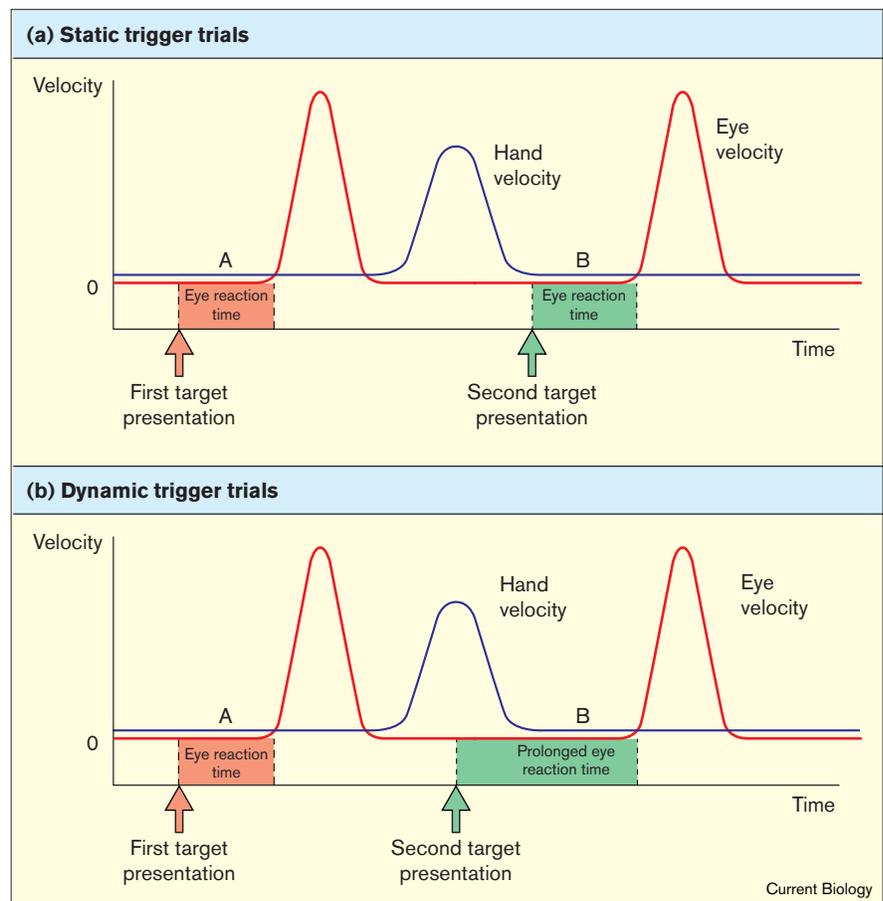
The results obtained by Neggers and Bekkering [7] provide hard evidence that participants could not initiate saccades to the second target until the hand had reached the first target, even though they attempted to do so. The saccade to the second target was severely delayed — relative to the onset of the second target — in the dynamic condition. Participants never initiated the second saccade until the arm movement was completed. Furthermore, there was no evidence that the second saccade could be planned during the terminal phase of the hand movement; no savings in reaction time for the second saccade were found once the hand had landed at the first target (Figure 2). A strong statistical relationship between the second saccade reaction time and the length of the deceleration phase of the pointing movement was found, also suggesting the normal saccade initiation process could not begin until the hand movement was completed.

Much like the earlier Fisk and Goodale [6] study described earlier, the Neggers and Bekkering [7] experiments suggest that eye movements are yoked to hand movements. Recently, patients have been described with neurological defects suggesting a pathological yoking of hand to eye, rather than eye to hand (think of the second explanation of Snyder *et al.*’s [4] results, referred to above). Our patient, Ms D., suffered from bilateral parietal lobe atrophy, related to corticobasal degeneration. She was unable to reach to targets that she was not allowed to look directly at (foveate). What was remarkable about Ms D. was the pattern of her reach errors: she inevitably reached to the place that she was fixating, acknowledged and apologised for her error, and proceeded to make the same error again and again. This ‘magnetic misreaching’ was a manifestation of the only route left available to her to generate accurate pointing movements to targets — a slavish dependence on eye position signals for guidance of the hand [8]. A patient with a similar sign has been described by Buxbaum and colleagues [9,10].

Buxbaum and her colleagues [9,10] favour an account of their patient, and other patients with misreaching disorders, in terms of difficulties with ‘coordinate transformations’ — the computational demands of taking ambiguous retinal signals and combining them with eye, head and arm position information in order to specify target position with respect to the hand, arm or shoulder. In fact, the interpretations of neurophysiological studies of the parietal lobe reflect a similar bias towards hierarchical models of transformations on the input side — that is,

Figure 2

Crucial conditions in the Neggers and Bekkering experiments [6] and schematic results from a single trial. Time is plotted along the X axis and velocity along the Y axis (not to scale). In the static trigger trials (a), the second target (for a saccade only) is presented after the hand has arrived at the first target. In the dynamic trigger trials (b), the second saccadic target appears when the hand is at peak velocity, some 300 milliseconds or so before the hand reached the first target. Note how the time to initiate the second saccade is similar to the time to initiate the first saccade *with respect to the end of the arm movement*, even though the first eye movement was completed when the second target was presented. A, eye movement reaction time to the first target; B, eye movement reaction time to the second target. Note how much longer B is in the dynamic trigger trial (b).



extraction of target location relative to some body reference point before any movement of any sort is made — of the complex sensorimotor loops which control visually guided reaching (see [11,12] for critiques). The Buxbaum and Coslett [9,10] model involves how target position in real space, or in space relative to an egocentric reference point, is reconstructed in the brain. Their model, like many others, says little about how the eyes, head and arm get to that point once it has been specified, or what role ‘on-line’ processes play in the interactions of eye and hand once movement has begun.

Although there is obviously *some* feedforward specification of eye and hand movements which influences properties such as their onset times — as revealed in the Fisk and Goodale [6] results, for example — much of the processing seems to happen at and after saccade initiation — as indicated by the results of Snyder *et al.* [4], Neggers and Bekkering [7] and Carey *et al.* [8] (see also Ferraina *et al.* [11]). As elegantly noted by Boussaoud and Bremmer [13], the functional utility of eye position signals in parietal and frontal cortex is probably not restricted to pre-movement encoding of target position in world space or arm

space. If eye-centred coding is used only to derive target position in egocentric coordinates, then that coding should be most prominent in early visual and visuomotor regions and less prominent in ‘downstream’ areas related to execution of arm movements — but they are not. So ‘where the action is’ in eye–hand coordination is not restricted to processes completed before we begin to move. The results of the neuropsychological studies could do much to inform future efforts in the neurophysiological laboratories designed to elucidate mechanisms necessary for coordinating eyes, heads and hands.

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