

Moving forward by looking away

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In one model of the brain, a central processing region is sandwiched between separate input and output areas. But studies of humans, and now monkeys, hint that this model may be too simplistic.

A conventional approach to studying the brain is to determine whether a particular signal or region is mainly sensory or motor in nature, reflecting what comes into the brain or what flows out, respectively. In this view, the input region (the sensory cortex) processes sensory signals to generate several neuronal representations of the information. Next, a central processor, found outside the sensory cortex, uses information about the goals of the task in hand to select the most appropriate sensory representation for directing motor output. This selection is the key step in the 'sensorimotor transformation'. But in another model, task-specific information influences the processing of incoming signals from an early stage. Pure sensory signals are rare, and the sensorimotor transformation is distributed throughout the brain. This view has begun to take hold among researchers who study the human brain¹. But convincing evidence is still needed. On page 971 of this issue, Zhang and Barash² provide just such evidence from studies of monkeys.

The task of moving one's eyes to a visual target involves a clear sensory input (from the target) and motor output (the eye movement), so it seems ideal for studying sensorimotor transformations. But experiments based on eye movements are often handicapped by a difficulty in distinguishing neuronal representations of what we see and what we plan to do. Imagine being inspired by the sight of a travel poster and deciding to visit London. Before you choose how and when to travel, your plan is best represented by the image on the poster — the poster is both the stimulus that evokes your plan, and an early representation of the plan itself.

A similar confusion occurs when studying directed eye movements. A simple way to introduce a distinction between representations of visual stimuli and plans to move the eyes to those stimuli is to study both prosaccades, which are eye movements towards a visual target, and antisaccades, eye movements away from the target³. The colour of a 'fixation spot' tells the subject whether to move their eyes towards or away from the target. This combination allows the researcher to determine whether neuronal activity is more closely related to the stimulus or the movement goal, and therefore where task-specific processing begins.

The lateral intraparietal area (LIP) in the posterior parietal cortex of monkey brains is likely to participate in, or even initiate,

sensorimotor transformations during saccades⁴. Neurons in this region link sensory and motor areas. Individual neurons are activated when a behaviourally relevant stimulus appears within the cell's receptive field. LIP neurons also fire shortly before an eye movement to a remembered or visible target in the receptive field.

Last year, Gottlieb and Goldberg⁵ recorded the activity of single neurons in the LIP while monkeys performed prosaccades and antisaccades. They found that most of the sampled neurons represented the location of the visual target. Few represented the direction of the eye movement; when they did, they fired quite late, around the time of the movement.

Zhang and Barash² have now repeated Gottlieb and Goldberg's experiment with a slight change, and obtained very different results. Rather than having the monkeys move their eyes as soon as they saw a target, Zhang and Barash trained the animals to delay their movements. In this way, signals time-locked to the sensory stimulus could be more easily distinguished from signals related to the motor response. Neuronal activity began hundreds of milliseconds before the signal to make the saccade and well after the sensory stimulus, reflecting the direction of the movement, not the location of the target. So, the sensorimotor transformation occurs in the LIP long after the stimulus appears but well before the eye movement begins.

Zhang and Barash also report evidence of an earlier sensorimotor transformation in the LIP. During both prosaccade and antisaccade trials, many LIP neurons become active shortly after a stimulus falls inside their receptive field. The authors show that a subset of these cells also becomes active soon after a stimulus appears outside their receptive field that will direct an antisaccade so that the stimulus falls into the field (Fig. 4b, page 973). Zhang and Barash refer to this as 'paradoxical activity'. These neurons show activity that is time-locked to the onset of the visual stimulus, suggesting that they are driven directly by visual inputs. But they also respond to a stimulus outside the receptive field on an antisaccade trial, consistent with an input that codes the end of the planned movement rather than the target's location. This activity probably represents the start of the sensorimotor transformation for an antisaccade.

But this transformation is incomplete on at least two counts. First, these neurons often fire when a stimulus outside their receptive

field directs an antisaccade back into that field. Yet when a stimulus appears inside the receptive field and directs a saccade to the outside, there is no complementary reduction in activity. Second, activity that encodes the upcoming direction of a saccade would be expected to persist until the movement occurs. But the paradoxical activity subsided long before the late activity began to build up. The fact that the representation of antisaccades in the LIP is incomplete is consistent with this sensorimotor transformation being spread out over several regions of the brain.

Why did Zhang and Barash², using delayed saccades, observe a partial early and a complete late sensorimotor transformation in LIP, whereas Gottlieb and Goldberg⁵ observed only sensory representations and rare motor responses during saccades? Antisaccades began in Gottlieb and Goldberg's task at a similar time to the paradoxical activity in the delayed task. Perhaps this activity was also present in Gottlieb and Goldberg's task but was obscured by the motor response, which occurred at about the same time. By delaying the saccade, Zhang and Barash's set-up may have allowed further time for both early (paradoxical) and late transformation signals to build up in LIP, increasing the chances that they would be observed. Or perhaps the insertion of a delay fundamentally changed the way in which the

animals solved the task. It would be worthwhile repeating the two experiments in the same animal and the same cells.

Nonetheless, Zhang and Barash's data² clearly show that, in a practised, delayed antisaccade task, the sensorimotor transformation is seen — and perhaps begins — in the LIP. The authors argue that the timing of the paradoxical activity preceding antisaccades suggests that it is produced by visual inputs (albeit non-standard inputs). They compare this to a report of a rerouting of visual inputs into the LIP⁶. Yet what Zhang and Barash describe is no mere rerouting of the sensory information. To decide whether to perform a prosaccade or an antisaccade, the animals must modify their behaviour on a trial-by-trial basis, requiring both sensory and non-sensory information. Fortunately, these are experimentally tractable issues and the stage is now set to address them. ■

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