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Through the Looking Glass. Focus on "Representation of an Abstract Perceptual Decision in Macaque Superior Colliculus"

Joshua I. Gold
University of Pennsylvania Department of Neuroscience, Philadelphia, Pennsylvania 19104

Oculomotor circuits have recently been used as a sort of looking glass, providing reflections of higher brain functions like reward expectation, target selection, and decision making (Glimcher 2003). One well-studied example is a decision about the direction of visual motion in a random-dot stimulus (Britten 2003). Monkeys are trained to make this difficult decision and indicate their answer with a saccadic eye movement in the direction of motion (Fig. 1*A*). In these monkeys, neural activity that prepares the saccadic response reflects the computations responsible for forming the decision (Horwitz and Newsome 1999; Kim and Shadlen 1999; Roitman and Shadlen 2002). In a new study, Horwitz and colleagues (this issue, p. 2281–2296), like Alice, step through the looking glass (Horwitz et al. 2004). Using a task in which the direction of the saccadic response is not a direct reflection of the decision (Fig. 1*B*), they find some oculomotor signals that nonetheless appear to encode the direction of the decision.

The looking glass is created by the task design. In the previous version of the task, the direction of the decision mirrors the direction of the response (e.g., if motion is upward, make an upward saccade). To solve this task, the brain appears to conflate the two, forming the decision and response together in a sort of neural portmanteau (Carroll 1991). That is, the computations that form the decision are reflected in the activity of neurons that form the saccadic response (Horwitz and Newsome 1999; Kim and Shadlen 1999; Roitman and Shadlen 2002). This appears to be a general phenomenon: intention-related neurons reflect sensory (and other) signals that play a role in movement selection.

These reflections have been enlightening. For example, they helped us to understand how the underlying neural computations give rise to performance (Gold and Shadlen 2003). They also show how specious the distinction between "sensory" and "motor" can be in some parts of the brain. However, studying reflections cannot answer some important questions like the source of the computations. If the oculomotor circuits merely reflect computations that occur elsewhere, then where do they occur? If the oculomotor circuits form the decisions themselves, then how and where are decisions formed that are not linked to specific eye movements?

The task used by Horwitz and colleagues provides a first step toward answering these questions. Their experiments are part of a welcome trend in which complex mechanisms that link sensory input to motor output are distinguished based on operational definitions from a behavioral task (e.g., Calton et al. 2002; Sato and Schall 2003). In their task, Horwitz and colleagues broke the association between the direction of the decision and the direction of the saccadic response. They could therefore identify mechanisms of decision formation that were independent of the response.

They found that, as expected, neurons that encode specific eye movements do not tend to encode the decision. Recording from the superior colliculus, they estimated that ~90% of the neurons do not respond selectively during motion viewing and the subsequent delay period, before the targets appear. Thus unlinking the decision from a specific saccadic response alters the flow of decision-related information in the brain, apparently excluding it in large part from oculomotor circuits.

They also found a small subset of collicular neurons with activity that predicted the monkey's decision even before the targets appeared. This was surprising. Consider, for example, a neuron that responded selectively on trials that the monkey decided motion was rightward. For the previous version of the task, this decision was indicated with a rightward saccade. Thus this neuron's selectivity for the direction of motion would be equivalent to its selectivity for the direction of the impending saccade; its responses could be thought of in terms of encoding an eye movement. For the new version of the task, a rightward decision was indicated with one of many possible saccades. Thus this neuron's selectivity for the direction of motion was independent of the saccadic response.

The results suggest that this "abstract" decision is encoded, at least in part, with respect to space, in the same reference frame in which saccades are encoded. Two qualifications should be noted. The first is that the spatial signals might correspond to the small spatial component of the saccadic response: a rightward decision is indicated by selecting the right-most target. Ongoing studies with a more abstract version of the task, in which the targets are distinguished by color and not their relative spatial locations (Gold and Shadlen 2003), should help to clarify this issue. The second qualification is that isolating the direction of the decision from the direction of the saccadic response might not be enough to identify the source of direction-selective neural signals. Other factors, like attention and working memory, might be encoded in a similar spatial framework. In fact, the authors present evidence that neurons in the supplementary eye field have similar direction-selective responses consistent with a role in remembering the direction of motion in object-centered coordinates (Olson and Gettner 1995). Further studies are needed to disentangle these factors from the computations responsible for forming the decision (Gold and Shadlen 2001).

Despite these qualifications, the experiments provide further evidence that oculomotor structures like the superior

Address for reprint requests and other correspondence: J. I. Gold, University of Pennsylvania, Dept. of Neuroscience, 116 Johnson Pavilion, 3610 Hamilton Walk, Philadelphia, PA 19104-6074 (E-mail: jigold@mail.med.upenn.edu).

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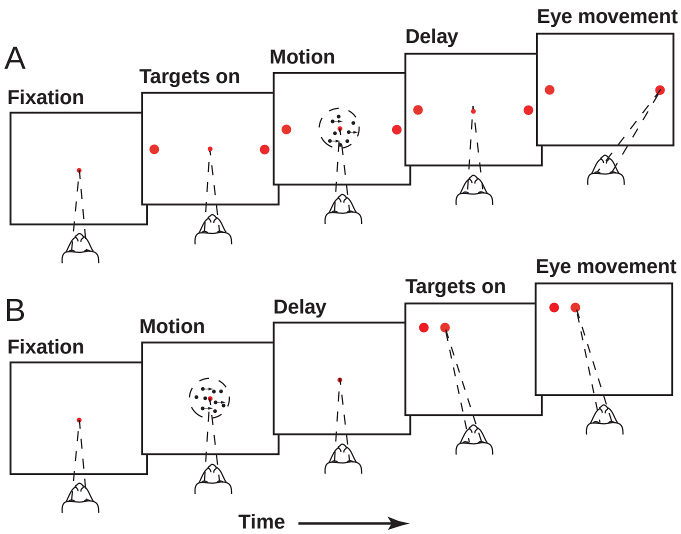

FIG. 1. *A*: task, used in previous studies, in which the direction decision is indicated with a saccadic eye movement to the target in the same direction. *B*: task, used by Horwitz and colleagues, in which the decision is indicated with a saccade to 1 of 2 targets that could appear at several locations.

colliculus play a general role in some aspects of spatial cognition. This role typically reflects the selection and preparation of eye movements. However, by stepping through the looking glass, we can begin to see the extent to which these computations have been usurped for higher functions like decision making, attention, memory, and whiffling through the tulgey wook.

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