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Weighing the evidence: how the brain makes a decision

Jeffrey D. Schall

Kim and Shadlen investigate how neurons of the prefrontal cortex interpret slowly accumulating signals from visual cortex to make a perceptual decision.

"...in the night, imagining some fear
How easy is a bush suppos'd a Bear?"
  – Shakespeare, A Midsummer Night's Dream, Act 5

As Shakespeare observed, even perception may require an active decision about how to interpret the raw data. On page 176 of this issue, Kim and Shadlen examine the neural basis of a simple visual perceptual decision. Their study, along with other recent work (see refs. 1–3 for reviews), illustrates how the subjective process of deciding may be soon be explained in terms of objectively observable brain processes.

Perceptual decisions involve several steps. First, a preliminary representation of the sensory stimulus is converted into higher-level explicit representations of the features that will form the basis for the decision. Second, one of the competing sensory representations must be selected; in other words, the ambiguous representation of the relevant features must be translated into an explicit representation of one of the possible alternatives. Finally, the sensory decision must lead to an appropriate behavioral response. A neural explanation of decision making must describe the neural basis of each of these steps.

Important insights into the first step have come from the work pioneered by William Newsome and colleagues[4], who have examined the sensory representations on which a perceptual decision is based. Meanwhile, other researchers have shown how behavioral responses are generated in the face of alternatives (reviewed in ref. 3).

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Kim and Shadlen have now begun to investigate the intermediate stage, in which the sensory evidence is evaluated to arrive at a decision.

The authors took advantage of a method developed in Newsome's laboratory, in which monkeys are trained to report the net direction of visual motion in an array of moving dots. They report their perception by making an eye movement to one of two targets that appear on either side of the display after the dots disappear. When all the dots move in the same direction, the task is easy, and monkeys can respond correctly on every trial. If some of the dots move in random directions, the motion signal is diluted, and as the fraction of randomly moving dots is increased, the task becomes harder and the proportion of correct responses decreases. Eventually, when all the dots are moving at random, there is no net motion signal, and so the monkey's response reflects preference in the absence of evidence.

This simple design allows precise measurements of both the stimulus and the response. The advantage of using motion as a cue is that the site of motion representation is well characterized; motion cues are represented in the extrastriate visual area MT, whose neurons respond preferentially to moving stimuli. Newsome and colleagues have shown that monkeys' performance in this task can be accounted for based on the activity of a small number (around 100) of MT neurons[5,6]. They have also shown that artificial stimulation of MT during the stimulus presentation influences the monkey's judgement in a predictable way, thereby demonstrating directly that neurons in MT provide the sensory representation on which the perceptual decision is based.

How then is this sensory representation converted into a behavioral outcome? In other words, how and where are the signals from MT read? The final behavioral response to the stimulus is an eye movement to one of two targets, so an obvious place to look is the frontal eye field and adjacent prefrontal cortex, which is known to be involved in producing eye movements, and also receives inputs from area MT. Moreover, prefrontal cortex is a region in which visual representations are combined with knowledge, goals and desires to generate action[7].
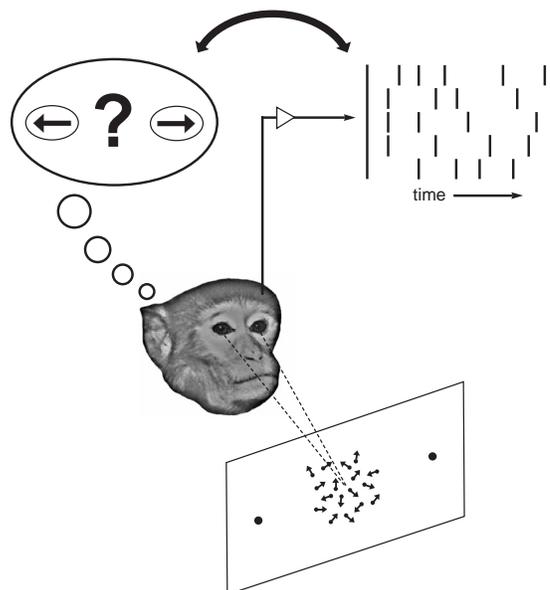
Fig. 1. To earn a reward, monkeys had to decide the net direction of motion of a stimulus composed of variable fractions of coherently and randomly moving dots. Monkeys reported their decision by making an eye movement to either of two targets. Psychologists seek to understand choice behavior in terms of computational or cognitive processes, symbolized by the bubble. Neurophysiologists seek to understand choice behavior in terms of neural activity monitored in particular parts of the brain, symbolized by the raster display. Ultimately, we would like to understand the relationship between the neural activity and the behavior and associated cognitive processes, symbolized by the arrow.

Kim and Shadlen therefore examined activity in this area, using a modified version of Newsome's original experimental design. In the original experiments, the monkey was required to report the direction of movement immediately after viewing the dots, but Kim and Shadlen introduced a delay between the presentation of the moving dots and the cue to make an eye movement. After the moving dots disappear, neurons in area MT cease to respond, indicating that the decision must be stored in some other area. Many studies have shown that neurons in the prefrontal cortex continue to fire during the delay period while the monkey remembers and plans what he is supposed to do[7]. By studying activity in the prefrontal cortex during the delay period, the authors could distinguish the representation of the decision having been made from the representation of the stimulus on which it was based.

In the original studies of area MT, the randomly moving dots were placed in the neurons' receptive field (so the neural response was to the dots themselves). For the present study of prefrontal neurons, the targets for the eye movements were instead placed in the neuron's receptive field. Thus, when a prefrontal cortex neuron fires in response to the moving dots, it does so not because the dots themselves are within the receptive field (they are not), but because the monkey has been conditioned to interpret a particular pattern of moving dots as an instruction to make an eye movement to the receptive field of that neuron.

Kim and Shadlen show that during the period when the moving dots are visible, neural activity grows in prefrontal cortex to signal one or the other choice. Importantly, the rate of growth and magnitude of activity during the viewing period was proportional to the quality of the evidence, that is, to the strength of the motion signal. The authors therefore propose that the gradual increase in prefrontal activity reflects the accumulation of sensory evidence. Although this interpretation is plausible, we should not overlook alternative explanations; for instance, the activity may reflect the preparation of the eye movement response, or the monkey's growing expectation that it will earn a reward. Distinguishing these alternatives will require not only further empirical work but also operational clarification of the concepts of preparation, expectation and so on. What is clear from the data, however, is that prefrontal neurons reach a state that predicts the monkey's choice while the moving dots are visible and maintain that state throughout the delay period when no dots are present until the monkey is given the opportunity to report its choice.

In some trials, there was no net motion, so the monkeys had to make choices in the absence of any compelling evidence for either alternative. In other trials, monkeys made errors, that is, a choice that contradicted the evidence. In both cases, prefrontal neural activity during the delay period corresponded to the choice and not to the evidence. This indicates that the prefrontal cortex neurons are signaling something more than just the sensory evidence during the delay period. Based on their location and properties, it is likely that most of the neurons Kim and Shadlen recorded are not directly involved in producing the eye movement. Thus, Kim and Shadlen reason, the neurons are encoding the decision in an abstract sense. Similar observations have been made in posterior parietal cortex[8] and the superior colliculus (G.D. Horwitz & W.T. Newsome, *Soc. Neurosci. Abstr.* 24, 1498, 1998).

Although prefrontal cortex has been studied before in conditions requiring an arbitrary response based on a visual discrimination[7], one major advance in Kim and Shadlen's study is the use of a stimulus with discriminability that could be manipulated in a psychophysical protocol. Another important aspect was the use of the random dot motion stimuli, for which the sensory representation was very well characterized. This provided for what may be the most important and innovative aspect of the study, a quantitative model of the decision process.

Presumably the prefrontal activity that the authors observe must be driven by responses in MT during the motion viewing period. The authors did not record from MT in these experiments, but based on earlier modeling of MT responses[6], they use signal-detection theory to suggest a model for how the prefrontal cortex reads the evidence from MT. In simple terms, their model supposes that a neuron in prefrontal cortex monitors the activity of two populations of MT neurons, each signaling motion in opposite directions, say left and right. However, the motion signals in MT are randomly variable across trials. To decide which direction the dots are moving, they propose that the input to the prefrontal cortex neuron represents a random sample of the activity of each population. Suppose the net motion is leftward. If the MT activity signaling 'left' exceeds the activity signaling 'right', then the monkey chooses 'left'. However, if by chance the activity signaling 'left' happens to be less than the activity signaling 'right', then the monkey will make an error. When a coherent motion stimulus evokes a strong leftward signal, then the total activity from a random sample of left-signaling neurons is greater than that of a sample of right-signaling neurons, so the monkey makes few errors. As the stimulus becomes less coherent, it evokes a weaker leftward motion signal. As a result, there is an increased probability that the activity signaling 'left' will be less than the activity signaling 'right', and so the monkey makes more errors. When Kim and Shadlen incorporate values for the magnitude and variability of the signals previously observed in MT, they can account for the performance of the monkeys and the responses of the prefrontal neurons.

Through research like that of Kim and Shadlen, neuroscience engages significant philosophical and ethical issues[9]. For example, if the neural events leading to a choice become publicly observable, then it should be possible to predict the choices made by an agent if the correct brain processes are monitored. This is not philosophical fiction. I have had the profound experience of being able to predict with high reliability the choice a monkey would make during a study of binocular rivalry[10], and Shadlen reports the same experience during this study (personal communication). It seems reasonable to assume that the same types of mechanisms may underlie other types of decisions, in our own brains as well as those of monkeys. Ultimately, philosophical arguments have been developed that reconcile a mechanistic explanation of decision making, one of the most sacrosanct of mental acts, with our own sense of free will, responsibility and dignity[11].

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