

Exploring the Neurophysiology of Decisions

Minireview

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A prerequisite for any animal's survival is the ability to make decisions about its sensory world. For a monkey to respond to a call signaling imminent danger, or a human to determine when to cross the street based on the flow of traffic, the brain must analyze the influx of fresh sensory information, integrate it with knowledge acquired recently or remotely, and select the appropriate behavior from perhaps many possible options. This nonreflexive linkage between sensory input and behavior involves interpretation and behavioral selection, what we refer to as a decision process. In this review, we discuss recent developments in brain electrophysiology that lend insight into the neural basis of decision formation.

A decision can only be studied in alert animals that can perform sufficiently complex tasks. In addition to this basic requirement, there are several key elements that are essential for any psychological task devised to study a decision process. First, the sensory stimulus should require an interpretation. Second, there must be some option as to whether one or another behavior ensues. Finally, the conversion from sensory processing to behavioral intention should take place over an identifiable epoch of sufficient duration to permit a physiological dissection.

Turning to physiology, what characteristics might one seek in neurons that play a role in a decision process? In principle, the brain could contain neurons whose sole purpose is to form pronouncements about interpretations, liberated in a sense from the fluctuating detail in the sensory stream or the particular behavioral option to be exercised. In fact, we know of no structure in the brain that contains an abstract representation of an interpretation or decision that is not either tied to an effector system or dependent on the continued presence of a sensory stimulus. Rather, the decision process seems to emerge at the nexus of sensory and motor processing—where sensory data give rise to a plan to enact some particular behavior. The neural elements therefore tend to one side or the other of what appears to be a sensory–motor continuum. Accordingly, a decision-related neuron should modulate its response during the acquisition of sensory information that leads to one interpretation or another. However, unlike a sensory neuron, it should continue to respond after the cue is removed—just as our decisions can persist after a sensory cue has vanished. Its response should also herald a particular action that would indicate one outcome and

not another. However, unlike a motor neuron, its response should not oblige an immediate movement—just as we can decide what to do without acting impulsively. *Decision-Related Activity on the Sensory Side* Neurons in the visual and somatosensory cortex are known to encode the sensory variables that govern performance in discrimination tasks (reviewed by Parker and Newsome, 1998). Can such neurons teach us anything about the decision process, beyond the simple fact that they encode the sensory data? It is often possible to find sensory neurons that respond differently to the variety of stimuli shown in an experiment, but one that responds differently to the same stimulus depending on the animal's interpretation might lend insight into the decision process.

For example, neurons in the motion-sensitive regions of the extrastriate visual cortex have been shown to encode the signals that permit a monkey to discriminate between two directions of random dot motion (Britten et al., 1992). In the paradigm depicted in Figure 1A, a weak motion cue instructs one of two behaviors (e.g., a saccadic eye movement to one or another target). Near psychophysical threshold, the same visual stimulus often gives rise to two different interpretations (e.g., leftward and rightward decisions). Interestingly, from trial to trial, neurons in MT, MST, and the superior temporal polysensory area (STPp) exhibit variation in the number of spikes evoked by identical visual stimuli, and this variation has been shown to correlate with the monkey's judgment of direction (Celebrini and Newsome, 1994; Britten et al., 1996; Thiele and Hoffmann, 1996).

The data in Figure 2A were obtained from an MST neuron during 60 trials in which the monkey was shown a random dot noise pattern containing no net motion. These trials represent a small fraction of the trials in which stimuli of a variety of motion strengths were shown to the monkey in random order. The responses tended to be larger, on average, when the monkey decided in favor of the neuron's preferred direction. This suggests that the monkey's decisions are influenced by the trial-to-trial variability in the responses of single cortical neurons. It is a remarkable observation that constrains theories of cortical organization. It implies that the decision mechanism reads out from pools of sensory neurons whose variable discharge covaries weakly—otherwise the variability of any one neuron would have only a random relationship with the behavior (Shadlen et al., 1996).

Binocular rivalry provides another example in which the same sensory stimulus gives rise to different interpretations. Rivalry and other bistable perceptual phenomena are not usually construed as involving a decision process, but they are relevant. As shown in Figure 1B, two visual stimuli, which are viewed separately by the left and right eyes, give rise to an alternating perception in which one or the other eye's image is seen. Scheinberg and Logothetis (1997) trained monkeys to indicate its perceptions by pressing one lever or another depending on which stimulus it sees. This is a challenging experiment because there is no way to know whether

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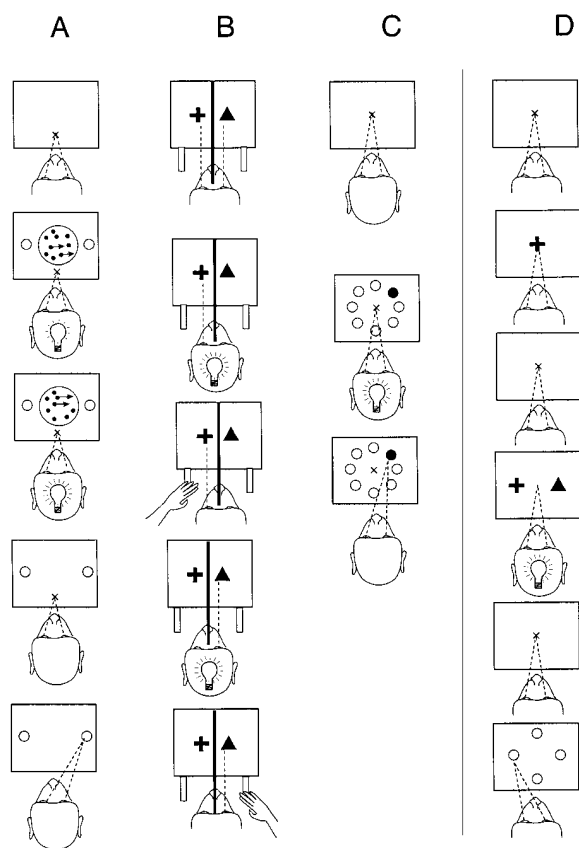


Figure 1. Four Tasks that Lend Insight into the Neural Basis of a Decision

In all tasks, the monkey interprets a visual stimulus and decides what behavior should ensue. The light bulb shown at various points in each task identifies the period in which the monkey forms its decision.

(A) Direction discrimination task. The monkey views a dynamic random dot motion display comprised of moving dots and random noise. The monkey is trained to indicate its judgment of direction by making an eye movement to one of two targets that appear to either side of the motion display. The random dot motion can be made arbitrarily difficult by varying the fraction of moving and random dots. When the task is difficult, the monkey arrives at a decision over a protracted epoch of motion viewing.

(B) Binocular rivalry task. Each eye views a separate stimulus, but only one of the two stimuli is perceptually dominant at any given time. The monkey indicates which stimulus is dominant by pressing a lever. The process leading to dominance of one stimulus over the other resembles a decision.

(C) Visual search task. The monkey is required to make an eye movement to the "oddball" target, which is easily distinguishable from the remaining "distractors."

(D) Delayed match-to-sample task. The monkey views a sample shape, and after a delay the same (match) stimulus is presented along with a second (distractor) stimulus. The monkey is required to make a saccade to the remembered location of the match stimulus.

the monkey is reporting its perception faithfully, but through a number of control experiments, Logothetis and colleagues demonstrated that the monkey's reports are likely to represent a pattern of alternating perception that resembles rivalry in humans.

The experimental protocol is similar to threshold psychophysics in the sense that one stimulus can give rise

to two different perceptions, which can be said to instruct one or another behavior. As illustrated in Figure 2B, neurons in the inferotemporal cortex (IT) alter their response in a manner consistent with a monkey's perceptual report during binocular rivalry (Scheinberg and Logothetis, 1997). These neurons respond to a preferred visual stimulus (e.g., a monkey's face) when it is shown alone in the neural receptive field, and when this preferred stimulus dominates the monkey's perception during binocular rivalry. Thus, they can be said to represent a decision about which eye's stimulus is perceptually dominant. Unfortunately, we do not know what takes place for the dominant percept to shift from the left to the right eye's view, and we do not know when this process occurs, only when it is completed.

Both motion- and form-sensitive neurons of the extrastriate visual cortex can be said to be "decision related" because they do not simply indicate what the experimenter presents on the video monitor but give some indication about the monkey's interpretation. However, certain observations limit the role of sensory neurons in the decision process. First, they do not respond when the stimulus is absent; yet, once formed, a decision can persist in the absence of continued sensory stimulation. Second, the observed covariation between the response of sensory neurons and the corresponding behavioral response seems to require an additional mechanism that reads out the weak and variable sensory responses (Shadlen et al., 1996). Thus, sensory neurons can encode the variables required to compute a decision, but they themselves neither carry out this computation nor represent its outcome.

Decision-Related Activity on the Motor Side

Many neurons in the parietal and frontal association cortex respond during the delay period between the presentation of a sensory instruction and an impending behavioral response. Such neurons are typically active from the time the sensory cue is first presented until the time a behavior is executed. This delay period activity might represent motor intention (Snyder et al., 1997), suppression of premature action (Hikosaka and Wurtz, 1989), working memory for the instruction (Funahashi et al., 1989), or attention to salient regions of the visual field (Gottlieb et al., 1998). The functional interpretation is often inferred from the neuron's connectivity or the behavioral consequences of lesions. Importantly, these neurons are commonly selective for a particular action, such as an eye movement of a particular size and direction.

Can such neurons teach us anything about the decision process, beyond the simple fact that they divulge the behavioral plan? A predominantly motor neuron is bound to respond differently to alternative behavioral options, but one that responds differently when the behavior is the same, but the sensory instruction differs, might also lend insight into the decision process (Zhang et al., 1997). Many neurons with delay-period activity appear to encode a mixture of sensory and motor properties and several laboratories have begun to investigate their role in tasks that require a decision.

Schall and colleagues (Thompson et al., 1997) recorded from neurons in the frontal eye field (FEF) while a monkey performed a visual search task (Figure 1C).

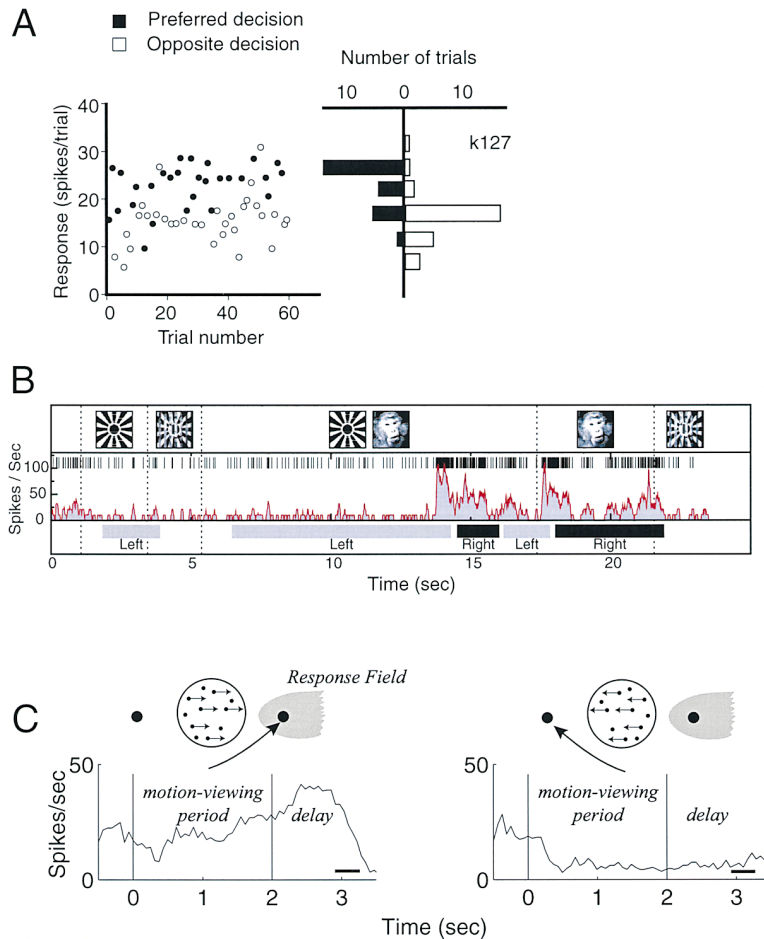


Figure 2. Three Examples of Decision-Related Neural Activity

(A) Responses of a motion-sensitive neuron during a direction discrimination task (Figure 1A) in which the monkey was required to judge whether motion was in the neuron's preferred or antipreferred direction. The plot shows responses obtained on the 0% coherent motion trials when there was no net movement of random dots. The trials are shown sequentially along the abscissa. Closed and open symbols denote trials in which the monkey decided that motion was in the neuron's preferred and antipreferred direction, respectively. The neural responses were larger, on average, when the monkey decided that motion was in the preferred direction of the neuron (From Celebrini and Newsome, 1994).

(B) Response of a neuron in the inferotemporal cortex during binocular rivalry. This neuron responded well when shown a photograph of a monkey face and poorly to a sunburst pattern. The monkey was instructed to press the left lever (indicated by shaded horizontal bar) whenever the sunburst pattern was seen and to press the right lever (solid horizontal bar) when it saw the face. The monkey was trained not to respond to blends of the stimuli, whether shown to one or both eyes. The neuron responded vigorously when the monkey indicated that the face stimulus was perceptually dominant, whether shown alone or during binocular rivalry. The times of action potentials are shown by the vertical tick marks. The instantaneous spike rate is approximated by the smoothed function, below (from Scheinberg and Logothetis, 1997).

(C) Response of a neuron in the parietal cortex (area LIP) during performance of the direction discrimination task shown in Figure 1A. The neuron's response field (RF) is shown in gray. The average spike rate from several trials is plotted as a function of time from the onset of random dot motion. The time of the monkey's saccadic eye movement is indicated by the horizontal line (mean \pm SD). The left column shows responses obtained when the monkey judged motion to be toward the response field and the monkey made an eye movement to the corresponding target. Responses on the right were obtained when the monkey decided in favor of motion away from the response field (from Shadlen and Newsome, 1996).

The monkey was trained to make an eye movement to one of eight stimuli arranged concentrically around the fixation point. Seven of the stimuli were identical in appearance; the eighth differed in color, shape, or texture and thus served as the "oddball." On "GO" trials the monkey was required to make a saccade to the location of the oddball stimulus. Approximately 80–150 ms after the stimulus array was turned on, the activity of FEF neurons began to discriminate the oddball from the "distractor" targets. Schall and colleagues propose that this response reflects the conversion of visual information into a plan to shift the gaze. They argue that the neurons are not simply encoding eye movements, because these same neurons also respond during "NOGO" trials when the monkey maintains its gaze on the fixation point (Thompson et al, 1997). These FEF responses may therefore reflect a visual selection process that underlies the monkey's decision to direct its gaze from one place to another. Unfortunately, the entire process occurs in an instant (typically, <100 ms), making it difficult to discern a finite epoch in which the sensory instruction gives rise to a planned behavior.

In an effort to expand the time of the decision process, Hasegawa et al. (1998) trained monkeys to perform a delayed match-to-sample task. In their task (Figure 1D), a delay period was imposed between the presentation of the sample stimulus and the presentation of the same (match) stimulus shown with an irrelevant distractor. Both the match and distractor stimuli were shown briefly at two locations in the periphery. Then, after another delay, the monkey indicated the match to sample by making an eye movement to the remembered location of the match stimulus. By imposing this second delay, the authors reasoned that the motor component of the neural response would be temporally separated from the portion of the response reflecting the decision process. Hasegawa et al. (1998) identified neurons in the area principalis of the frontal lobe (mainly Walker area 46) that responded before saccades made to particular directions and to particular sample stimuli. Similar observations have been made by Miller and colleagues (Rao et al., 1997).

The neural responses observed in these experiments appear to reflect both the decision-relevant sensory cue

and a specific type of behavioral response. They offer a glimpse of what may be a physiological basis of the decision process. However, the decisions the monkeys are required to make in these tasks are based on supra-threshold stimuli. Consequently, the decision is made as soon as a monkey sees the oddball or match stimulus, making it difficult to attribute any portion of the neural response to anything other than what the monkey sees or plans to do. In other words, these tasks allow us to observe neural responses related to sensation and action but offer only a brief glimpse of the nexus in between. To appreciate a neural correlate of the decision process and not just its foundation or result, it is necessary to expand the period of sensory-motor indeterminacy.

Threshold psychophysics may fulfill this desire. Here, the interpretation of a weak sensory stimulus can be said to instruct a behavioral response. For many tasks, moreover, observers are known to benefit from prolonged exposure to sensory cues and seem to arrive at a decision gradually, as if accumulating the sensory evidence toward a categorical judgment. It would be informative to study the type of neurons described above during the period that a decision is forming about a weak visual stimulus.

Shadlen and Newsome (1996) recorded from neurons in the posterior parietal cortex (area LIP) during the motion discrimination task described earlier (Figure 1A). Neurons in area LIP emit sustained activity when a monkey plans an eye movement to a region of the visual field, termed the response field (RF) (Barash et al., 1991; Colby et al., 1996; Platt and Glimcher, 1997). Shadlen and Newsome used the random dot motion stimulus to instruct an eye movement into or away from the neuron's RF. The strength of motion was varied by manipulating the percentage of dots that moved coherently in a common direction. Consequently, on some trials the monkey's decision was a simple one, whereas on other trials it was more difficult.

The responses of neurons in area LIP reveal the monkey's decision about the direction of motion. A typical example is shown in Figure 2C. When the random dot motion was toward this neuron's RF (left plot), the response was large, presumably reflecting the monkey's intention to shift its gaze to the RF. Conversely, when motion was away from the RF, the response was attenuated. The response began to predict the monkey's choice during the period of motion viewing when the monkey was forming its decision—seconds before the monkey actually moved its eyes. The response predicted the monkey's choice whether the sensory stimulus was strong (i.e., easy) or weak, and it predicted the errors the animal made when forced to make decisions about subthreshold stimuli. Most interestingly, many neurons responded differently to motion stimuli of different strengths, modulating more intensely when the stimulus motion was stronger. Thus, the neural response indicated what action the monkey was going to take but also reflected the quality of the evidence upon which this action was based. Such observations are not confined to the visual system. A similar mixture of sensory "evidence" and motor response has been reported in recordings made in the primary motor cortex during a

tactile speed categorization task (Salinas and Romo, 1998). Like LIP, these "predominantly motor" neurons appear to accumulate sensory information toward a categorical plan.

The results obtained in threshold discrimination tasks provide the most compelling evidence yet for a neural correlate of a decision mechanism, but many questions remain. What computation do these neurons perform? Is there a discrete moment when the decision process achieves a binary state? How much specificity is there in the neural circuitry for a particular type of stimulus or instruction? Would the same neurons discharge if a different discrimination were chosen to instruct the behavior, or is the circuitry specialized for particular sensory-motor contingencies?

Clearly, we are just beginning to understand the neural circuits that underlie the brain's ability to link sensory interpretations with the appropriate behavioral options. While there is more to cognition than making decisions about simple sensory stimuli, we expect the principles gleaned from these experiments to generalize to many activities in which we plan and choose behaviors from a limited repertoire based on information sensed a short time ago.

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