The neurophysiology of decision-making as a window on cognition

Michael N. Shadlen[1] and Joshua I. Gold[2]

[1] Howard Hughes Medical Institute, Department of Physiology & Biophysics and National Primate Research Center, University of Washington Medical School, Box 372790, Seattle, WA 98195-7290

[2] Department of Neuroscience, University of Pennsylvania, Philadelphia, PA 19104-6074

"Would any one trust in the convictions of a monkey's mind, if there are any convictions in such a mind?"

Charles Darwin (1881, *letter to W. Graham*)

Nervous systems extract sensory information from the environment to guide behavior. The underlying neural mechanisms have been studied extensively, in part by identifying neurons with responses linked deterministically to sensory and motor events. Higher nervous systems are also capable of widespread cognitive abilities, including interpretation, decision-making, valuation, intention, language, and learning. The mechanisms underlying these abilities is less clear, in part because they seem beyond the scope of the machine-like behavior of sensory and motor neurons. This chapter examines this conundrum: How do properties of neurons and neural circuits give rise not just to reflexive sensory and motor abilities, but to cognition, as well? We suggest that an answer can be found in circuits that link sensory input to motor output. Here, transformations of sensory and motor signals reflect the kinds of nuance and flexibility that are hallmarks of cognition.

Several lines of evidence show that sensory-motor and cognitive mechanisms interact in the brain. Psychophysical measurements illustrate the many ways in which mechanisms that link sensation and action are not reflexive: they take a variable amount of time that can depend on the subject’s strategy and other factors (Luce, 1986); they can involve flexible associations between different sensory stimuli and different actions (Murray et al., 2000; Wise and Murray, 2000); and they can be influenced by psychological factors like bias, attention, and expected costs and benefits (Carpenter and Williams, 1995; Reddi and Carpenter, 2000). Clinical observations of patients with damage to “association” areas of cortex, particularly in the parietal and frontal lobes, have shown deficits in both sensoryguided behavior and cognitive functions (Mesulam, 1985; Feinberg and Farah, 1997). Neuroimaging studies have also shown co-localization of function, with similar patterns of activation in these association areas during certain sensory-motor and cognitive tasks (Corbetta et al., 1998; Acuna et al., 2002; Simon et al., 2002; Astafiev et al., 2003).

Combined electrophysiology and psychophysics in monkeys provides an opportunity to study how properties of neurons and circuits of neurons provide these sensory-motor and cognitive abilities. Here we describe advances in understanding the neural mechanisms responsible for making a decision about visual motion (Fig. 1). In part I, we quantify decision formation in terms of a trade-off between speed and accuracy. In part II, we show that the underlying mechanisms involve neural activity that tends to persist beyond sensory and motor events, accumulates over time a "weight of evidence" that supports or opposes the alternative decisions, and is related to motor intention. In part III, we discuss the broader implications of these findings. The mechanisms of decision formation appear well suited for a variety of roles, from sensory-motor processing to more complex aspects of cognition.

I. Psychophysics of decision-making

Decisions about noisy sensory signals involve an inherent trade-off between speed and accuracy. Deciding quickly can mean missing important signals. Taking more time can provide more or better signals, but that time might be wasted. We use the motion task to study the mechanisms responsible for this trade-off. The random-dot stimulus supplies a continuous source of noisy signals that can take hundreds of msec for the brain to accumulate and interpret. Thus, we can study the underlying mechanisms on a time scale that is relatively long for neurons. Here we analyze performance and show that information from the motion stimulus appears to be accumulated over time until sufficient evidence has been gathered to render a decision.

The most direct evidence for a temporal accumulation of motion information comes from experiments in which the time given to view the stimulus was varied randomly from trial to trial (Fig. 1A). The percentage of coherently moving dots was also varied. Performance accuracy was affected by both variables (Fig. 2). At high motion coherence (top curve), performance was perfect (no errors) with greater than ~200 msec of motion viewing. At lower motion coherences, performance improved with increased viewing time, measured out to 700 msec, but never reached perfect accuracy. The smooth curves fit to the data allow us to infer properties of the signals in the brain that are used to make the decision (Gold and Shadlen, 2000; Gold and Shadlen, 2003). Information from the stimulus appears to be accumulated throughout motion viewing without loss, as long as it is needed to improve performance. Information gained in the first 100 msec is simply added to information gained in the next 100 msec, and so forth. This perfect accumulation persists over a time scale that is at least an order of magnitude longer than the time scale of neural computations in the sensory cortex, which must keep up with changes in the environment.

In a second set of experiments, the monkey, rather than the experimenter, controlled the period of motion viewing (Fig. 1B). The results from this type of experiment are shown in Figure 3. In addition to a *psychometric* function describing accuracy (Fig. 3A), we also obtain a *chronometric* function of behavioral response time (RT) versus motion strength (Fig. 3B). The RT was measured from the time the random dots first appear to the time that the monkey initiates an eye movement to indicate its choice of direction. For high coherences, the task was easy and the monkey took a short time to reach a decision. For progressively lower coherences, the task was more difficult and the monkey took progressively longer to reach a decision.

Performance on the RT task is also consistent with a decision process that accumulates noisy motion evidence over time. In this case, the decision process terminates and monkey issues a response when the amount of evidence in favor of one of the alternatives reaches a criterion level. The analysis of this kind of process has roots in sequential analysis (a branch of statistical hypothesis testing) and psychology (Wald, 1947; Stone, 1960; Laming, 1968; Link, 1992; Ratcliff and Rouder, 1998; Gold and Shadlen, 2002; Usher et al., 2002). Here we emphasize an analogy to the diffusion of a particle toward absorbing barriers that lie on either side of its starting point (Fig. 4).

Random-dot motion causes the brain to generate signals that depend on the direction and strength of the motion stimulus but are highly variable from moment-to-moment

(Shadlen and Newsome, 1994, 1998). We assume that the accumulation of these signals will tend to drift in one direction or the other, depending on the stimulus, but because of the variability will meander like a particle in Brownian motion. The process stops when the accumulation reaches one of two barriers at ±B (Fig. 4; here the barriers are stationary as a function of time, but, in principle, that does not need to be the case). If the accumulation reaches +B, a decision is rendered in favor of one direction; if the accumulation reaches –B, the brain renders the opposite decision. The value of B controls the trade-off between speed and accuracy: larger values imply more time to reach the barrier and thus more time to accumulate signals, resulting in fewer errors (i.e., crossing the wrong barrier). The variability in the signals being accumulated ensures that one of the barriers will be reached, even when the evidence favors neither alternative on average (i.e., 0% coherence), and accounts for both errors and trial-by-trial differences in RT.

The smooth curves in Fig. 3 illustrate how well the diffusion-to-barrier model can account for performance on the RT task. The sigmoid curve fit to the RT data (Fig. 3B) describes the hitting time of a particle in 1-dimensional

Brownian motion:

$$t(c) = \frac{B}{kc}\tanh(Bkc) + t_{nd} \quad , \qquad (1)$$

where c is motion strength (percent coherence) and k, B and t_{nd} are fitted parameters (for derivations of Eqs. 1 and 2, see Link, 1992; Ross, 1996). t_{nd} is the non-decision component of the RT; it includes, for example, the time needed to propagate information from the stimulus to the circuits that form the decision and to execute the eye movement once the decision has been made. The term involving tanh describes the amount of time for an accumulation at one sample per msec of a normally distributed random number with mean kc and variance 1 to reach a criterion level, $\pm B$.

The same diffusion-to-barrier model also predicts the monkey's choices. It specifies how often the accumulation will reach $+B$ first. This is quantified as a logistic function for the probability of correct choices:

$$p(c) = \frac{1}{1 + e^{-2k|c|B}} \qquad (2)$$

Equation (2) describes the sigmoid curve in Fig. 3A, but it is not a fit to the data. It is a prediction from the chronometric function. The scaling factor, k, and barrier distance, B, were determined by fitting the RTs. This leaves no free parameters to fit the psychometric function, which nonetheless lies close to the data points. This close match is emblematic of the success this kind of model has had in explaining psychophysical data, including percent correct, mean RT, and distributions of RT, on a wide range of perceptual tasks (Link, 1992; Ratcliff and Rouder, 1998).

Both the variable-duration and RT experiments suggest that there is a gradual evolution of a quantity, termed a decision variable, that determines the monkey’s decision. The decision variable grows, on average, in proportion to the motion strength and viewing time. It represents the accumulated evidence in favor of one proposition and against another. As described in the next section, such a decision variable has been identified in the brain of the monkey.

II.Neurophysiology of decision-making

Early brain mapping studies using electrical microstimulation in awake patients undergoing brain surgery exposed extensive “silent” regions of neocortex that did not seem tied to particular sensations or motor outputs

(Penfield and Roberts, 1974). These regions, found in the parietal, temporal, and frontal lobes, were eventually assumed to subserve higher “associative” functions. Electrophysiological measurements in alert monkeys have shown that neurons in these areas have complicated response properties that are not simply locked to sensory or motor events. Instead, the neural activity tends to persist throughout delay periods. Such persistent activity is likely to be a hallmark of the capacity for temporal integration – holding a level of response until perturbed to a new value – that underlies the computation of decision variables. Here we describe neural signals that appear to integrate over time a “weight of evidence” that supports or opposes the alternative direction interpretations on the motion task, thereby linking the interpretation of sensory input to a motor output (in this case, the eye-movement response).

In one set of experiments, we recorded from neurons in the lateral intraparietal area (LIP; Fig. 5A) (for reviews, see Colby and Goldberg, 1999; Andersen and Buneo, 2002). Using a saccade-to-target task, we selected neurons with activity that persisted in a delay period between flashing the target in the periphery and instructing the monkey to initiate an eye movement to the target (Figure 5B). These neurons are not purely sensory because they respond when there is nothing present in the visual scene (after the target has been turned off). They are also not purely motor, because their discharge does not obligate an immediate action. In our experiments, the persistent activity corresponded to particular target locations, termed the neuron's response field (RF). This term is a descriptive hybrid of "receptive field", which implies visual processing of the target, and "motor field", which implies processing the metrics of the impending eye movement.

We used the motion task to test whether this persistent activity represented a decision variable. Instead of a flashed target, the direction of random-dot motion indicated which eye movement to make. Not surprisingly, the LIP neuron predicted whether or not the monkey made an eye movement into the RF; that is, it reflected the outcome of the process that formed the direction decision. What is perhaps more surprising is that the LIP responses also reflected the computations underlying the decision process itself.

This result is best appreciated in the RT version of the motion task (Roitman and Shadlen, 2002). The advantage of this task is that the monkey indicates the end of the decision process on every trial. Thus, we can study LIP activity in the time epoch in which the monkey is forming a decision but has not yet committed to an answer. The results are summarized in Fig. 5C. Following onset of the targets (not shown), activity is robust (~35 spikes/sec on average) until ~100 msec following onset of the motion stimulus. The activity then undergoes a stereotyped dip and recovery that does not reflect the motion stimulus or the eye-movement response. We think this activity might represent a reset of an integration process that appears to begin ~200 msec after motion onset and continues until the decision is formed.

The integration process is evident as ramp-like changes in LIP activity. The ramps represent accumulations of motion evidence that, on average, correspond to the monkey’s decisions. For the decision associated with the target in the neuron’s RF, the activity ramps upward (solid curves). For the alternative decision, the activity ramps downward (dashed curves). Higher coherence provides more evidence, corresponding to steeper ramps. Lower coherence provides less evidence, corresponding to shallower ramps. Even zero coherence, which provides no net motion information but still must be interpreted by the monkey to reach a decision, is treated as noisy evidence that ramps gradually towards the monkey's choice. Note that the responses in Fig. 5C are averages from many individual trials. For any one trial, LIP activity is probably more like the meandering path of a particle in Brownian motion.

The upward and downward ramps, apparent for individual neurons, suggest that the motion evidence being accumulated is a difference in activity favoring the two directions. For example, an LIP neuron with a rightward RF would accumulate the difference between rightward and leftward direction signals. Rightward motion would tend to cause a positive (upward) accumulation, whereas leftward motion would tend to cause a negative (downward) accumulation. A recent study provided direct experimental support for this difference operation (Ditterich et al., 2003). Such a difference approximates the logarithm of the likelihood ratio—or "weight of evidence"—in favor of one or the other alternative (Gold and Shadlen, 2001). Thus, accumulating this difference to a criterion value approximates a statistical process known as the sequential probability ratio test (Wald, 1947; Stone, 1960; Laming, 1968; Link, 1992).

Consistent with the sequential probability ratio test and the “diffusion-to-barrier” model (see Fig 4), the LIP activity appears to reach a criterion value that indicates the end of the decision process. On the right side of figure 5C, the same responses are shown aligned to the beginning of the eye movement response. In contrast to the ramps on the left, the rising responses are stereotyped. They seem to reach a common value ~100 msec before the eye movement response, regardless of their trajectory to this point. This is more apparent when the data are sorted by RT instead of motion strength (Fig. 5D): the responses reach an apparent decision threshold rapidly for fast decisions but take a more meandering approach to the same threshold when the decision takes longer. In contrast, there is no common end point for the declining responses associated with the opposite decision (Fig. 5C, dashed curves). Presumably, a second set of neurons accumulates evidence in the opposite direction. When their activity reaches the criterion value, a movement into their RF is triggered and all decision processes are terminated.

LIP is just one of several brain structures with neurons that show this kind of activity on the motion task. Similar activity has been found in other cortical association areas, including the frontal eye field (FEF) and dorsolateral prefrontal cortex, and in subcortical structures including the superior colliculus (Kim and Shadlen, 1999; Horwitz and Newsome, 2001). The relative contributions these different structures make to the decision process are not known. For example, it is not clear whether they all help to compute the decision variable or some simply reflect computations performed elsewhere. Nevertheless, one common feature of these structures is evident: they are all involved in preparing the eye-movement response (Funahashi et al., 1991; Schall, 1997; Sparks, 2002).

Thus, a decision that links sensation to action appears to be formed by structures involved in motor preparation. From one perspective, this seems odd. The direction decision clearly depends on the sensory input but seems unrelated to how the answer will be communicated. Indeed, one might predict that the motor systems that control the behavioral response should be engaged only after the decision is reached. These motor systems should not be concerned with the evolving sensory evidence. This prediction turns out to be incorrect.

We examined how much of the decision process is communicated to the oculomotor system while the monkey performs the motion task (Fig. 6A). In effect, we perturbed the oculomotor system to find evidence of the decision variable. As in some of the behavioral experiments, the monkey was given a variable amount of time to view the motion stimulus. At the exact time that the motion was turned off, a brief train of microstimulation pulses was applied to the FEF. These pulses evoked a short-latency saccadic eye movement. After another ~100 msec, the monkey, having recognized the offset of random-dot motion and thus the end of the trial, made a second, voluntary eye movement to one of the choice targets to indicate its direction decision.

The trajectory of the evoked saccade was influenced by an evolving decision variable. The trajectory was similar to those measured on control trials when the monkey simply fixated a central spot (Fig. 6B, *fix*). However, on discrimination trials, the trajectory tended to deviate in the direction of the subsequent voluntary eye movement

(Fig. 6B, *up* and *down*). This deviation appeared to reflect an ongoing plan to make this movement while viewing the motion stimulus. Importantly, this deviation was not an all or none phenomenon but instead, like the decision variable, depended on the strength and duration of motion (Fig. 6C). Thus, the accumulated weight of evidence in favor of one direction versus the other is represented in the commands related to the behavioral response.

III. A window on cognition: perspectives and future directions

Several principles appear to govern the formation of decisions about motion. Sensory input is converted into a weight of evidence to support or oppose the alternative direction decisions. The weight of evidence is accumulated over time. The accumulation stops when a criterion value is reached. This process is represented in structures that prepare the behavioral response. Here we discuss the broader implications of these principles for sensory-motor processing and cognition.

Sensory information as weight of evidence. The monkey's direction decisions appear to be based on the difference in activity between pools of motion-sensitive neurons with preferences for the two alternative directions. This difference provides a weight of evidence that quantifies the relative likelihoods of the alternatives given the sensory activity. Thus, the decision is not simply a reflex that associates a pattern of sensory activity with an appropriate behavioral response (an eye movement). Instead, the decision is a process of interpretation that uses the weight of evidence to make sense of noisy, distributed sensory information to reach a categorical judgment.

The usefulness of the weight of evidence is not limited to decisions about motion. In general, it can be used to maximize the probability of deciding correctly between two alternatives (Good, 1979; Gold and Shadlen, 2001; Gold and Shadlen, 2002). The basic principles can even be extended to decisions with many alternatives (Laming, 1968; Usher et al., 2002), although it is unknown whether the brain uses this method for such complicated problems.

The weight of evidence is also easy to compute. Motion direction is represented systematically in the middle temporal area (MT or V5) of extrastriate visual cortex

(Zeki, 1974; Albright et al., 1984). Other sensory parameters, including location, orientation, and disparity, are similarly mapped in sensory cortex. A simple difference in activity within any of these maps represents a weight of evidence that can distinguish between different values of the mapped parameter. In principle, differences computed from other representations can also be used as a weight of evidence; for example, the difference between sensory activity and memory activity could help to distinguish between sequentially presented stimuli.

Finally, the weight of evidence constitutes a currency that allows signals with dissimilar origins to be compared and combined. By analogy, monetary currency can define the relative values of seemingly unrelated quantities, like an hour’s labor versus a new car. Similarly, the weight of evidence can, in principle, be used to compare the information provided by different sources, sensory or otherwise, to make decisions. For example, the evidence provided by a sensory stimulus can be weighed against other factors like bias, reward expectation, and utility (Gold and Shadlen, 2001; Gold and Shadlen, 2002; Montague and Berns, 2002; Glimcher, 2003). Indeed, such a confluence of factors is evident in the activity of neurons in association areas of cortex (Leon and Shadlen, 1999; Platt and Glimcher, 1999; Amador et al., 2000; Hikosaka and Watanabe, 2000; Tremblay and Schultz, 2000).

Accumulation of evidence over time. Time is needed to form the direction decision. At any given moment, the weight of evidence provided by the stochastic motion stimulus is too vague to reach a decision. However, the motion signals are presented continuously over time. Appropriately, the decision appears to be formed by accumulating over time the moment-by-moment weight of evidence. Thus, less time implies less accumulated evidence and lower accuracy. More time implies more evidence and higher accuracy.

Accumulation is undoubtedly just one of many strategies that the brain uses to interpret incoming sensory information. For the motion task, a continuous accumulation is appropriate for a continuously arriving signal. For other tasks, different temporal functions might be more appropriate if, for example, information arrives at separate, predictable intervals. The point is that decisions about stochastic stimuli like the dots are not simply processes that take time. Rather, they are processes that can use strategies like accumulation to interpret information that arrives at different times. This capacity is central to organizing behavior that is not tied to the immediacy of a particular sensory input or motor output (Fuster, 1985).

In general, mechanisms that establish a logical relationship between sensory input and motor output but are not invariably tied to either exemplify the close relationship between sensory-motor and cognitive function in the brain. For example, in the association cortex, activity that persists between sensory and motor events has been implicated in short term (working) memory (Fuster and Alexander, 1971; Miyashita and Chang, 1988; Goldman-Rakic et al., 1990; Quintana and Fuster, 1992; Miller et al., 1996l; Graziano et al., 1997; Romo et al., 1999), allocation of attention (Colby and Goldberg, 1999), motor planning (Crammond and Kalaska, 1989; Andersen and Buneo, 2002), motor sequencing (Shima and Tanji, 2000), the representation of motor set or rules (Evarts and Tanji, 1974; di Pellegrino and Wise, 1993; Hoshi et al., 2000; Tanji and Hoshi, 2001; Wallis et al., 2001), and, as we have discussed, the formation of decisions (Schall, 2001; Glimcher, 2003; Romo and Salinas, 2003). It is intriguing to think that these higher functions have co-opted mechanisms that evolved to solve more mundane problems in sensory-motor processing. For example, persistent activity in certain brainstem nuclei holds the gaze in a fixed position. This activity arises through a process resembling integration with respect to time: eye position is the integral of a pulse-like motor command signal, which controls eye velocity (Robinson, 1989). By analogy, neurons in association areas might integrate over time the “pulses” of evidence that bear on decisions.

Thus, cognition appears to rest, in part, on mechanisms that liberate the brain from time constraints imposed by the environment and the body. However, this freedom poses new problems. How does the brain organize in time computations that are not linked to immediate sensory or motor events? When do the computations begin and end? How can they take into account sensory input from the past? Or affect future behavior? To solve these problems, time itself is likely to be represented explicitly in brain structures with persistent activity. Indeed, recent experiments suggest that elapsed time is represented in the parietal cortex (Leon and Shadlen, 2003). The representation of this and other time parameters will likely emerge as an important future direction in the pursuit of the neural mechanisms of higher brain function.

Commitment to one alternative when a criterion level of evidence is reached. To form the direction decision, the weight of evidence appears to be accumulated until a criterion level or "barrier height" is reached. Setting the barrier height controls the trade-off between speed and accuracy. A low barrier provides fast-but-uncertain decisions. A high barrier provides slow-but-certain decisions. This process—accumulating a difference to a barrier—can explain not just decisions about motion, but also a wide variety of laws of sensation and perception. These include Weber's Law, which governs the appreciation of increments, and both Fechner's and Stevens' Laws, which explain estimates of subjective magnitude of sensory experience (Link, 1992).

The barrier crossing also represents a form of temporal control. For the RT task, it determines the end-point of decision processing and the beginning of motor execution. In principle, a barrier crossing could help control how cognitive processing is organized in time, as well. It could determine the end-point of decision processing and a commitment to a more abstract proposition than an immediate behavior, like more computations. In this sense, accumulations to barriers seem intimately related to internal representations of time. This mechanism could help control the brain’s ability to process sequences of sensory inputs, plan sequences of behavior, and in general cascade sequences of operations on a flexible time scale.

Representation of the decision variable in brain structures that control the motor response. In monkeys trained to indicate their direction decision with an eye movement to a predictable location in the same direction, formation of the decision and formation of the eye-movement response seem to be closely linked in the brain. Neurons in several structures involved in oculomotor preparation, including area LIP, the FEF, the dorsolateral prefrontal cortex, and the superior colliculus, represent both the impending eye-movement response and the accumulation of motion evidence used to select that response. Indeed, the decision variable appears to be represented in the very motor commands that ultimately generate the eye-movement response.

These results certainly reflect the design of the task. If the monkeys were trained to indicate their decision with an arm movement, not an eye movement, we would expect the decision variable to be represented in neurons that prepare arm movements. It seems to be, in part, a matter of efficiency. When the decision is associated with a particular, predictable, and impending motor response, there is a continuous flow of up-to-date information about the decision – both sensory and psychological – in the circuits that prepare the response (Bichot et al., 2001).

The same principles can be extended to include decisions not linked to specific movements. This is illustrated with a new version of the motion task. This task requires the monkey to indicate its direction decision with an eye movement to a target not at a particular location but of a particular color: red for rightward motion, green for leftward motion. Critically, the locations of the targets are not known until after the decision is formed. FEF microstimulation confirms that, for this task, the decision variable is not represented in commands to generate a specific eye movement (Gold and Shadlen, 2003). Instead, the brain might construe incoming motion information as evidence for implementing a particular behavioral rule. The possible rules are "When two targets appear, look at the red one" or "look at the green one." Thus, the decision can still be formed in an intention-oriented framework, but the intention – a behavioral rule – is more abstract than a specific movement.

An obvious question is whether intention-related structures form the decisions or simply reflect computations performed elsewhere. As a practical issue of determining what those computations are, the answer might not matter: studying the computations themselves or their faithful reflections will yield similar insights. To understand the flow of information in the brain, however, the answer certainly does matter. Is information that arrives in intention-related structures already processed thoroughly, having been sent there by higher-order circuits that do the hard work of cognition? If so, where are those circuits? If not, what are the implications of high-order brain function being processed in an intention-oriented framework?

We do not know the answers to these questions. However, there is reason to speculate that intention-related structures indeed play pivotal roles in forming decisions. In our view, the most compelling reason is that decision-making implies a goal. The most obvious goals are behaviors and consequences of behaviors: to get from here to there, to avoid bad things, to get good things. Thus, brain structures involved in achieving these goals – that is, structures that determine what to do and how and when to do it – seem likely to make decisions. With flexible representations of behaviors and behavioral goals, along with a flexible currency like the weight of evidence, it seems unnecessary to posit other structures to do the hard work.

The generalization of this principle shifts the emphasis of brain function from the descriptive analysis of sensory data to the informed control of behavior. Intention-related mechanisms provide goals. These goals establish the utility and meaning of sensory and psychological signals, which are used as evidence to help decide among alternatives and achieve these goals. Thus, intention-related structures provide the framework for both sensory-motor processing and the rudiments of higher cognitive function. These ideas on the centrality of intention to perception and higher brain function have a long tradition. For example, Helmholtz suggested that the perception of space, including the interpretation of curvature and straightness, could be understood in terms of the way our motor systems are organized to rotate our eyes along great circles (Helmhotz, 1925). These ideas also emerge under various guises in philosophy, notably in the writings of Merleau-Ponty and other descendants of Heidegger, who recognized that the properties of things are related in a profound sense to their utility (Heidegger, 1962; Merleau-Ponty, 1962; Clark, 1997; O'Regan and Noë, 2001).

An intention-based framework for information processing might also point the way towards understanding one of the deepest mysteries of neuroscience: consciousness. Our understanding of consciousness seems stymied by the same conundrum posed at the beginning of this article. Consciousness, like cognition, seems unrelated to the operations that neurons perform. For example, there seem to be too few constraints to explain the leap from raw sensory information to the coherence and salience of conscious perception. How can we group the elements of visual scenes into meaningful wholes and background, despite the combinatorial complexity posed by the raw data of light, edges, and color (see Figure 7)? To solve this kind of problem, many theories of consciousness posit a central interpreter, or homunculus. The intention-based framework provides an alternative view. According to this view, our conscious experience is indeed constrained. Conscious perception derives from, in effect, questions related to behavior (e.g., is that something I can grab? Can I walk there?). Sensory and memory signals are interrogated for evidence that can be used to provide answers. Thus, our conscious experiences – and the underlying neural computations – are constrained to what is being asked and what is answered. Because the questions are determined from the repertoire of possible behaviors, the underlying mechanisms of consciousness are intimately tied to the fact that the brain controls a body.

This intention-based architecture seems to take the hard work of consciousness away from the homunculus. However, another, equally mysterious mechanism seems to be required. If sensory information flows to circuits where it can exert leverage on intentions, plans, and rules, what controls the flow? Which intentions, plans, and rules are under consideration at any moment? The need for a homunculus has apparently been replaced by the need for a traffic cop.

We speculate that, unlike for the homunculus, we already have insights into the brain mechanisms that serve as traffic cop. These are the same mechanisms that allow an animal to explore its environment; that is, to forage. Foraging is about connecting data in the environment to a prediction of reward through complex behavior (Gallistel, 2000). However, in principle, the mechanisms of foraging, like the mechanisms of decision-making, do not need to be tied to overt behaviors. The same principles that apply to visits to flowers could direct the parietal lobe to query the visual cortex for evidence needed to answer a question about motion. More generally, foraging might be related to the leaps our brains make to replace one percept with another (e.g., binocular rivalry), to escape one behavioral context for another, or to explore new ideas. For cognitive neuroscientists, these ideas inspire research on how reward expectation influences sensory-motor and higher processing in association areas of the brain. For the philosopher of mind, these ideas provide an inkling of how properties of the brain give rise to agency and, perhaps, free will.

Conclusions

When designing an experiment to study decision-making and other cognitive functions, among the critical questions we ask is, where should we put our electrodes? That is, where in the brain will we find neurons that contribute to these higher functions? We and others are finding success by recording from neurons at the nexus of sensory-motor processing. By studying how sensory information is converted into a categorical decision that guides behavior, we gain insight into flexible and efficient mechanisms that could subserve cognitive functions, as well. These mechanisms provide a common currency for integrating information from a variety of sources, sensory or otherwise; they disengage information processing from the immediacy of sensory and motor events; and they establish rules for committing to a proposition. The mechanisms we study also hint at a broad principle of brain organization: behavior and behavioral goals are the hubs around which other information is organized. These hubs define, for example, how utility and meaning should be ascribed to sensory signals. This organization lights the path to future research in cognition and perhaps even consciousness.

Bibliography

Acuna BD, Eliassen JC, Donoghue JP, Sanes JN (2002) Frontal and parietal lobe activation during transitive inference in humans. Cereb Cortex 12:1312-1321.

Albright TD, Desimone R, Gross CG (1984) Columnar organization of directionally selective cells in visual area MT of macaques. J Neurophysiol 51:16-31.

Amador N, Schlag-Rey M, Schlag J (2000) Reward-predicting and reward-detecting neuronal activity in the primate supplementary eye field. J Neurophysiol 84:2166-2170.

Andersen RA, Buneo CA (2002) Intentional maps in posterior parietal cortex. Annu Rev Neurosi 25:189-220.

Astafiev SV, Shulman GL, Stanley CM, Snyder AZ, Van Essen DC, Corbetta M (2003) Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. J Neurosci 23:4689-4699.

Bichot NP, Chenchal Rao S, Schall JD (2001) Continuous processing in macaque frontal cortex during visual search. Neuropsychologia 39:972-982.

Carpenter R, Williams M (1995) Neural computation of log likelihood in control of saccadic eye movements. Nature 377:59-62.

Clark A (1997) Being There: Putting brain, body, and world together again. Cambridge, MA: MIT Press.

Colby CL, Goldberg ME (1999) Space and attention in parietal cortex. Annu Rev Neurosci 22:319-349.

Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL (1998) A common network of functional areas for attention and eye movements. Neuron 21:761-773.

Crammond DJ, Kalaska JF (1989) Neuronal activity in primate parietal cortex area 5 varies with intended movement direction during an instructed-delay period. Exp Brain Res 76:458-462.

di Pellegrino G, Wise S (1993) Visuospatial versus visuomotor activity in the premotor and prefrontal cortex of a primate. J Neurosci 13:1227-1243.

Ditterich J, Mazurek M, Shadlen MN (2003) Microstimulation of visual cortex affects the speed of perceptual decisions. Nat Neurosci 6:in press.

Evarts EV, Tanji J (1974) Gating of motor cortex reflexes by prior instruction. Brain Res 71:479-494.

Feinberg TE, Farah MJ, eds (1997) Behavioral neurology and neuropsychology. New York: McGraw-Hill.

Funahashi S, Bruce C, Goldman-Rakic P (1991) Neuronal activity related to saccadic eye movements in the monkey's dorsolateral prefrontal cortex. J Neurophysiol 65:1464-1483.

Fuster J (1985) The prefrontal cortex and temporal integration. In: Cerebral Cortex (Peters A, Jones E, eds), pp 151-177. New York: Plenum.

Fuster JM, Alexander GE (1971) Neuron activity related to short-term memory. Science 173:652-654.

Gallistel CR (2000) Time, Rate, and Conditioning. Psychological Review 107:289-344.

Glimcher P (2003) The neurobiology of visual-saccadic decision making. Annu Rev Neurosci 26:133-179.

Gold JI, Shadlen MN (2000) Representation of a perceptual decision in developing oculomotor commands. Nature 404:390-394.

Gold JI, Shadlen MN (2001) Neural computations that underlie decisions about sensory stimuli. Trends Cogn Sci 5:10-16.

Gold JI, Shadlen MN (2002) Banburismus and the brain: decoding the relationship between sensory stimuli, decisions, and reward. Neuron 36:299-308.

Gold JI, Shadlen MN (2003) The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands. J Neurosci 23:in press.

Goldman-Rakic PS, Funahashi S, Bruce CJ (1990) Neocortical memory circuits. Cold Spring Harb Symp Quant Biol 55:1025-1038.

Good IJ (1979) Studies in the history of probability and statistics. XXXVII A.M. Turing's statistical work in World War II. Biometrika 66:393-396.

Graziano MSA, Hu XT, Gross CG (1997) Visuospatial properties of ventral premotor cortex. J Neurophysiol 77:2268-2292.

Heidegger M (1962) Being and Time. New York: Harper and Row.

Helmhotz Hv (1925) Chapter 28. The monocular field of vision. In: Helmholtz's Treatise on Physiological Optics (Southall JPC, ed). Menasha, Wisconsin: The Optical Society of America and George Banta Publishing Company.

Hikosaka K, Watanabe M (2000) Delay activity of orbital and lateral prefrontal neurons of the monkey varying with different rewards. Cereb Cortex 10:263-271.

Horwitz GD, Newsome WT (2001) Target selection for saccadic eye movements: prelude activity in the superior colliculus during a direction-discrimination task. J Neurophysiol 86:2543-2558.

Hoshi E, Shima K, Tanji J (2000) Neuronal activity in the primate prefrontal cortex in the process of motor selection based on two behavioral rules. J Neurophysiol 83:2355-2373.

Kim J-N, Shadlen MN (1999) Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. Nat Neurosci 2:176-185.

Laming DRJ (1968) Information theory of choice-reaction times. London: Academic Press.

Leon MI, Shadlen MN (1999) Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. Neuron 24:415-425.

Leon MI, Shadlen MN (2003) Representation of time by neurons in the posterior parietal cortex of the macaque. Neuron 38:317-327.

Link SW (1992) The wave theory of difference and similarity. Hillsdale, NJ: Lawrence Erlbaum Associates.

Luce RD (1986) Response times: their role in inferring elementary mental organization. New York: Oxford University Press.

Merleau-Ponty M (1962) Phenomenology of Perception. London: Routledge & Kegan Paul Ltd.

Mesulam M-M (1985) Principles of behavioral neurology. Philadelphia: F.A. Davis.

Miller EK, Erickson CA, Desimone R (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. J Neurosci 16:5154-5167.

Miyashita Y, Chang H (1988) Neuronal correlate of pictorial short-term memory in the primate temporal cortex. Nature 331:68-70.

Montague PR, Berns GS (2002) Neural economics and the biological substrates of valuation. Neuron 36:265-284.

Murray EA, Bussey TJ, Wise SP (2000) Role of prefrontal cortex in a network for arbitrary visuomotor mapping. Exp Brain Res 133:114-129.

O'Regan JK, Noë A (2001) A sensorimotor account of vision and visual consciousness. Behav Brain Sci 24:in press.

Penfield W, Roberts L (1974) Speech and brain-mechanisms. Atheneum, New York: Princeton University Press.

Platt ML, Glimcher PW (1999) Neural correlates of decision variables in parietal cortex. Nature 400:233-238.

Quintana J, Fuster J (1992) Mnemonic and predictive functions of cortical neurons in a memory task. Neuroreport 3:721-724.

Ratcliff R, Rouder JN (1998) Modeling response times for two-choice decisions. Psychological Science 9:347-356.

Reddi BA, Carpenter RH (2000) The influence of urgency on decision time. Nat Neurosci 3:827-830.

Robinson DA (1989) Integrating with neurons. Annu Rev Neurosci 12:33-45.

Roitman JD, Shadlen MN (2002) Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. J Neurosci 22:9475-9489.

Romo R, Salinas E (2003) Flutter discrimination: neural codes, perception, memory and decision making. Nat Rev Neurosci 4:203-218.

Romo R, Brody C, Hernandez A, Lemus L (1999) Neuronal correlates of parametric working memory in the prefrontal cortex. Nature 399:470-473.

Ross S (1996) Stochastic Processes, Second Edition Edition. New York City, NY: John Wiley & Sons.

Schall JD (1997) Visuomotor areas of the frontal lobe. In: Cerebral Cortex (al Re, ed), pp 527-638. New York: Plenum.

Schall JD (2001) Neural basis of deciding, choosing and acting. Nat Rev Neurosci 2:33-42.

Shadlen MN, Newsome WT (1994) Noise, neural codes and cortical organization. Curr Opin Neurobiol 4:569-579.

Shadlen MN, Newsome WT (1998) The variable discharge of cortical neurons: implications for connectivity, computation and information coding. J Neurosci 18:3870-3896.

Shadlen MN, Movshon JA (1999) Synchrony unbound: a critical evaluation of the temporal binding hypothesis. Neuron 24:67-77.

Shima K, Tanji J (2000) Neuronal activity in the supplementary and presupplementary motor areas for temporal organization of multiple movements. J Neurophysiol 84:2148-2160.

Simon SR, Meunier M, Piettre L, Berardi AM, Segebarth CM, Boussaoud D (2002) Spatial attention and memory versus motor preparation: premotor cortex involvement as revealed by fMRI. J Neurophysiol 88:2047-2057.

Sparks DL (2002) The brainstem control of saccadic eye movements. Nat Rev Neurosci 3:952-964.

Stone M (1960) Models for choice-reaction time. Psychometrika 25:251-260.

Tanji J, Hoshi E (2001) Behavioral planning in the prefrontal cortex. Curr Opin Neurobiol 11:164-170.

Tremblay L, Schultz W (2000) Reward-related neuronal activity during Go-nogo task performance in primate orbitofrontal cortex. J Neurophysiol 83:1864-1876.

Usher M, Olami Z, McClelland JL (2002) Hick's law in a stochastic race model with speed-accuracy tradeoff. J Math Psych 46:704-715.

Wald A (1947) Sequential Analysis. New York: Wiley.

Wallis JD, Anderson KC, Miller EK (2001) Single neurons in prefrontal cortex encode abstract rules. Nature 411:953-956.

Wise SP, Murray EA (2000) Arbitrary associations between antecedents and actions. Trends Neurosci 23:271-276.

Zeki SM (1974) Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. J Physiol 236:549-573.

Acknowledgments. We thank Jochen Ditterich and Alex Huk for helpful comments on the manuscript. This research was supported by the Howard Hughes Medical Institute, the National Eye Institute (EY11378), the National Center for Research Resources (RR00166), the McKnight Foundation, and the Burroughs-Wellcome Fund.

Figure Legends

Figure 1. Two versions of the motion task used to study decision-making in monkeys. This task was formerly used to study the relationship between the properties of neurons in the visual cortex and the limits of perception (see Parker and Newsome, 1998). The monkey decides whether the net direction of random-dot motion is in one of two directions, here right or left. The ease and difficulty of the task can be controlled by varying the percentage of dots that are moving coherently in one of the two directions. The remaining dots merely appear and disappear at random locations. The monkey does not know beforehand what percentage of dots will be moving coherently or in which direction they will be moving. Even the moving dots are not shown for more than ~40 msec before being replotted elsewhere. Thus, the decision depends on assessing the net motion across all the dots and across time. The monkey is trained to look at a target to the right for rightward motion, to the left for leftward motion, etc. The monkey is also trained to handle stimuli with different directions, speeds, and locations in the visual field. To study sensory processing, the random-dot stimulus is placed in the receptive field of a direction-selective neuron. To study decision-making, one of the targets that signals the

monkey's commitment to a particular choice is placed in a neuron's response field. **A**, In the variable-duration version of the task, the viewing time is a random value drawn from an exponential distribution with minimum and maximum times shown. The experimenter controls the duration of motion viewing. The monkey indicates his choice when the fixation point is extinguished. **B**, In the response-time (RT) version of the task, the monkey controls the viewing duration. Whenever ready, he makes an eye movement to one of the choice targets. The RT is the time from the onset of random-dot motion to the beginning of the eye movement.

Figure 2. Performance on the variable-duration version of the discrimination task depends on motion coherence and viewing time. Solid lines are best-fitting functions based on a model for the decision using signal detection theory. The best fits suggest that the internal signals are proportional to motion strength and viewing time. N=45,511 trials from 32 experiments using two monkeys. Reprinted with permission from Gold and Shadlen, 2003.

Figure 3. Accuracy and speed of decisions in the response-time version of the motion task. Data points are from two monkeys. **A**, Psychometric function depicting accuracy as a

function of motion strength. **B**, Chronometric function depicting response time as a function of motion strength. The solid curve in B is the fit of Equation 1 to the data. It describes the amount of time it would take accumulating evidence to reach a criterion level were it to diffuse like a particle in Brownian motion with average drift proportional to motion coherence (see Fig. 4). The sigmoid curve in A is the predicted psychometric function based on the model fit to the response-time data.

Figure 4. Diffusion-to-barrier as a model for decision-making. In 1-dimensional Brownian motion of a particle, random displacements are accumulated in a trajectory that stops at ±B. The displacements at each moment are drawn from a normal distribution (insert). Decisions about direction are based on an accumulation of evidence, which is the difference in spike rates from ensembles of direction selective neurons in the visual cortex.

Figure 5. A neural correlate of a decision process in the parietal cortex. **A**, The right hemisphere of the macaque brain. Experiments focus on neurons in the lateral intraparietal area (LIP), which lies on the lateral bank of the intraparietal sulcus. It receives input from direction-

selective neurons in area MT, along the superior temporal sulcus, and projects to structures involved in eye-movement control. **B**, Persistent activity from an LIP neuron recorded during memory-guided saccadic eye movements. Targets appeared in one of 8 locations arranged around a circle. The responses are aligned to the onset of the target that was flashed on and immediately off. The monkey made an eye movement to the remembered location of the target when the fixation point was extinguished (triangles). Rasters and peristimulus time histograms are arranged to illustrate the position of the target. The response histograms do not include activity after the initiation of the saccadic eye movement. The polar graph at the center of the figure shows the memory-period response as a function of target location. This neuron exhibited activity in the delay period before saccadic eye movements to the left. Adapted from Shadlen and Newsome, 2001. **C**, Time course of LIP activity in the RT version of the motion task. Traces are averaged responses from 54 LIP neurons. Responses are grouped by motion strength and choice as indicated by color and line type, respectively. The task is arranged so that one of the choice targets is in the neuron’s RF. The other target and the random dots are outside the RF, as indicated by the icons. On the left, responses are aligned to the onset of stimulus motion. Response averages in this portion of the graph show only activity accompanying motion viewing. They stop at the median RT for each motion strength and exclude any activity within 100 msec of eye movement initiation. On the right, responses are aligned to initiation of the eye-movement response. Response averages in this portion of the graph show the build up and decline in activity at the end of the decision process. They exclude any activity within 200 msec of motion onset. The average firing rate was smoothed using a 60 msec running mean. **D**, Time course of activity on trials with similar RT. Curves are population average responses for trials that end with an eye movement to the choice target in the RF. The responses are aligned to saccade initiation. Color designates the RT of the trials included in the average, which fall within 25 msec of the time indicated (e.g., 400-425 msec). All spikes are included in these averages (N=54 neurons). Average firing rate was smoothed using a 60 msec running mean. Panels C and D adapted from Roitman and Shadlen, 2002.

Figure 6. An evolving decision variable is represented in brain structures that prepare the motor response. Microstimulation of the frontal eye field (FEF, which is

located in the anterior bank of the arcuate sulcus; see Fig. 5A) evokes a stereotyped saccadic eye movement. When evoked at a random time during motion viewing, this eye movement reflects the evolving direction decision. **A**, The monkey performs the motion task as in Fig. 1A. The axis of the direction discrimination is aligned perpendicular to the direction of stimulation-evoked eye movements. On some trials, a brief train of stimulating current (50 msec of biphasic stimulation, 20-70 µA) evokes an eye movement. After ~100 ms, the monkey makes a second, voluntary eye movement to indicate its direction decision. **B**, Examples of eye movement trajectories. Fixation point is at the origin. The two larger circles are the choice targets. The random-dot stimulus (not shown) was centered on the fixation point. The symbols mark eye position in 2 ms steps. Stimulation during fixation, in the absence of motion and choice targets, elicited a rightward saccade (trace marked 'fix'). Stimulation while viewing upward and downward motion induced saccades that deviated in the direction of the subsequent, voluntary eye movements. **C**, The average amount of deviation depends on motion strength and viewing time. The amount of deviation toward the chosen target was estimated using the evoked saccades from 32 stimulation sites (14,972 trials). This result shows that the oculomotor system is privy to information about the evolving decision, not just the final outcome of the decision process. Adapted from Gold and Shadlen, 2001.

Figure 7. An example of a binding problem. A famous problem in visual perception concerns the ability to combine the elements of the representation of vision into appropriate groups – that is, to determine which elements are bound to a common object and which are not. To perceive this scene, the brain must combine information from small regions of the visual field (dashed ellipses) corresponding to the receptive fields of neurons in visual cortex. For example, the contours falling in the receptive fields *x* and *y* are bound to a common object. The contours falling in *y* and *z* are not bound despite their colinearity and shared color. The brain performs this task with little effort despite the large number of ways that information about surface order, border ownership, and other properties of the objects could be combined in principle. An intention-based architecture would tame this combinatorial explosion by restating the problem in terms of potential actions that could be performed, interrogating the visual cortex for evidence supporting hypotheses of the form: if the topmost arrowhead is moved, which other contours are likely to be displaced?

The answer is presumably based on the way the contours trace paths that support or oppose a hypothesis of continuity. The underlying mechanisms seem likely to be related to those that form the motion decision, because in both cases sensory evidence is assembled across space and time to support a particular action. Adapted from Shadlen and Movshon, 1999.

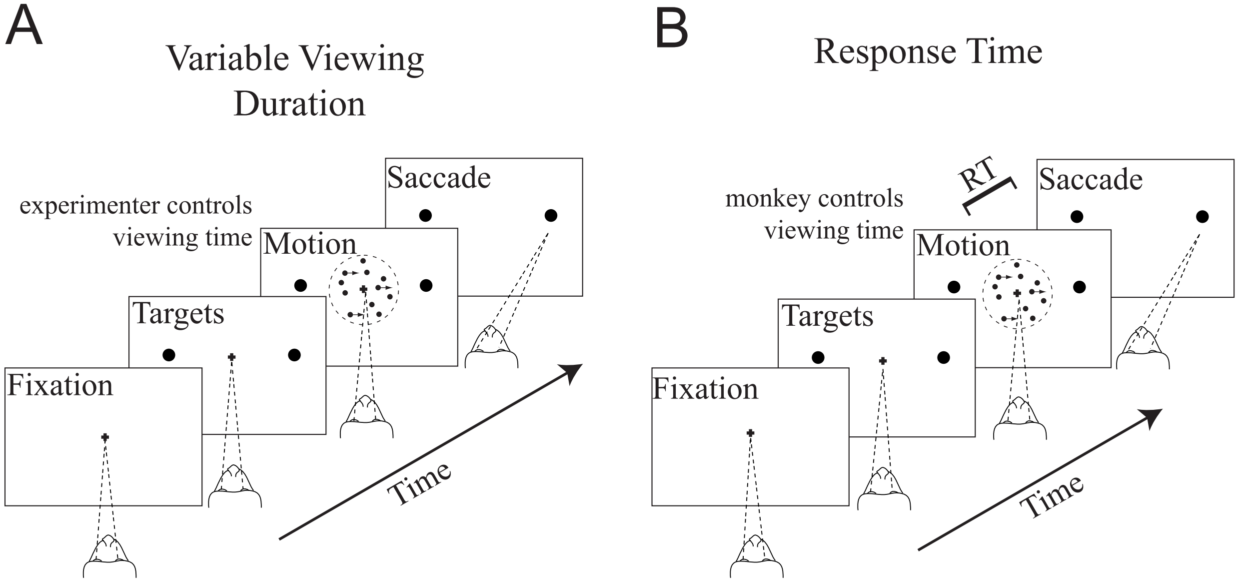


Figure 1
Shadlen & Gold

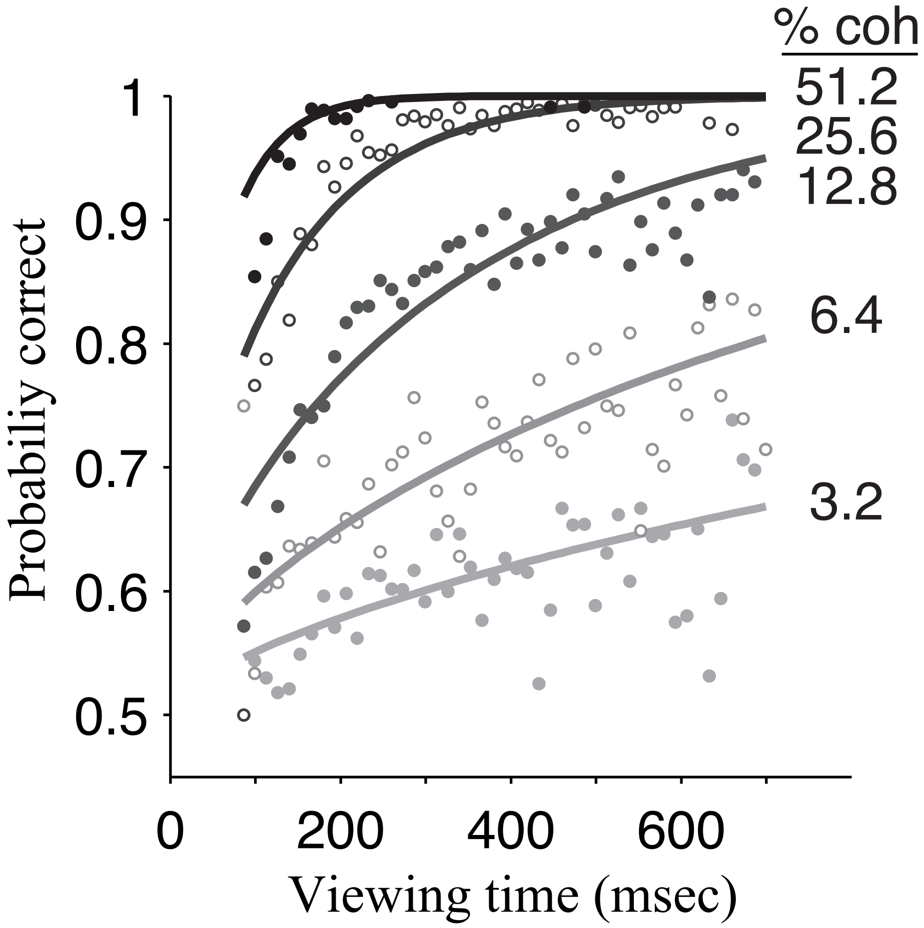


Figure 2 (black & white)
Shadlen & Gold
(see Fig2_color.pdf)

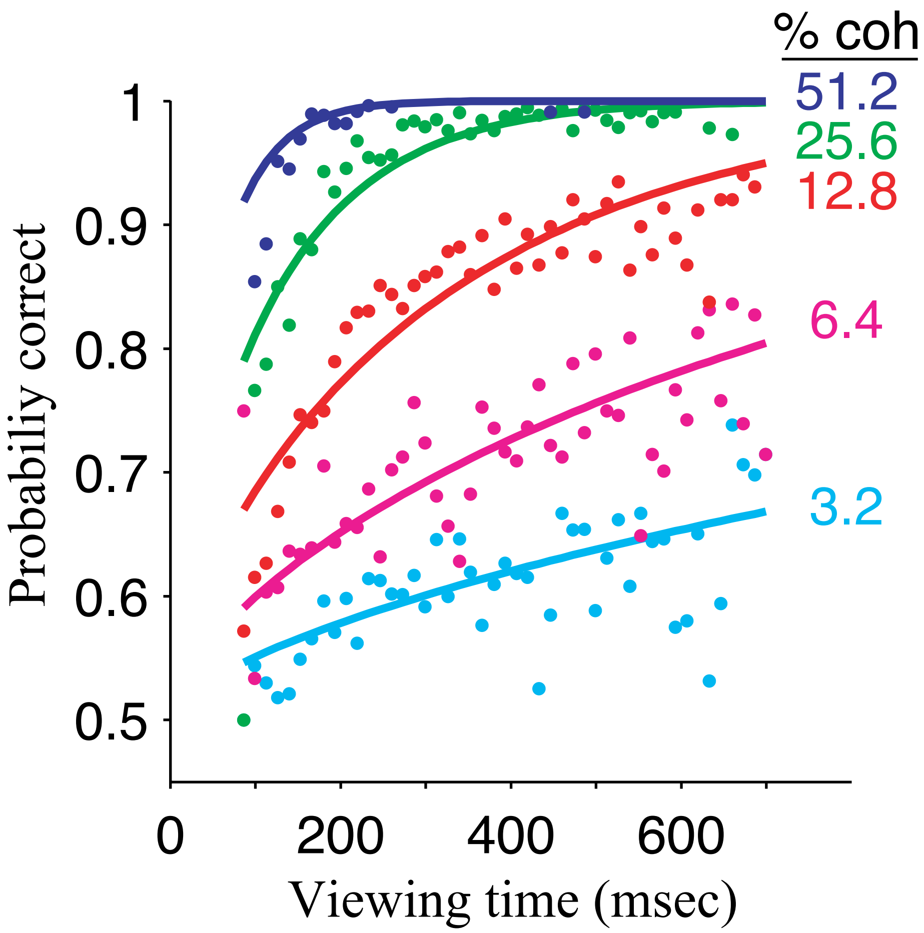


Figure 2 (color version)
Shadlen & Gold

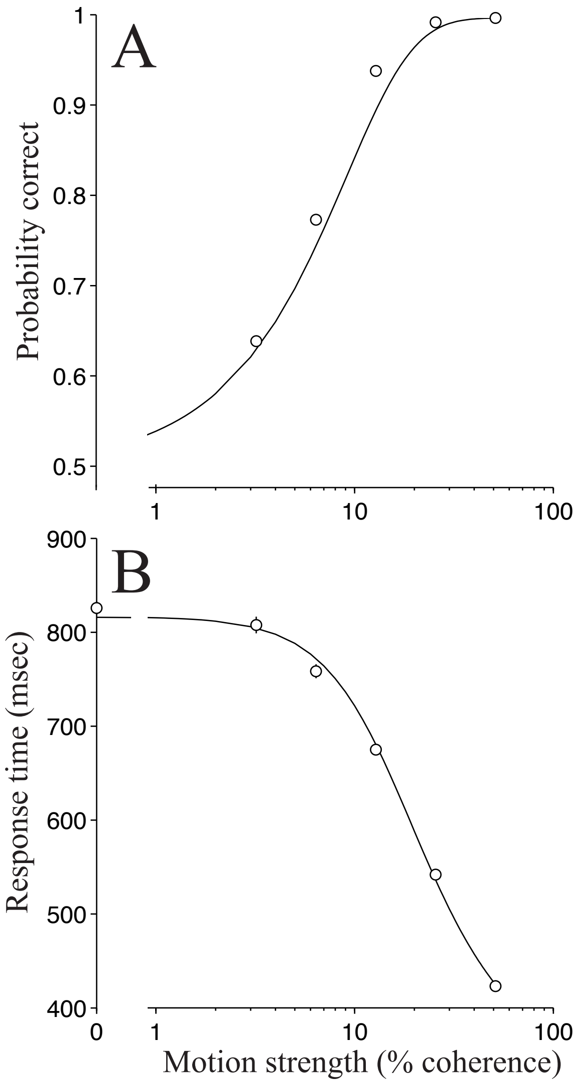


Figure 3
Shadlen & Gold

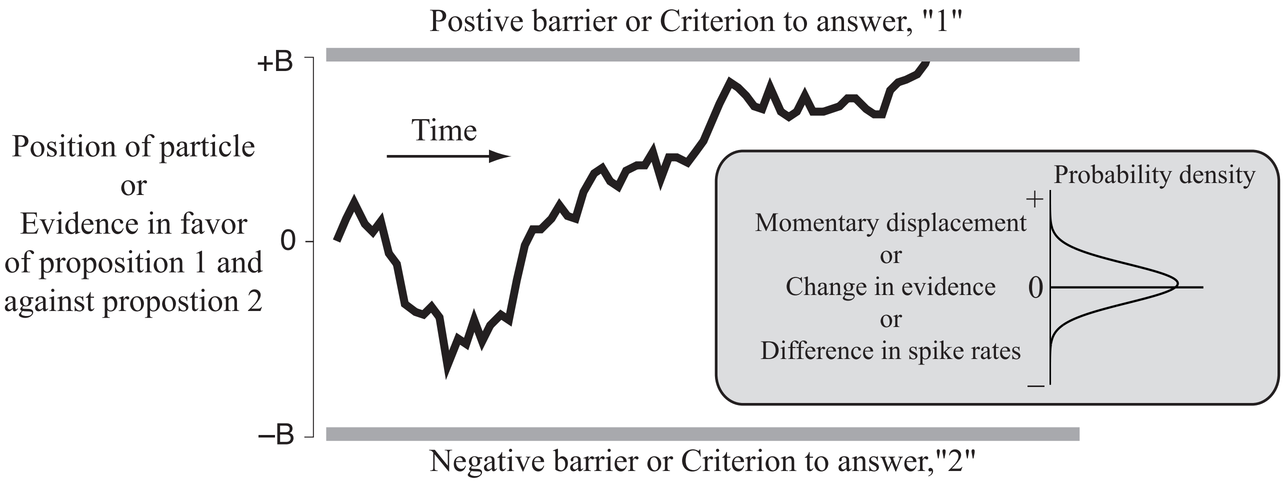


Figure 4
Shadlen & Gold

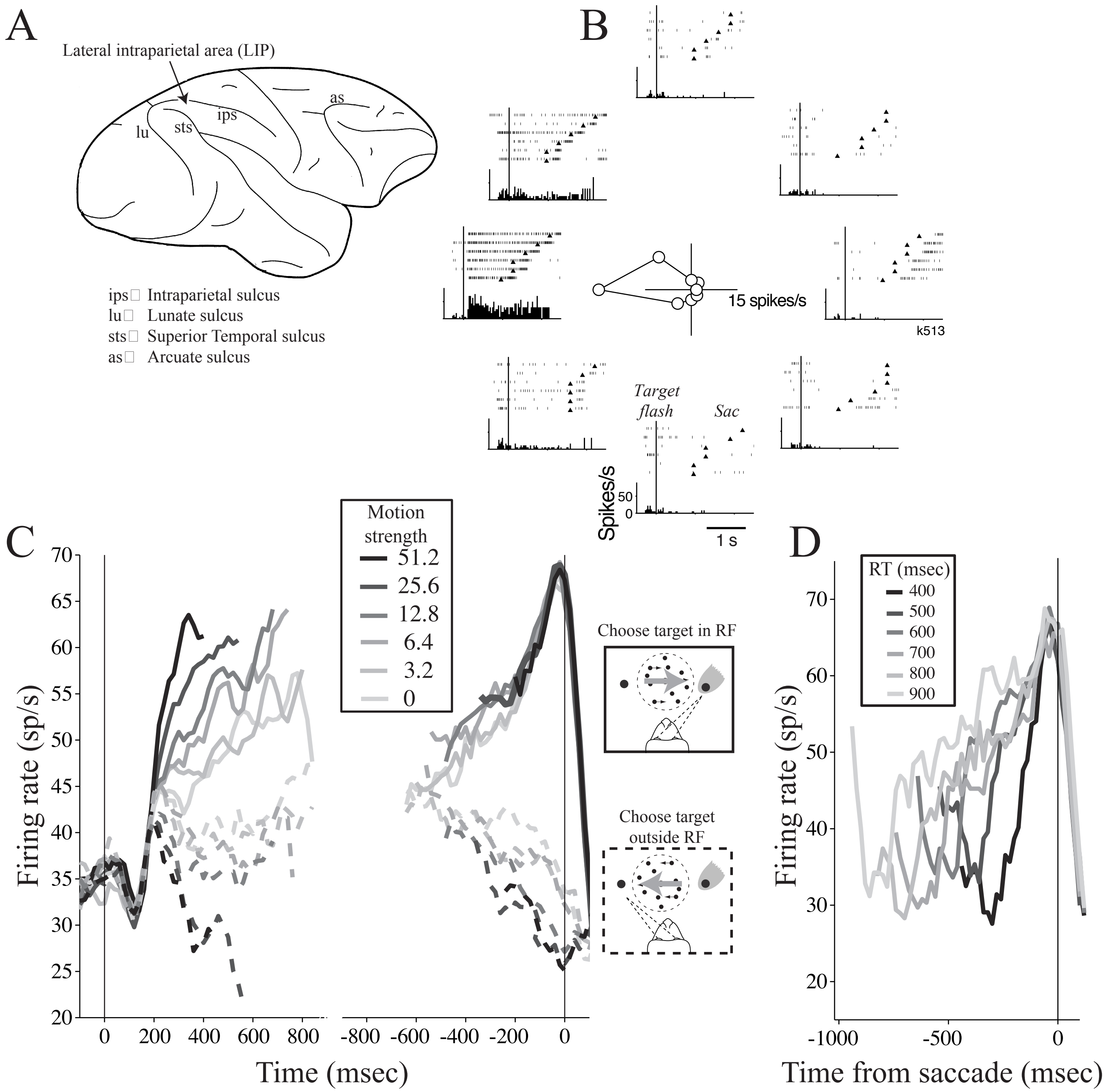
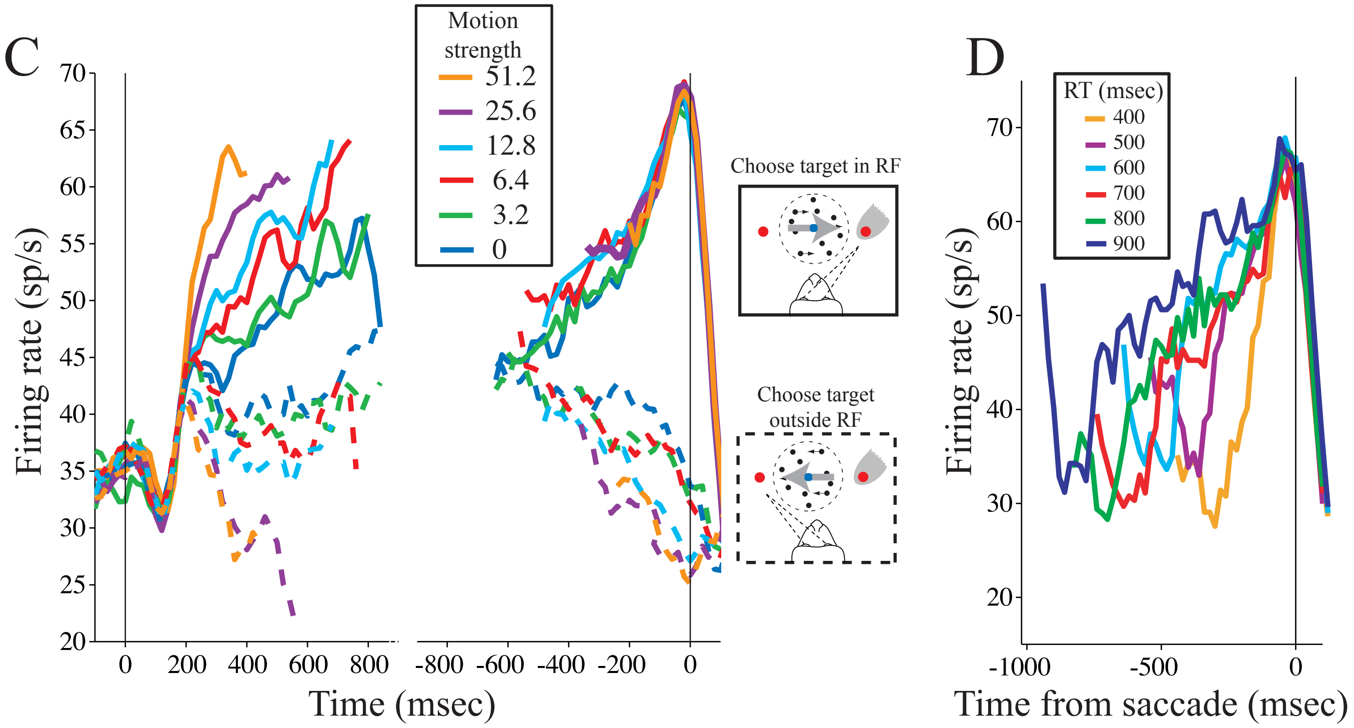


Figure 5 (black & white)
Shadlen & Gold
see Fig5_CD_color.ai



Figures 5C & 5D (with color)
Shadlen & Gold

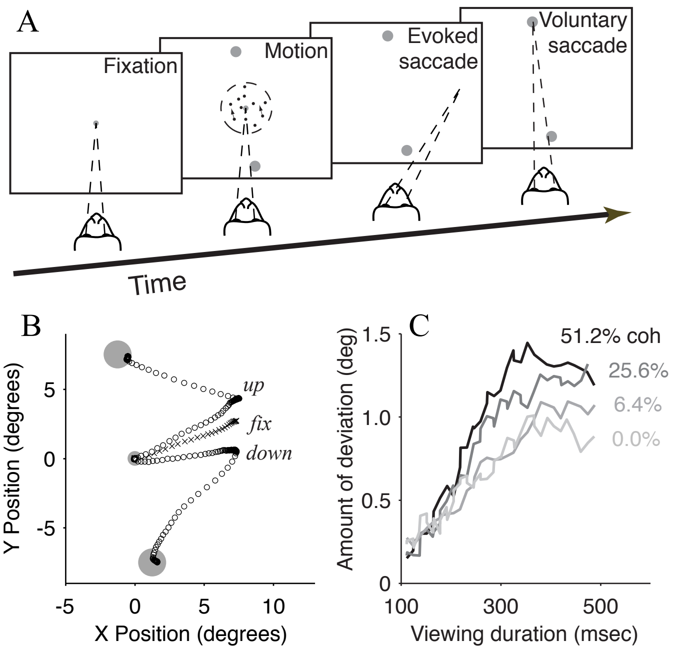


Figure 6
Shadlen & Gold

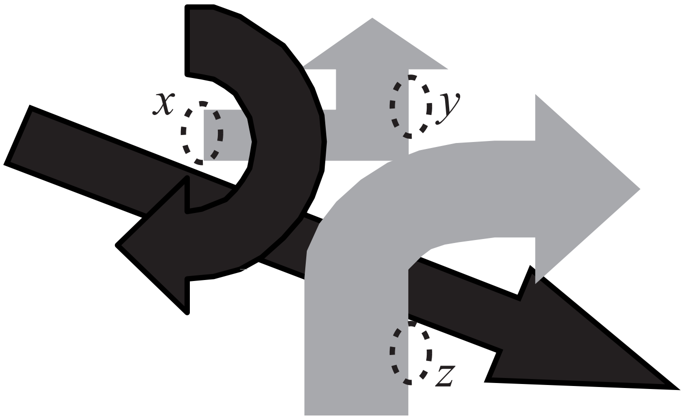


Figure 7
Shadlen & Gold