# Neurobiology of Decision Making

# An Intentional Framework

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#### Abstract

The aim of statistical decision theories is to understand how evidence, prior knowledge, and values lead an organism to commit to one of a number of alternatives. Two main statistical decision theories, signal detection theory and sequential analysis, assert that decision makers obtain evidence—often from the senses—that is corrupted by noise and weigh this evidence alongside bias and value to select the best choice. Signal detection theory has been the dominant conceptual framework for perceptual decisions near threshold. Sequential analysis extends this framework by incorporating time and introducing a rule for terminating the decision process. This extension allows the trade-off between decision speed and accuracy to be studied, and invites us to consider decision rules as policies on a stream of evidence acquired in time. In light of these theories, simple perceptual decisions, which can be studied in the neurophysiology laboratory, allow principles that apply to more complex decisions to be exposed.

The goal of this chapter is to "go beyond the data" to postulate a number of unifying principles of complex decisions based on our findings with simple decisions. We make speculative points and argue positions that should be viewed as controversial and provocative. In many places, a viewpoint will merely be sketched without going into much detail and without ample consideration of alternatives, except by way of contrast when necessary to make a point. The aim is not to convince but to pique interest.

The chapter is divided into two main sections. The first suggests that an intentionbased framework for decision making extends beyond simple perceptual decisions to a broad variety of more complex situations. The second, which is a logical extension of the first, poses a challenge to Bayesian inference as the dominant mathematical foundation of decision making.

# **A Common Framework**

Progress in understanding the neurobiology of decision making stems from simple experimental paradigms. Several pivotal studies (reviewed in Gold and Shadlen 2007) have emphasized tasks in which decision making reduces to a choice among actions. These studies have exploited the fact that when a decision bears on a particular act, the steps toward formation of the decision (i.e., the decision process) affect the neurons in the higher-level association areas of the brain that are identified with motor planning. Here, we suggest that the success of this enterprise is a consequence of a principle of brain organization, and we explore some of the extensions of these principles.

# **Intentional Organization**

Information flow in the brain is effectively channeled into structures that are organized in terms of behavior. To a visual neuroscientist, it might seem that the point of visual processing is to elaborate more complex features and scene properties, as well as to generalize over invariants for purposes of object classification and recognition. Although the initial stages of visual processing can be considered automatic and oriented toward extraction of features, we think it is mistaken to assume that the goal of visual processing is the automatic extraction of such features. Viewed from the perspective of decision making, information in the sensory cortex merely supplies evidence bearing on propositions. The way this evidence is organized-the transformation of information and the functional architecture in support of maps-facilitates and constrains the accessibility of this evidence. We would be mistaken, however, to identify the representation of the sensory data as giving rise directly to perception (He et al. 1996; Naccache et al. 2002; Jiang et al. 2006). Perception, like decision making, arises by asking and answering questions that bear on specific propositions. Importantly, evidence-gathering mechanisms are organized in the brain in association with structures that control the body. This constrains the possible meanings of information and connects the analysis of vision to embodied perception, affordances, and intentionality (Gibson 1950; Merleau-Ponty 1962; Churchland et al. 1994; Rizzolatti et al. 1997; Clark 1997; O'Regan and Noë 2001; Cisek 2007).

# Lessons from the Intraparietal Sulcus

Let us consider the organization of the posterior parietal lobe of the rhesus monkey.

*Sensory modality specific.* The posterior/lateral bank of the intraparietal sulcus seems to receive predominantly visual input. The regions anterior and medial to it receive somatosensory and proprioceptive input. The more anterior parts of the sulcus (toward the temporal lobe) appear to receive auditory input (Poremba et al. 2003). Based on connectivity with frontal structures and input from sensory structures, the emerging picture is a regional organization (cm scale) respecting sensory modality and an area organization (mm scale) respecting modes of motor function (Petrides and Pandya 1984; Cavada and Goldman-Rakic 1989; Lewis and Van Essen 2000a, b; Colby and Goldberg 1999).

*Gnosis versus praxis.* Neurologists recognize that loss of parietal function leads to a loss of appreciation for the significance of contralateral space. The frame of reference for the designation "contralateral" can be the visual field, body, or an external landmark such as an object. Importantly, it is the knowledge of space (gnosis), not the ability to move around in the space (praxis), that is affected, at least at a gross level (Critchley 1953).

At a finer level of resolution (e.g., millimeters), it is becoming clear that the areas comprising this part of the brain have more specific associations with motor regions. The lateral intraparietal area (LIP), for example, is connected to structures involved in moving the gaze and therefore probably also in shifting spatial attention. Neurons in this area seem to be concerned with places in space, especially when the place contains a potential target of an eye movement. The parietal reach region (PRR), which is only millimeters away from LIP, is connected to frontal lobe structures involved in reaching movements. Its neurons respond to places in extrapersonal space, especially when the place contains a potential target of a reach. The anterior intraparietal region (AIP) connects to frontal lobe structures that control the shape of the hand. Neurons in AIP respond to the shapes of objects. Although there is heterogeneity of neuron response preferences in each of these areas, there is an emerging support for the concept that these areas associate visual information with particular modes of utilizing that information (Anderson and Buneo 2002; Scherberger and Andersen 2007; Scherberger et al. 2003; cf. Levy et al. 2007).

The three parietal areas—LIP, PRR and AIP—are not motor in the traditional sense: their activity does not cause an immediate movement of a body part, nor do they encode movement parameters such as force, velocity, or tension. Instead, we think they allow us to know that something is present as well as an intended purpose. Their activity might be viewed as an interrogation or query of the evidence in the visual cortex. They effectively construe this information as evidence for (or against) embodied hypotheses and propositions—statements about what the body might do to its world. We refer to this as an "intentional architecture" for information flow. It does not provide answers to complex problems in perception (e.g., constancies, segmentation, binding of parts of objects into wholes) but it does tell us where in the brain we might look for neural correlates of these capacities, and it adds constraints to problems in perception that could pave the way to progress (e.g., Shadlen and Movshon 1999). We know far less about regions of the parietal lobe that receive predominantly auditory information (Poremba et al. 2003). It seems reasonable to predict that further research will expose the organization of the parietal lobe as being in the service of gathering specific forms of information (i.e., particular sensory submodalities) to guide potential action.

## Challenges and Extensions to Intentional Architecture

When a decision about a state of the world necessitates a particular action, it may not be surprising to some that a slightly elaborated sensorimotor integration area, like LIP, might represent the evolving decision variable. However, we should be surprised by this! After all, we do not feel as if we make decisions with our eye movements but instead make decisions about the stimulus and then communicate the outcome of the decision in whatever way we are instructed. We decide that motion is rightward, for example, and then communicate this by making an eye movement, pushing a button, or making a verbal response.

If decisions are made by neurons that are connected to specific action modalities, then there are at least three challenges: First, if a decision can be made by eye, hand, or verbal response, what prevents these systems from reaching different decisions? Second, the design seems wasteful: why not make the decision in some central spot and allow a "central executive" to deliver the answer to whatever motor modality is used to communicate the outcome? Third, how do we make a decision if the mode of response is not specified ahead of time?

Agreement is natural. In many instances, decisions are determined by the evidence from the environment or the noisy evidence in sensory maps. If different effector systems examine the same evidence, they will naturally reach the same conclusion. This statement rests on an assumption about the source of variability in the decision process, an assumption that is likely to hold when accuracy is valued. Recall that for difficult perceptual decisions, the variations in choice rendered from trial to trial are explained by considering the signal and noise affecting the decision. As long as the noise is in the stimulus or in the sensory representation, it will explain the choice. Therefore, even if several decision makers work in parallel, as long as they access the same evidence, they will reach the same decision. This is because both the signal and the noise that determine the outcome of a single decision can be traced to the sensory evidence. If eye, hand, and language access the same evidence, they reach the same conclusion, correct or incorrect.

This is actually a quantitative argument. It boils down to an analysis of the noise contributions in brain regions that represent momentary evidence and areas that represent the decision variable. When accuracy is a desired goal, evidence is allowed to accumulate before the decision is terminated with a choice. Consequently, the noise introduced by neurons that represent the decision

variable (e.g., neurons in LIP) does not contribute substantially to the error rate. In contrast, under speed stress, the decision terminates after very little averaging. In these circumstances, noise at the level of the decision makers can actually affect which choice is made. In that case it ought to be possible for different motor response modalities to reach different decisions, which, in the absence of further coordination among the response modalities, would result in incongruent responses. However, coordination of responses is feasible, and there is plenty of information in the decision outcome to provide a basis for it. For example, different modalities may reach their decisions at different times, and we might know that the first process to terminate could be an outlier and choose to delay until a few more systems weigh in.

One might argue that this parallel intentional architecture is inefficient. That may be true from the perspective of energy conservation, but it seems highly efficient to us from an evolutionary perspective. It allowed our brains to develop complex higher functions (contingency, deliberation) using a minor variation on a theme already developed for sensorimotor integration. No new wiring scheme was required!

In any case, our experiments tell us that when the action mode is known in advance, the high-level intentional structures represent partial information. If there were a central executive, it seems to pass on its deliberations to neurons concerned with motor planning while the decision evolves (Gold and Shadlen 2000, 2003; Spivey et al. 2005). Thus, it does not act as a central executive in that setting.

*Abstract decisions.* It is not difficult to understand how the intentional architecture can be extended to explain abstract decisions. In fact it helps to consider a simple case: a perceptual decision among two alternatives performed in a setting in which the action used to communicate the decision is not specified until after the decision is made.

Consider a monkey trained to decide between leftward and rightward motion of a random dot kinematogram. This is the same task as the one used to study neurons in LIP except for one important difference: there are no choice targets shown during the period of motion viewing. The monkey will ultimately communicate a choice by making an eye movement to a target, but it does not know where they will appear. When they do appear, one is red and the other is green. The monkey is trained to make an eye movement to the red target if the motion is rightward and to the green if it is leftward.

Monkeys can perform this task about as well as the version of the task described in our earlier work. When they do, it is clear that they have decided about right- or leftward direction and not which way they will make an eye movement. Indeed, on each trial, the monkey seems to embrace the proposition, "right" or "left." In this case, structures in the oculomotor pathways do not represent a decision variable. Instead, the brain seems to make the kind of abstract decision that does not involve intention. Or does it?

To picture this decision process, consider the accumulation of evidence toward a commitment to a plan, only here it is not a plan to make a particular eye movement but instead to select a red or a green target when they appear. We can think of the motion as instructing the implementation of a rule: when two targets appear, make an eye movement toward the red (or green) one. We have no trouble imagining neurons that accumulate evidence toward implementing this plan or rule, and we can imagine that this rule is enacted by selecting the appropriate circuits in the brain that allow a simple sensorimotor decision to ensue. Choose a target for an eye movement based on its color. This is just a decision to make a certain kind of decision.

*Functional and anatomical considerations.* Where would we expect to find such neurons? They should be in areas of the brain that project to the association areas. A reasonable candidate for the neurons in the red/green motion task are the parts of the dorsolateral prefrontal cortex (area 46) that project to area LIP (Cavada and Goldman-Rakic 1989). Neurons with the requisite properties have been found in this area, but experimental evidence is not all that compelling in our view. The problem with the experiments is that there is currently no way to sample neurons in A46 efficiently, based on their projection pattern to LIP (or other areas).

Although our hypothesis is not able to be tested at the present, there is some support for the idea that some A46 neurons carry on the kind of computations we have in mind. Wallis et al. (2001) described neurons in A46 that represent rules, and we have shown in one monkey that some neurons in A46 accumulate evidence for direction in this task (Gold and Shadlen 2001b). However, we view these studies with healthy skepticism because there is no obvious clustering of response patterns in A46 indicative of a functional architecture. Thus the reports (including ours) are based on a small fraction of randomly encountered neurons that happen to bear on the hypothesis. This concern about electrophysiology in A46 is not limited to the study of decision making.

Nonetheless, there are many parts of the association cortex in the nonhuman primate that map other association areas. They could achieve the computation we are proposing. The important conceptual point is that the computations underlying abstract decisions, which are not tied to specific actions, are probably similar formally to the computations we have studied in a simpler context: accumulation of information for a purpose and the representation of a plan to enact. In this case, the plan is to implement a rule.

*If-then logic.* Let us take this one step further. Consider that the plan of action is to enable a variety of circuits, not just one eye movement to red/green, but also several possible rules. This is then a means to establish a nested logical flow. It is a way for the brain to implement an if-then logic. Indeed, it does not seem improbable to consider that more areas that map the areas that select the sensorimotor circuits allow further nesting of this if-then logic. We are

only hinting at the variety of functions that this functional architecture could achieve. Our main point is that the intentional architecture studied in simple decision-making tasks is likely to share common features and principles with the brain architecture that gives rise to complex functions. Figure 4.1 illustrates this scheme. The 25 million years of evolution between macaque and humans has probably served to expand the cortical mantle in the service of this nested intentional architecture. This seems far more likely to have occurred than the evolution of brand new principles of neural computation.

#### **Value-based Decisions**

Our research on perceptual decisions has focused on the way the brain combines evidence across time as well as from multiple sources. We have also studied the effect of prior probability in these tasks and see a clear connection (in our human studies) with asymmetric reward schedules, which should also promote a bias. These studies emphasize decisions that are based primarily on the evidence. Value-based decisions, on the other hand, emphasize the component of decision making that is predicated on weighting alternatives based on expected utility. These are often the types of decisions that mimic foraging for food.

It is not controversial to assert that, at the level of formalisms, evidenceand value-based decisions are fundamentally similar. Just about any theory of decision making posits that the decision variable or the criterion to which it is subjected is affected by values placed on the choices and their probable outcomes. How similar is the neurobiology in these cases? We argue that it is likely to be very similar. This is controversial for two reasons. First, the kinds of quantities that are involved in value-based decisions are poorly understood and seem to be quite different from the kind of information that is represented in the visual cortex. Second, the patterns of behavior observed in value-based decisions are thought by many to require a stage of strategic (i.e., deliberate) randomness in the decision-making process. We believe that this is incorrect and perhaps misguided.

# Quantities in Value-based Decisions

All decisions are ultimately decisions about value. In evidence-based decisions, the value is in being correct. As such, value is implicitly represented in the decision variable (DV) and the criterion that is applied to it. In this way, the quantities that underlie the decision itself are similar in the two situations. What differ are the sources of signals that inform those quantities.

The representation of value and its association with places, features, foods, etc. seems to be conveyed by dedicated structures. Evidence from several groups point to the orbitofrontal cortex (OFC). A recent study from Padoa-Schioppa and Assad (2006) asserts that the value or utility of a potentially









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rewarding experience is represented in units that would combine naturally with evidence: the firing rate encodes a quantity that contributes linearly to choice preference in units of log odds (see also Deaner et al. 2005; Gold and Shadlen 2001a). Thus the basic framework for making decisions is likely to be preserved. On the other hand, elucidation of mechanism will force us to study processes in brain regions like the OFC, anterior cingulate cortex, amygdala, and striatum, which presumably represent valence and establish termination rules (McCoy and Platt 2005; McCoy et al. 2003; Paton et al. 2006; Lo and Wang 2006; Kawagoe et al. 2004; Watanabe et al. 2003; Tremblay and Schultz 1999; Hikosaka and Watanabe 2000; Montague and Berns 2002).

We note one final point, which is also relevant to the following section: The kinds of quantities that contribute to the DV (and criteria for terminating) are not limited to evidence, priors, and value of reward or punishment. They also include premiums and penalties for taking time, for exploration, or for persisting. How a premium for exploration is calibrated against evidence is an open question, but it is likely to be no more mysterious than the standard mix of ingredients in decisions. In the end, all quantities in the DV add in units of a common currency, namely spike rate.

## Randomness (of Choice) Arises from Noise Not Strategy

The conversion from DV to the expression of choice is commonly treated differently for evidence- and value-based decisions. Here, however, is a peculiar distinction, which we think is incorrect: less than perfect performance is attributed to noise in evidence-based decisions but to probabilistic behavioral response in value-based decisions. Consider a binary decision between options A and B. In both evidence- and value-based decisions, a DV summarizes the merits of A relative to B. For one type of decision, the DV is based mainly on evidence; for the other it is based primarily on utilities. We have already pointed out that a single framework (and a common neurobiology) can accommodate both DVs. The DV has some relationship with probability.

Both evidence- and value-based decisions appear to be stochastic from the point of view of the experimentalist. The sigmoid curve in Figure 4.2 could describe the probability that a monkey chooses rightward as a function of the strength of motion evidence to the right, or it could describe the probability of choosing the red location based on the experienced value of this choice as inferred from recent history of food collection. Neither behavior appears stochastic for extreme values of the *x*-variable. Near the middle of the graph, however, the responses are distributed probabilistically. Indeed a sequence of answers—especially from a practiced and highly motivated subject—appears nearly indistinguishable from the sequence of heads and tails produced by a weighted coin. Current theories of evidence- and value-based decisions diverge in their accounts of the neurobiological mechanism underlying this phenomenon.



**Figure 4.2** Choice function. The support might be evidence for choice "A" or an expected value that is associated with "A."

For value-based decisions, the brain represents a quantity related to relative utility of one of the choices. It is assumed that this value is explicitly converted to a probability, which then governs a process that is formally identical to flipping a coin (Figure 4.3). The specific mathematical operations are not important to the argument here, save for one: there is a conversion of a number (or vector) to a probability. For two choices this is like inverting a logistic to a parameter p (and 1-p), which is realized as a random event (a so-called Bernoulli trial). For more than two choices, the idea naturally extends to inversion of a vector to a multinomial parameter  $p_1, p_2, ..., p_n$ , also realized as a random event. Thus, even when the relative utility of one choice is registered by the brain as the better choice, it is not always selected. Contrast this to the following.

For evidence-based decisions, the DV represents a quantity related to the likelihood that one proposition is true. Rather than converting this to a probability, the brain simply makes the best choice it can. Again, the details of the computation are not important. If the quantity is proportional to the log likelihood ratio, then zero marks the criterion at which evidence favors one or the other choice. However, any quantity that is monotonically related to relative likelihood will do, as long as it is accompanied by the appropriate criterion. The randomness to the behavior results because the DV is noisy. This is consistent with all accounts of neurophysiology, especially in the regime in which decisions are difficult; that is, a weak rightward stimulus gives rise to a representation of evidence that is noisy. Although a perfect transducer would always favor a right- over leftward direction, the fact is that on some fraction of trials, the brain represents a value with the wrong sign relative to the criterion.

Contrast the two ideas: in value-based decisions, the brain knows what the better option is but behaves randomly, depending on how much better. In evidence-based decisions, the brain makes the best choice it can, based on the available evidence, which may be faulty. Is this distinction artificial or real?



**Figure 4.3** Components of simple decisions. (a) Flow used to explain perceptual- and evidence-based decisions. A decision variable is established from the evidence. A criterion is applied to achieve the best choice. The notion of "best" incorporates valuation, which is commonly incorporated in the criterion. (b) Flow used to explain value-based decisions. The choice is a realization of a random event (coin flip) to match a probability. We are critical of this concept.

We propose that such a distinction does not exist in the brain. The representation of a DV is noisy, whether it is constructed from sensory evidence or from knowledge of reward values. This is a fact of neurobiology (Softky and Koch 1993; Shadlen and Newsome 1994, 1998). This noise underlies the apparent randomness of choices in both evidence- and value-based decisions. Thus the neurobiology of these two types of decision is similar, and the seemingly stochastic behavioral response in neither of them is due to an explicit random number generator in the brain. In addition to the noise in the DV, there are other sources that contribute to the variability of behavioral responses. For instance, the subject often tries to reach a balance between exploitation of the existing knowledge and exploration of new possibilities. Exploration is more prominent in value-based decisions when the reward values can change (e.g., Sugrue et al. 2004). A tendency to explore the environment should not be mistaken with a deliberate randomization of behavior; it should just remind us of the complexity of the decision process. The DV can incorporate the anticipated costs and dividends associated with exploration and persistence. The random number generator in Figure 4.2 should be regarded as a mathematical convenience, rather than a neurally motivated computational principle, to lump multiple sources of variability together. Indeed, it spells out the wrong principle.

What led to the idea of a random stage in value-based decisions? The main reason was an absence of noise in psychological theories. Signal/noise relations have a long tradition in sensory physiology (Hecht and Mintz 1939; Barlow et al. 1971; Parker and Newsome 1998) and in psychophysics (Green and Swets 1966; Cohn et al. 1975; Tanner 1961; Thurstone 1959; Link 1992), but they are generally absent from psychological theories of choice (Luce 1959; Herrnstein 1961; Herrnstein and Vaughan 1980; Kahneman 2002, but see Manski 1977).

Absent noise, some sort of random number generator seems to be required. Enthusiasm for inclusion of a random number generator in the mechanism of value-based decisions is also partly rooted in game theory (Dorris and Glimcher 2004; Glimcher 2003, 2005; Lee et al. 2004; Lee et al. 2005; Barraclough et al. 2004). The optimal strategy in competitive games often necessitates random behavior to stop an intelligent opponent from exploiting predictable patterns in one's own behavior. However, such omniscient opponents are rarely present in real-life situations. In fact, the behavior of subjects in value-based decisions can often be successfully characterized by the history of subject's decisions and payoffs even for competitive games (Lee et al. 2005; Barraclough et al. 2004; Corrado et al. 2005; Lau and Glimcher 2005). We argue that in these successful behavioral models the random number generator can be replaced by noisiness in the representation of evidence and value via a DV.

#### **Summary of Generalized Intentional Framework**

The intentional framework that we have characterized extends to a broad variety of decision-making situations using a cascade of the basic machinery that has been uncovered through studies of simpler decisions. In simple perceptual decisions, sensory neurons provide evidence about the current status of the external environment. This evidence is accumulated into a DV in structures that are associated with particular plans of action which would instantiate the outcome of the decision, should it come out one way or another (gray-shaded region of Figure 4.1). Such instantiation might be an immediate behavior, enactment of a behavioral rule (e.g., if-then logic), or more generally, activation of a specific neural circuit. The DV also incorporates information about prior probability, value, temporal costs, and any other factors that bear on the decision. The underlying machinery of this is simply a race model where the process that reaches the bound first results in the implementation of the corresponding decision outcome. There can be as many processes as necessary to underlie the possible decision outcomes. Furthermore, there can be cascades of decisions, where the outcome of one determines the nature of a subsequent deliberation through the appropriate circuit activation.

The basic building blocks of a decision establish a functional architecture, which in turn hints at the critical neurobiology. As shown in Figure 4.1, there must be accumulators: neurons whose rate of discharge depends on the history of the moment-by-moment fluctuations in the evidence furnished by sensory neurons. Many of the cells that demonstrate persistent activity, which is thought to play a role in working memory, motor planning, representation of context, etc., may also be capable of acting as accumulators. Such cells are ubiquitous in the association cortex.

To establish a termination rule or bound, there must be neurons that can sense a level crossing in the accumulators. These neurons can use temporal and reward-related information to set and implement the appropriate level. This is

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presumably achieved by the basal ganglia, perhaps in concert with its targets, the substantia nigra pars reticulata, the thalamus, and their targets (ultimately the neocortex). Other structures that represent value are also likely to participate (e.g., ventral tegmentum, nucleus accumbens, amygdala, OFC).

The decision ends in a signal that stimulates another structure into action. In the case of simple real-time RT tasks, this might be neurons that generate movements of body parts; in other cases it might be a structure that activates another decision (Figure 4.1c). Further, we think that at least two other signals must accompany the declaration of the decision outcome. There must be some degree of confidence associated with the content and some prediction of the expected time that the decision should lead to an action, anticipated outcome, reward, or punishment. Little is known about the neurobiological correlates of these putative signals. We will not discuss the anticipated time signal except to say that it seems essential for a variety of functions, including learning. The "confidence" signal might also play a role in learning, but as discussed in the next section, it seems essential to negotiate between competing decisions or to interpolate rationally when the outcome from separate decision processes must be combined.

# **Decision Making Is Not Bayesian Inference**

The relationship between Bayesian inference and decision making has held center stage in theorizing about the neural mechanisms for choice behavior. We question the wisdom of this paradigm. In particular, we focus on an important distinction between the Bayesian approach and what we term "decision as intention." The idea stems from the intentional architecture concept discussed above. That architecture suggests that decisions are not made in the abstract about states of the world but instead guide a choice among a discrete set of possible behaviors.

It may be sensible to preface the argument with a short list of caveats. Our argument is not anti-Bayesian. Indeed it endorses many of the key components of Bayesian decision making, as will be clear. It is not concerned with the nature of probability; it is not an embrace of the frequentist school of probability theory. It is instead a critique of the notion that posterior probability distributions are calculated explicitly, represented and used to guide decisions.

#### The Bayesian Paradigm: "Decision As Inference"

Any sensible formulation of the problem of decision making must consider at least three main factors: (a) evidence pertaining to choices, (b) prior knowledge about states of the world, and (c) costs and rewards associated with the decision. The Bayesian paradigm assumes that the brain represents a posterior probability distribution over the possible states of the world. Decisions, actions, estimates, and confidence ratings all stem from this posterior.

Within this framework, decisions among discrete hypotheses are regarded as a special case of inference. In the context of decision making, the posterior is used to forecast expected cost and benefit associated with the consequences of each choice. The latter calculation can take a variety of forms, which incorporate different assumptions about utility, but all involve evaluation in light of the probable states of the world as represented by the posterior. For simple decisions among *N* alternatives, "decision as inference" postulates that decisions arise by placing criteria on the quantities calculated from posteriors.

The key to the Bayesian paradigm is that the posterior is used to achieve the projected prediction of utility. It is an independent entity, which can be used for a variety of purposes. We do not question the merit of this perspective in general, but we do question its direct application to the neurobiology of decision making; that is, whether the brain actually represents posterior probability distributions.

# A Critique of the Data in Support of the Representation of Posterior Probabilities

The main experimental evidence in support of the explicit representation of posterior probability distributions involves integration of evidence from diverse sources. These are behavioral studies in perception and motor control (Ernst and Banks 2002; Rosas et al. 2005; Mamassian and Landy 2001; Landy et al. 1995; Trommershauser et al. 2005; Yuille and Bulthoff 1996; Knill and Saunders 2003; Kording and Wolpert 2004a; Brainard and Freeman 1997; van Ee et al. 2003; Kersten 1999; Kersten and Yuille 2003; Kersten et al. 2004). For example, when a subject is asked to judge the angle  $\alpha$  of an object in space based on disparity and texture cues (i.e., binocular depth and perspective), the judgments reflect information from both sources, weighted in accordance with the relative reliability of the two sources. To achieve this, the brain must keep track of at least two numbers per cue: an estimate bearing in the decision and the degree of uncertainty/reliability.

The brain can achieve this in a number of ways. Clearly, if the brain represents two posterior probability distributions over possible angles,

$$P(\alpha | e_{disparity}) \text{ and } P(\alpha | e_{texture}),$$
 (1)

it can combine these distributions to obtain

$$P(\alpha | \boldsymbol{e}_{disparity}, \boldsymbol{e}_{texture}).$$
<sup>(2)</sup>

This is not necessarily as simple as multiplying the distributions, as will be discussed below (see section, "Conditional Dependencies Render Bayesian

Inference Impractical"). That is the Bayesian approach. A simpler idea is to use each source as a decision maker. Rather than combining probabilities over all possible values of angle, the brain makes two choices based on disparity and texture, respectively, and takes a weighted average based on the level of uncertainty, reliability, or confidence. Different weighting schemes translate into different valuations on error (see Kording and Wolpert 2004b). Thus, it is broadly consistent with Bayesian decision making. However, the approach is less versatile than the full representation of posterior probability distributions. We do not know how the brain actually solves a cue combination task such as the one described. Our point is simply that it need not represent posterior probability distributions explicitly to do so.

We are unaware of an experimental result that would necessitate a representation of posterior probability distributions over a simpler shortcut like combining estimates in accordance with their uncertainties. Also we do not know how the brain estimates uncertainty, reliability, and confidence. Some insights are forthcoming, however, from experiments that test the mechanism underlying the combination of evidence with prior probability in simple two-choice decisions (Shadlen et al. 2006b).

#### **Decision Making from Decision Variables, Not Posteriors**

Decisions are made by placing a criterion on a DV, which is a quantity that is calculated from diverse ingredients: evidence, priors, costs. At face value, this statement is compatible with decision making as Bayesian inference. Indeed, everything we are about to say about DVs can be translated to quantities that we could calculate in the Bayesian framework. Nonetheless, biology need not calculate the DV by an algorithm that adheres to a particular set of operations even if, in some cases, there is functional equivalence with the results produced by these operations. In particular, our experiments lead us to suspect that the brain does not represent posteriors explicitly.

We focus on three observations that arise in the study of decisions based on the sequential sampling of evidence: (a) the nature and necessity of a termination rule; (b) constraints imposed on the decision process by a finite set of choices; and (c) the simplification of conditional dependencies. All three may be viewed as heuristics that arise naturally in the framework of sequential sampling of evidence.

#### In a Decision Variable, Probability Is Not Dissociated from Other Terms

In most circumstances, decisions are not based on all the available evidence but instead incorporate a termination rule, thereby deciding based on some *quantum satis* of belief. This is beneficial when there is value associated with saving time or when there is cost associated with gathering evidence. Indeed these are the situations we face in almost all circumstances, for instance, to move from one decision to the next. By controlling the time spent on each decision, we can maximize reward per unit time. In these settings, a decision rule must specify the mapping of DV to choice, and a stopping rule must determine when to terminate the process. In some cases, the stopping rule and the decision rule operate on the same DV. The DV, or a race among several DVs, mediates both the outcome of the process (i.e., the choice) and the time that the process terminates.

The class of bounded accumulator models (Figure 4.1b) has been applied to a variety of decisions in perception, cognition, cryptography, quality control, and economics (Link 1992; Wald 1947; Smith and Ratcliff 2004; Ratcliff and Rouder 1998, 2000; Good 1979; Karlin and Taylor 1975). It has roots in optimality theory and is deeply connected to Bayesian inference (Wald and Wolfowitz 1947; Jaynes 2003; Bogacz et al. 2003; McMillen and Holmes 2006; Ma et al. 2006). In our studies of perceptual decisions using random dot motion, bounded accumulation explains the speed and accuracy of choice in human and nonhuman primate subjects. There is considerable experimental support for the computations: accumulation of noisy evidence and a termination bound in the responses of neurons in parietal cortex and elsewhere (for reviews, see Gold and Shadlen 2007; Shadlen et al. 2006a).

The simplest version of bounded accumulation is Wald's sequential probability ratio test (SPRT) (Wald 1947; Wald and Wolfowitz 1947). We will explain its connection to Bayesian decision making and use it to highlight the ways that the neural mechanisms depart from the Bayesian ideal. In SPRT, there are just two choices among states,  $s_1$  and  $s_2$ . As each piece of evidence  $e_i$ arrives, it is converted to a log likelihood ratio (logLR),

$$\log\left[p\left(e_{i}\left|s_{1}\right)\right/p\left(e_{i}\left|s_{2}\right)\right],\tag{3}$$

and added to the accumulation. The process stops when the accumulated logLR reaches a predefined positive or negative bound. The process is Bayesian in the sense that we are using this term: the posterior probability is explicitly represented in the DV. The bounds are the log of the posterior odds,

$$\log\left[p\left(s_1 \mid e_1, \dots, e_n\right) \middle/ p\left(s_2 \mid e_1, \dots, e_n\right)\right],\tag{4}$$

and the same holds for the partial sums (e.g., the first *m* samples of evidence). In this simple case, the DV, the stopped DV and the termination rule would all satisfy the desire for an explicit representation of posterior probabilities. For example, if there were two sources of evidence bearing on the decision, we could combine estimates from the two terminated processes by adding log posterior odds, determined by their respective stopping rules. The SPRT can incorporate priors and loss functions without compromising this feature.

More commonly, however, a termination rule tends to render the posterior probability far less accessible, even for a simple binary choice. The main reason for this is that there is often missing information, which precludes the conversion of evidence to units of logLR. The motion discrimination task is an example. Consider a decision between  $s_1 = up$  and  $s_2 = down$ . Assume the evidence to the decision maker is a sample of a difference in firing rates from two populations of neurons: one responds more when motion is upward whereas the other responds more when motion is downward. A single piece of momentary evidence,  $e_i$ , is the difference in the two spike rates (upward minus downward) measured in some brief epoch  $\Delta t$ . Positive values of this difference favor upward. These assumptions are supported by experimental findings (Ditterich et al. 2003; Huk and Shadlen 2005).

To carry out SPRT, we would convert the  $e_i$  to logLR based on our knowledge of the two sampling distributions, the probability of observing the possible values of  $e_i$  under  $s_1$  and  $s_2$ , and therein lies the problem. Even in this simple experiment, we cannot do this because of one additional detail: there are a variety of stimulus strengths. For each decision, not only is the direction of motion randomized, so too is the intensity of the motion (i.e., the percentage of random dots that move coherently from one video frame to the next). Therefore, the sampling distributions depend on this motion strength.

For example, when motion is weak, a small positive difference, say e = 1 sp/s, often occurs for either direction of motion. It is only slightly more likely when motion is upward. Therefore, the logLR for up is only slightly larger than 0: weak evidence for upward motion. In contrast, when the motion is strong, the same e=1 sp/s constitutes strong evidence. Consider, when motion is strongly downward, it would be a rare occurrence for the upward preferring neurons to respond more strongly than the downward preferring neurons. Therefore, the logLR for upward is a value much larger than 0. To make the conversion from evidence to logLR, the brain would need to know the motion strength. However, it does not know this at the beginning of the trial. This example illustrates why SPRT cannot be properly implemented. In a task with stimuli of varying difficulty, there is no unique relationship between evidence and logLR. Thus, there is no proper way to implement SPRT.

For the purpose of making a decision about direction, the motion strength is a nuisance parameter. From the perspective of Bayesian inference, one would like to marginalize out this variable. This proves to be difficult in general and imprudent in this case (and many like it). Impracticality results from the requirement of solving integrals, a problem that is well known to Bayesians but not the crux of our argument. We wish to emphasize a different point that arises in the context of sequential sampling. For this experiment, the nuisance parameter remains fixed for all samples until a decision is made. The brain cannot know the value of the motion strength at the beginning of viewing, but it can exploit the fact that it is the same for all samples of evidence.

There are two points. First and most germane to the argument here, it would be unwise to marginalize motion strength to its expectation over all possible stimuli. That would only make sense if each sample of evidence were drawn from the larger pool of all possible motions strengths at each time step  $\Delta t$ . This, however, is not the case: until a decision is completed, the evidence is drawn from a particular source associated with just one motion strength. Second, the assumption of a stationary nuisance parameter over the time course of the decision—in this case justified, but a heuristic more generally—can be exploited. For example, as time passes, if the decision has not terminated, it is probably because the motion strength is low. The brain appears to exploit this knowledge (Shadlen et al. 2006b). In theory, it is possible to develop a Bayesian inference framework that exploits the information about the passage of time, but it would be extremely cumbersome (e.g., involving elapsed time in the conversion of firing rates to probability).

Whenever different stimulus strengths are possible, the termination bound no longer represents the log of the posterior odds. It does so only in a convoluted sense. It is the log of the posterior odds of a correct choice at each of the motion strengths. As shown in Figure 4.2, the subject typically answers correctly when motion is stronger. Thus the bound does not have a unique mapping to log posterior odds. Instead, the stopping rule is to terminate when the DV—the accumulated firing rate difference—reaches a critical level. This is what the physiology indicates, and it explains with a single rule both the reaction times and the error rates in the motion experiments. This success comes at a cost, however. In contrast with Bayesian inference, there is no explicit representation of posterior probability.

#### Value and Utility Are Time Dependent

How do we interpret the stopping rule? If the DV does not represent posterior probability, then the bound is not a level of posterior probability. Nonetheless, there is an insight from SPRT that might be exploited. Assuming that the nuisance parameter(s) are fixed for a trial (by which we mean a decision on a stream of evidence), then at least in principle, one could apply SPRT. That means that any bound is a log posterior odds. What is missing is the magnitude of the setting. Again, we do not know the value of the bound in units of log posterior odds, because we do not know the nuisance parameters. However, we can adjust it to achieve a desired policy (e.g., maximum utility per unit time).

In some instances, like the random dot motion task, elapsed time conveys information about the nuisance parameters. In general, as time elapses, it is increasingly likely that the stimulus is low coherence. Indeed there are probably many instances in which less reliable evidence leads to slower accumulation toward a decision bound (a counterexample is when unreliability is caused by a change in variance rather than signal strength). If this is known (or assumed), then whatever the value of bound was in units log posterior odds at early times, it is worth less as time passes. It follows that the representation of expected value (or utility) is time dependent.

We have tested this idea directly in experiments in which the prior probability of up or down is manipulated in a block of trials. Briefly, a fixed prior is incorporated in the DV dynamically as elapsed time effectively discounts the posterior that would be represented by the terminated DV (Shadlen et al. 2006b). This heuristic is likely to be both useful and appropriate when there is reason to believe that the nuisance parameters are stationary over the time spanned by a single decision.

The important point is that a terminated DV lacks a unique, straightforward mapping to a posterior. We have illustrated this using binary decisions with nuisance parameters—aspects of the sources of evidence that affect the conversion to logLR. The problem is likely to be worse with more than two choices because a multidimensional SPRT is not uniquely specified (see McMillen and Holmes 2006; Bogacz et al. 2006). Thus the main feature of Bayesian inference, the posterior probability, is absent. It can be approximated with knowledge of nuisance parameters and/or elapsed time, but it is not represented explicitly nor is it accessible.

# The Constraint on the Choice Space Is Not Trivial

The argument in this section is a natural extension of the "intentional architecture" introduced earlier in this chapter. When we process information in general, but especially in the context of making a decision, we construe it as evidence that bears on a set of competing hypotheses. At first glance, this statement seems perfectly compatible with decision making as Bayesian inference. However, the neurobiology suggests that the framework tends to dissipate any meaningful notion of a posterior probability distribution. In the end, this is because the neural architecture is concerned with a limited choice space; that is, the repertoire of possible actions, intentions, and "decisions about decisions."

Placing criteria on posteriors (or their transformed functions of expected value and utility) only approximates a decision process in which termination rules apply. To illustrate the concept with a simple case, consider the decision of whether direction of motion,  $\theta$ , is to the left or right. The Bayesian inference approach is to represent the posterior  $P(\theta \mid observations)$  and to simply choose left or right based on which is more likely (or to satisfy some other loss function besides accuracy). The question we raise here is how knowledge of the space of possible choices affects the decision process.

*Placing priors on the possible states is an appealing approach, but it too has limitations.* Here we start with the prior that  $P(\theta)=0$ ,  $\forall \theta \neq left \text{ or right}$ . Using Bayes's rule, the posterior can only achieve nonzero probability at left and right. This approach remains Bayesian inference because it asserts an explicit representation of the posterior,  $P(\theta)$ , although there are only two possible values for which this posterior can be nonzero. We think this approach leads to difficulties for termination of the decision process, as described below.

The rules for termination are affected by the choice space. This poses a deeper problem. For example, knowledge that there are 2 or 4 or 8 possible choices affects the policy governing when to terminate decisions. This can probably be formulated as Bayesian inference, but it is not parsimonious and it is ultimately wanting. Above, we explained why a bound is not a posterior when there are different degrees of reliability associated with the members of a class of items upon which a decision is to be made. The same argument applies here, but there is an interesting extension. If the termination rule were to be based on a relative degree of belief, we would have to imagine adjusting this value differently for different N and for different stimulus strengths. A termination rule based on  $P(\theta \mid observations)$  is cumbersome when the reliability of the evidence (observations) is not known. Such a termination rule is also inconsistent with experimental results: achieving a criterion on uncertainty or posterior probability cannot explain a performance function—the error rates as a function of evidence quality (e.g., strength of motion).

The intended goal of the decision process can be achieved without representing the posteriors. The brain can exploit regularities that arise under sequential sampling. For example, as described above, the reliability of the evidence may not be known, but it is presumed to be stationary during the evidence gathering. The brain can also exploit time-dependent factors. For example, the longer the decision process takes, the lower the quality of evidence. The effect of time and stationary evidence on the outcome of the decision process is affected by the number of choices. These factors can be easily incorporated in a decision variable toward an intended goal (i.e., the intentional framework) without any need for explicit representation of the posterior probability. More importantly, the experimental data suggests that the brain uses a decision variable that governs both choice and decision time, effectively abandoning the exact posterior in favor of something simpler and more efficient that satisfies the intentions.

#### Conditional Dependencies Render Bayesian Inference Impractical

Even without nuisance parameters, it is far from straightforward to compute a posterior for a large class of even simple decisions. To compute a posterior, it is often necessary to combine probabilities from sources of evidence that arrive in a stream,  $e_1$ ,  $e_2$ ,  $e_3$ ,.... If the likelihoods,  $P(e_i | S_j)$ , are known, and in particular if they are independent, then the posterior  $P(S | e_1, e_2, e_3, ...)$ can be calculated using Bayes's rule. However, for a wide class of decisions, even when  $e_1, e_2, e_3, \ldots$  are sampled independently, they are not independent, conditional on S. Hence the likelihoods are not independent! Here we wish to make three points: (a) this is a common situation, (b) the sequential sampling poses obstacles to representing the true likelihood, (c) the brain does not appear to respect this reality but instead presumes conditional independence.

This last heuristic might have interesting implications for so-called irrational decision making.

*Conditional dependence.* Often we gather evidence bearing on some state of the world, S, that holds as true or false. For example, S might be left- or rightward, and the evidence we gather is a sample of motion energy taken from a video display or the spikes from direction selective neurons in the visual cortex. In this case, if the samples are independent, then they are also conditionally independent. In contrast, there are many types of decisions in which the evidence we gather has a bearing on S: Will I arrive at Frankfurt on time? There are separate factors to sample (e.g., weather in Seattle, weather in Frankfurt, traffic patterns, airline labor issues, airplane equipment failures, a terrorist event, etc.) that are presumably independent. They are not sampled conditionally on S = "on time" or S = "late" but instead bear on that outcome.

The situation is so common that it might come as a surprise to discover that it is largely ignored in standard applications, at least the ones we know. For example, in the theory of signal detection, it is assumed that if the  $e_1, e_2, e_3, \ldots$  are sampled independently, such that  $P(e_1, e_2) = P(e_1)P(e_2)$ , then the likelihoods are conditionally independent:  $P(e_1, e_2 | S) = P(e_1 | S)P(e_2 | S)$ . This is a natural assumption because we think of sampling evidence under conditions where one state holds. That is the case for the sequential sampling of evidence about direction of motion in the preceding examples. On any one trial, motion is, for example, either up or down. If the evidence samples are independent, then they are also conditionally independent, because they are always sampled under one condition (up or down). However, that is exactly what is not true in situations in which samples of evidence affect S.

We are not arguing that it is impossible to learn statistical dependencies. For example, every medical student develops an intuition about whether the joint occurrence of headache and fever bear on the possibility of meningitis in a manner that is not predicted by the product of their likelihoods. What we are saying is that conditional independence does not hold in a variety of circumstances when at face value there is no obvious reason to suspect this. The variant of the so-called "weather prediction" task studied by Yang and Shadlen (2007) provides one example. These issues are discussed in more detail in the supplementary material to that paper.

*It is hard (but not impossible) to accommodate conditional dependencies in a decision variable.* In principle, a DV and termination rule ought to be able to incorporate conditional dependencies, but it is costly. To put it simply, there is no easy update rule and no way to exploit marginal probabilities. This problem is especially severe under sequential sampling of evidence. The same piece of evidence will affect the current estimate of probability differently depending on what other evidence has arrived.

A relevant experiment. We trained monkeys to make predictions about the location of a reward based on observing a sequence of four shapes. Each shape affects the probability of the outcome (reward at the red or green target). Our findings suggest that in these experiments, the brain gathers evidence under an assumption of conditional independence. In other words, it takes the observations associated with outcomes and makes the correct inference that they have independent effects on outcome. It, however, makes the incorrect inference that the probabilities of the observations are independent from one another, conditional on the outcome. Thus each shape increases or decreases the decision variable by a fixed amount, regardless (approximately) of when it appears in the sequence and regardless (again approximately) of what other shapes were displayed before it (Yang and Shadlen 2007).

# **Implications and Speculations**

The arguments above raise new questions about decision making and the underlying neurobiology. Here are some examples.

#### The Traffic Cop Problem

The intentional architecture discussed earlier resolves several long-standing problems in perception, mainly by casting them as chimeras. For example, there is no need for a central interpreter of information—the so-called homunculus or little man that sits in the brain and makes sense of the data. Similarly, the "combinatorial explosion" that supposedly arises when trying to assemble the atoms of vision (small receptive fields) into coherent percepts vanishes. Both of these problems are seen to arise from a mistaken assumption that the data stream gives rise to one out of a vast set of possible interpretations. Instead, according to the intentional architecture, the data only bear evidence on a finite (large perhaps, but manageable) set of hypotheses that are currently under consideration. Admittedly, this creates a new set of problems.

What is it that establishes the question that the brain is asking about the data? What establishes the set of hypotheses? What establishes the intention or list of possible intentions at any moment? We do not know the answer to these questions, but we suspect they will turn out to be more tractable than the problems they replace. For example, the organism learns which tasks to consider—decisions about decisions—based on conceptual cues. Perhaps we forage in a landscape of possible tasks using mechanisms similar to the ones that underlie value-based decisions in a landscape of potential sources of nutrition and predators.

#### Agency without a Central Executive

Begin with the premise that value-based and perceptual decisions are mediated by a common framework. Consider decisions about choice of task as a problem akin to foraging. Instead of looking for a tree with better fruit, we are searching a task space for a better project. Recall that abstract decisions are simply decisions about which questions sensorimotor-like structures should be asking of the evidence. Thus, searching for the right question is like looking for the right task. It is a value-based decision where the search is for a task that is likely to pay off in some way. There are probably costs and dividends associated with exploration, exploitation, and perseverance. Thus looking for the right questions is just another kind of decision.

This is the way the animal exercises its own rapport with the world. It is what the philosophers refer to as agency. However, what we have described (albeit vaguely) can operate without any explicit awareness of the steps. It can have the kind of automaticity that is referred to as subconscious. From the outside, it has all the qualities of purposeful, autonomous choice. When we are aware of these choices, we express ownership of our behavior and experience our "free will." What we do in the subconscious version of this, however, is not capricious and thus just as much a candidate for free will. After all, as long as the choices are not capricious, they are expressions of the relative weights the brain assigns to evidence, value, and policy (e.g., balancing time pressure against deliberation).

It should be obvious that the neural computations discussed earlier should be capable of achieving these foraging decisions. Although we do not know as much about the neurobiology of value-based decisions as we do about evidence-based decisions, the key ingredients are not mysterious. For example, termination rules lead to a switch of task rather than an action. On the other hand, we do not have a good idea about what neural events occur that distinguish the awareness of a foraging decision from the ones we make "unconsciously."

One possibility is that awareness is just a decision to activate the circuits that mediate "actions" (e.g., engaging items in the world, reporting, forming narrative internally, and interrogating). Thus when a subconscious process of decision making leads to a choice to engage, we experience the world (or an item in it) as consciously attended. We are aware. Indeed, the establishment of consciousness after sleep, anesthesia, or coma might be regarded as an unconscious decision to engage the world at all (Shadlen and Kiani 2007).

#### **Extensions of the Foraging Idea**

#### Bistability and Rivalry

There are examples of perceptual phenomena that seem like they might be mediated by the kinds of mechanisms at play in this "foraging" mode of query. If we approach problems in visual recognition as a set of queries (e.g., How should I hold my hand to grasp this object? If I move this edge, which bit will move with it? Should I scrutinize this further? Does this appeal to me?) then we can think about the brain perseverating away at the analysis of a scene that contains features worthy of further query. We can also consider the possibility of the brain abandoning this immediate set of queries to search for alternatives.

It seems that we experience something like this search for alternatives when we view bistable figures and when we experience binocular rivalry. Perhaps the study of rivalry might expose some of the computational principles that are common to value-based decisions that resemble "foraging." It might be fruitful to compare and contrast standard foraging behavior with the intervals between perceptual alternations, including regularities in the sampling schedules brought on by differences in the salience of competing images.

#### Mental Disorders

This is a rather large leap, but it seems possible that some mental disorders may be better understood from the perspective of decision making. Consider the two primary ways that we might expect foraging to fail. It could favor exploration at the expense of deliberation and deeper interrogation of evidence pertaining to the task at hand (i.e., the current workspace). This would lead to peripatetic behavior, flightiness, and deficits in concentration. The other failure mode is too little exploration. This would appear as a lack of interest in things external to the current workspace. Severely autistic children meet this description (Kanner 1973). Perhaps some of the odd expertise exhibited by some autistic patients (typically mild autism) reflects a lack of exploration. Perhaps a brain that tends to be stuck in the deliberative exploitation of the current workspace tends to acquire expertise.

# **Concluding Remarks**

This essay should be regarded as a speculative exercise. We have tried to elaborate a set of principles that have been elucidated in the experiments on the neurobiology of decision making in nonhuman primates. Naturally, these experiments (reviewed in Gold and Shadlen 2007) use simple paradigms suitable for laboratory investigations in animal subjects. We have extracted key insights from these investigations and extrapolated beyond the data to demonstrate how a simple architecture might underlie the wonderfully complex landscape of human decision making. We have tried to paint a picture of functional architecture that is aimed primarily at choosing among possible actions. We extended this principle to choices among possible tasks or decisions. Among other things, we think this perspective hints at the way in which the bigger cerebral cortex in humans provides the basis for higher cognitive functions.

The functional architecture is also a computational architecture. Viewed from this perspective, we question the popular wisdom that the brain operates as an information-processing device that performs probabilistic inference. These points are likely to be regarded as controversial (or just plain wrong) by many readers. We are less wed to the conclusions than to the motivation: decisions among possible courses of action invite us to formulate inference differently than the formulations derived from probability theory and statistics (Jaynes 2003). If our tone was overly polemical, it was not intended to be so. We do not see ourselves as anti-Bayesian. Indeed, in many instances the brain's decision variables can be seen as a way to implement aspects of Bayesian decision making.

Ours is not an argument against Bayesian inference but an embrace of the intentional architecture. The goal of information processing is not to identify content or estimate parameters but to answer questions concerning choices among possible actions, including posing the next question.

#### Acknowledgments

We are grateful to Mehrdad Jazayeri, Peter Meilstrup and Tianming Yang for input and discussions. We thank the organizers of the Ernst Strüngmann Forum and the members of the working group on the neural basis of decision making for comments and many insights. Our research is supported by the Howard Hughes Medical Institute, the National Eye Institute (EY11378), the National Institute of Drug Abuse (DA022780), the National Center for Research Resources (RR00166), and the James S. McDonnell Foundation.

#### References

- Andersen, R. A., and C. A. Buneo. 2002. Intentional maps in posterior parietal cortex. *Ann. Rev. Neurosci.* **25**:189–220.
- Barlow, H. B., W. R. Levick, and M. Yoon. 1971. Responses to single quanta of light in retinal ganglion cells of the cat. *Vision Res. Suppl.* **3**:87–101.
- Barraclough, D. J., M. L. Conroy, and D. Lee. 2004. Prefrontal cortex and decision making in a mixed-strategy game. *Nature Neurosci.* **7(4)**:404–410.
- Bogacz, R., E. Brown, J. Moehlis, P. Holmes, and J. D. Cohen. 2006. The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced choice tasks. *Psychol. Rev.* 113:700–765.
- Bogacz, R., J. M. Moehlis, E. T. Brown, P. Holmes, and J. D. Cohen. 2003. Neural mechanisms for decision optimization. In: 2003 Abstract Viewer/Itinerary Planner, Program No. 197.6. Washington DC: Society for Neuroscience.
- Brainard, D. H., and W. T. Freeman. 1997. Bayesian color constancy. J. Opt. Soc. Am. A 14(7):1393–1411.
- Cavada, C., and P. Goldman-Rakic. 1989. Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. J. Comp. Neurol. 287:422–445.

- Churchland, P. S., V. S. Ramachandran, and T. J. Sejnowski. 1994. A critique of pure vision. In: Large-Scale Neuronal Theories of the Brain, ed. C. Koch and J. L. Davis, pp. 23–60. Cambridge, MA: MIT Press.
- Cisek, P. 2007. Cortical mechanisms of action selection: The affordance competition hypothesis. *Phil. Trans. Roy. Soc. Lond. B* **362**:1585–1599.
- Clark, A. 1997. Being There: Putting Brain, Body, and World Together Again. Cambridge, MA: MIT Press.
- Cohn, T. E., D. G. Green, and W. P. Tanner. 1975. Receiver operating characteristic analysis. Application to the study of quantum fluctuation in optic nerve of Rana pipiens. J. Gen. Physiol. 66:583–616.
- Colby, C. L., and M. E. Goldberg. 1999. Space and attention in parietal cortex. *Ann. Rev. Neurosci.* 22:319–349.
- Corrado, G.S., L. P. Sugrue, H. S. Seung, and W. T. Newsome. 2005. Linear-nonlinear-Poisson models of primate choice dynamics. J. Exp. Anal. Behav. 84(3):581–617.
- Critchley, M. 1953. The Parietal Lobes. New York: Hafner Publ. Co.
- Deaner, R. O., A. V. Khera, and M. L. Platt. 2005. Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Curr. Biol.* **15(6)**:543–548.
- Ditterich, J., M. Mazurek, and M. N. Shadlen. 2003. Microstimulation of visual cortex affects the speed of perceptual decisions. *Nature Neurosci.* **6**:891–898.
- Dorris, M. C., and P. W. Glimcher. 2004. Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* **44(2)**:365–378.
- Ernst, M. O., and M. S. Banks. 2002. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* **415(6870)**:429–433.
- Gibson, J. J. 1950. Perception of the Visual World. Boston: Houghton Mifflin.
- Glimcher, P. W. 2003. Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics. Cambridge, MA: MIT Press.
- Glimcher, P. W. 2005. Indeterminacy in brain and behavior. *Ann. Rev. Psychol.* **56**:25–56.
- Gold, J. I., and M. N. Shadlen. 2000. Representation of a perceptual decision in developing oculomotor commands. *Nature* 404(6776):390–394.
- Gold, J. I., and M. N. Shadlen. 2001a. Neural computations that underlie decisions about sensory stimuli. *Trends Cogn. Sci.* **5**:10–16.
- Gold, J. I., and M. N. Shadlen. 2001b. Neural correlates of an abstract perceptual decision in monkey area 46. *Soc. Neurosci. Abstr.* **27**:237.6.
- Gold, J. I., and M. N. Shadlen. 2003. The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands. J. Neurosci. 23(2):632–651.
- Gold, J. I., and M. N. Shadlen. 2007. The neural basis of decision making. *Ann. Rev. Neurosci.* **30**:535–574.
- Good, I. J. 1979. Studies in the history of probability and statistics. XXXVII A.M. Turing's statistical work in World War II. *Biometrika* **66(2)**:393–396.
- Green, D. M., and J. A. Swets. 1966. Signal Detection Theory and Psychophysics. New York: Wiley.
- He, S., P. Cavanagh, and J. Intriligator. 1996. Attentional resolution and the locus of visual awareness. *Nature* 383(6598):334–337.
- Hecht, S., and E. U. Mintz. 1939. The visibility of single lines of various illuminations and the retinal basis of visual resolution. *J. Gen. Physiol.* **22**:593–612.
- Herrnstein, R. J. 1961. Relative and absolute strength of response as a function of frequency of reinforcement. J. Exp. Anal. Behav. 4:267–272.

- Herrnstein, R. J., and W. Vaughan. 1980. Melioration and behavioral allocation. In: Limits to Action: The Allocation of Individual Behavior, ed. J. Staddon, pp. 143– 176. New York: Academic Press.
- Hikosaka, K., and M. Watanabe. 2000. Delay activity of orbital and lateral prefrontal neurons of the monkey varying with different rewards. *Cerebral Cortex* **10(3)**:263–271.
- Huk, A. C., and M. N. Shadlen. 2005. Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. J. *Neurosci.* 25(45):10,420–10,436.
- Jaynes, E. T. 2003. Probability Theory: The Logic of Science. Cambridge: Cambridge Univ. Press.
- Jiang, Y., P. Costello, F. Fang, M. Huang, and S. He. 2006. A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proc. Natl. Acad. Sci.* 103(45):17,048–17,052.
- Kahneman, D. 2002. Nobel prize lecture: Maps of bounded rationality: A perspective on intuitive judgment and choice. In: Nobel Prizes 2002. Nobel Prizes, Presentations, Biographies, and Lectures, ed. T. Frangsmyr, pp. 419–499. Stockholm: Almquiest and Wiksell Intl.
- Kanner, L. 1973. The birth of early infantile autism. J. Autism Child Schizophr. **3(2)**:93–95.
- Karlin, S., and H. M. Taylor. 1975. A First Course in Stochastic Processes, 2nd ed. Boston, MA: Academic Press.
- Kawagoe, R., Y. Takikawa, and O. Hikosaka. 2004. Reward-predicting activity of dopamine and caudate neurons: A possible mechanism of motivational control of saccadic eye movement. J. Neurophys. 91(2):1013–1024.
- Kersten, D. 1999. High-level vision as statistical inference. In: The Cognitive Neurosciences, ed. M. S. Gazzaniga, pp. 353–363. Cambridge, MA: MIT Press.
- Kersten, D., P. Mamassian, and A. Yuille. 2004. Object perception as Bayesian inference. Ann. Rev. Psychol. 55:271–304.
- Kersten, D., and A. Yuille. 2003. Bayesian models of object perception. Curr. Op. Neurobiol. 13(2):150–158.
- Knill, D. C., and J. A. Saunders. 2003. Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Res.* **43(24)**:2539–2558.
- Kording, K. P., and D. M. Wolpert. 2004a. Bayesian integration in sensorimotor learning. *Nature* 427(6971):244–247.
- Kording, K. P., and D. M. Wolpert. 2004b. The loss function of sensorimotor learning. *Proc. Natl. Acad. Sci.* 101(26):9839–9842.
- Landy, M. S., L. T. Maloney, E. B. Johnston, and M. J. Young. 1995. Measurement and modeling of depth cue combination: In defense of weak fusion. *Vision Res.* 35(3):389–412.
- Lau, B., and P. W. Glimcher. 2005. Dynamic response-by-response models of matching behavior in rhesus monkeys. *J. Exp. Anal. Behav.* **84(3)**:555–579.
- Lee, D., M. L. Conroy, B. P. McGreevy, and D. J. Barraclough. 2004. Reinforcement learning and decision making in monkeys during a competitive game. *Cogn. Brain Res.* 22:45–58.
- Lee, D., B. P. McGreevy, and D. J. Barraclough. 2005. Learning and decision making in monkeys during a rock-paper-scissors game. *Cogn. Brain Res.* **25**:416–430.
- Levy, I., D. Schluppeck, D. J. Heeger, and P. W. Glimcher. 2007. Specificity of human cortical areas for reaches and saccades. *J. Neurosci.* 27(17):4687–4696.

- Lewis, J. W., and D. C. Van Essen. 2000a. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J. Comp. Neurol.* **428(1)**:112–137.
- Lewis, J. W., and D. C. Van Essen. 2000b. Mapping of architectonic subdivisions in the macaque monkey, with emphasis on parieto-occipital cortex. *J. Comp. Neurol.* **428**(1):79–111.
- Link, S. W. 1992. The Wave Theory of Difference and Similarity. Hillsdale, NJ: Lawrence Erlbaum.
- Lo, C. C., and X. J. Wang. 2006. Cortico-basal ganglia circuit mechanism for a decision threshold in reaction time tasks. *Nature Neurosci.* **9**(7):956–963.
- Luce, R. D. 1959. Individual Choice Behavior: A Theoretical Analysis. New York: Wiley.
- Ma, W. J., J. M. Beck, P. E. Latham, and A. Pouget. 2006. Bayesian inference with probabilistic populaton codes. *Nature Neurosci.* 9(11):1432–1438.
- Mamassian, P., and M. S. Landy. 2001. Interaction of visual prior constraints. *Vision Res.* **41(20)**:2653–2668.
- Manski, C. 1977. The structure of random utility models. *Theory and Decision* 8:229–254.
- McCoy, A., J. Crowley, G. Haghighian, H. Dean, and M. Platt. 2003. Saccade reward signals in posterior cingulate cortex. *Neuron* **40(5)**:1031–1040.
- McCoy, A. N., and M. L. Platt. 2005. Risk-sensitive neurons in macaque posterior cingulate cortex. *Nature Neurosci.* 8(9):1220–1227.
- McMillen, T., and P. Holmes. 2006. The dynamics of choice among multiple alternatives. J. Math. Psychol. 50:30–57.
- Merleau-Ponty, M. 1962. Phenomenology of Perception. London: Routledge and Kegan Paul Ltd.
- Montague, P. R., and G. S. Berns. 2002. Neural economics and the biological substrates of valuation. *Neuron* **36(2)**:265–284.
- Naccache, L., E. Blandin, and S. Dehaene. 2002. Unconscious masked priming depends on temporal attention. *Psychol. Sci.* **13(5)**:416–424.
- O'Regan, J. K., and A. Noë. 2001. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24(5):939–973.
- Padoa-Schioppa, C., and J. A. Assad. 2006. Neurons in the orbitofrontal cortex encode economic value. *Nature* **441(7090)**:223–226.
- Parker, A. J., and W. T. Newsome. 1998. Sense and the single neuron: Probing the physiology of perception. *Ann. Rev. Neurosci.* 21:227–277.
- Paton, J. J., M. A. Belova, S. E. Morrison, and C. D. Salzman. 2006. The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature* 439(7078):865–870.
- Petrides, M., and D. N. Pandya. 1984. Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *J. Comp. Neurol.* **228**:105–116.
- Poremba, A., R. C. Saunders, A. M. Crane, M. Cook, L. Sokoloff et al. 2003. Functional mapping of the primate auditory system. *Science* 299(5606):568–572.
- Ratcliff, R., and J. N. Rouder. 1998. Modeling response times for two-choice decisions. *Psychol. Sci.* **9**:347–356.
- Ratcliff, R., and J. N. Rouder. 2000. A diffusion model account of masking in twochoice letter identification. J. Exp. Psychol. Hum. Perc. Perf. 26(1):127–140.
- Rizzolatti, G., L. Fogassi, and V. Gallese. 1997. Parietal cortex: From sight to action. *Curr. Op. Neurobiol.* 7:562–567.

- Rosas, P., J. Wagemans, M. O. Ernst, and F. A. Wichmann. 2005. Texture and haptic cues in slant discrimination: Reliability-based cue weighting without statistically optimal cue combination. J. Opt. Soc. Am. A. Opt. Image Sci. Vis. 22(5):801–809.
- Scherberger, H., and R. A. Andersen. 2007. Target selection signals for arm reaching in the posterior parietal cortex. *J. Neurosci.* 27(8):2001–2012.
- Scherberger, H., M. A. Goodale, and R. A. Andersen. 2003. Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. J. Neurophys. 89(3):1456–1466.
- Shadlen, M. N., T. D. Hanks, A. K. Churchland, R. Kiani, and T. Yang. 2006a. The speed and accuracy of a simple perceptual decision: A mathematical primer. In: Bayesian Brain: Probabilistic Approaches to Neural Coding, ed. K. Doya et al., pp. 209–237. Cambridge, MA: MIT Press.
- Shadlen, M. N., T. D. Hanks, M. E. Mazurek, R. Kiani, T. Yang et al. 2006b. The brain uses elapsed time to convert spike rate to probability. Program No. 605.6. Neuroscience Meeting Planner Atlanta: Soc. for Neuroscience.
- Shadlen, M. N., and R. Kiani. 2007. Neurology: An awakening. *Nature* **448(7153)**: 539–540.
- Shadlen, M. N., and J. A. Movshon. 1999. Synchrony unbound: A critical evaluation of the temporal binding hypothesis. *Neuron* 24(1):67–77.
- Shadlen, M. N., and W. T. Newsome. 1994. Noise, neural codes and cortical organization. *Curr. Op. Neurobiol.* **4**:569–579.
- Shadlen, M. N., and W. T. Newsome. 1998. The variable discharge of cortical neurons: Implications for connectivity, computation and information coding. J. Neurosci. 18:3870–3896.
- Smith, P. L., and R. Ratcliff. 2004. Psychology and neurobiology of simple decisions. *Trends Neurosci.* 27(3):161–168.
- Softky, W. R., and C. Koch. 1993. The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSPs. *J. Neurosci.* **13(1)**:334–350.
- Spivey, M. J., M. Grosjean, and G. Knoblich. 2005. Continuous attraction toward phonological competitors. *Proc. Natl. Acad. Sci.* 102(29):10,393–10,398.
- Sugrue, L. P., G. S. Corrado, and W. T. Newsome. 2004. Matching behavior and the representation of value in the parietal cortex. *Science* **304(5678)**:1782–1787.
- Tanner, W. P. Jr. 1961. Physiological implications of psychophysical data. Ann. NY Acad Sci. 89:752–765.
- Thurstone, L. L. 1959. The Measurement of Values. Chicago: Univ. Chicago Press.
- Tremblay, L., and W. Schultz. 1999. Relative reward preference in primate orbitofrontal cortex. *Nature* **398**:704–708.
- Trommershauser, J., S. Gepshtein, L. T. Maloney, M. S. Landy, and M. S. Banks. 2005. Optimal compensation for changes in task-relevant movement variability. *J. Neurosci.* 25(31):7169–7178.
- van Ee, R., W. J. Adams, and P. Mamassian. 2003. Bayesian modeling of cue interaction: Bistability in stereoscopic slant perception. *J. Opt. Soc. Am. A* **20(7)**:1398–1406.
- Wald, A. 1947. Sequential Analysis. New York: Wiley.
- Wald, A., and J. Wolfowitz. 1947. Optimum character of the sequential probability ratio test. Ann. Math. Statist. 19:326–339.
- Wallis, J. D., K. C. Anderson, and E. K. Miller. 2001. Single neurons in prefrontal cortex encode abstract rules. *Nature* 411:953–956.
- Watanabe, K., J. Lauwereyns, and O. Hikosaka. 2003. Neural correlates of rewarded and unrewarded eye movements in the primate caudate nucleus. J. Neurosci. 23(31):10,052–10,057.

- Yang, T., and M. N. Shadlen. 2007. Probabilistic reasoning by neurons. *Nature* 447(7148):1075–1080.
- Yuille, A., and H. H. Bulthoff. 1996. Bayesian decision theory and psychophysics. In: Perception as Bayesian Inference, ed. D. C. Knill and W. Richards, pp. 123–162. Cambridge: Cambridge Univ. Press.