

Neural correlates of decisions

Michael L Platt

Once considered the province of philosophy and the behavioral sciences, the process of making decisions has received increasing scrutiny from neurobiologists. Recent research suggests that sensory judgements unfold through the gradual accumulation of neuronal signals in sensory–motor pathways, favoring one alternative over others. Stored representations of the outcome of prior actions activate neurons in many of these same areas during decision-making. The challenge for neurobiologists lies in deciphering how signals from these disparate areas are integrated to form a single behavioral choice and the mechanisms responsible for selecting the appropriate information upon which decisions should be informed in particular contexts.

Addresses

Department of Neurobiology, Center for Cognitive Neuroscience, and Department of Biological Anthropology and Anatomy, Duke University Medical Center, 327G Bryan Research Building, Research Drive, Box 3209, Durham, North Carolina 27710, USA;
e-mail: platt@neuro.duke.edu

Current Opinion in Neurobiology 2002, **12**:XXX–XXX

0959-4388/02/\$ – see front matter

© 2002 Elsevier Science Ltd. All rights reserved.

DOI 10.1016/S0959-4388(02)00302-1

Abbreviations

FEFs	frontal eye fields
LIP	lateral intraparietal area
MT	middle temporal
SC	superior colliculus
SNr	substantia nigra pars reticulata
S1	primary somatosensory area

Introduction

Consider the following ethological observations made by primatologists Dorothy Cheney and Robert Seyfarth. In an effort to reveal what monkeys know about social relationships within their own groups, these researchers performed vocalization playback experiments on wild monkeys in Africa, by hiding a loudspeaker in the brush near groups of female monkeys sitting near each other (vervets, *Cercopithecus aethiops* [1] and baboons, *Papio cynocephalus* [2]). In one experiment, Cheney and Seyfarth played the pre-recorded distress call of a juvenile monkey from the hidden speaker and noted the behavior of each of the females. The mother of the infant whose alarm call was played looked in the direction of the loudspeaker (Figure 1b, Monkey B), demonstrating that monkeys recognize their offspring by voice and can use this information to plan an appropriate orienting response. More intriguingly, other females in the group (Figure 1b, Monkey A) looked at the mother of the juvenile, suggesting that monkeys, in addition to recognizing individuals by their calls, also know the kinship relationships between other monkeys in their group, and can use this information to orient in the

appropriate direction. Cheney and Seyfarth further demonstrated that, in social situations like this, a monkey is more likely to come to the aid of another monkey if such friendly interactions have been reciprocated in the past.

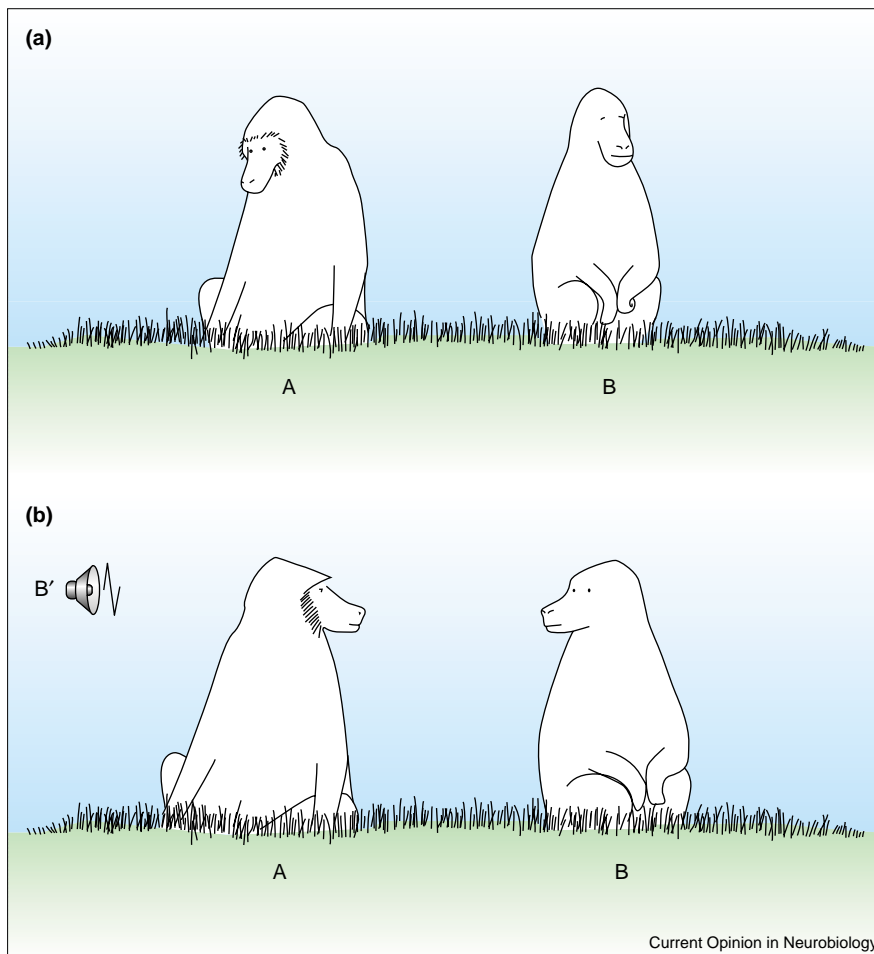
These observations demonstrate that a single sensory cue, such as the distress call of a juvenile monkey, can generate multiple different behavioral responses, depending on context, learned associations, and memory for the outcome of prior actions. This selection of one out of several potential behavioral responses, in a given situation, is often referred to as decision-making [3,4]. As illustrated by the study mentioned above, the decision process can involve sensory judgements as well as an evaluation of competing goals and potential outcomes, in order to choose an appropriate course of action.

Although behavioral scientists, including psychologists, economists, and behavioral ecologists, have made great strides in describing principles underlying both perceptual judgements and goal-oriented choices [5–7], the neural mechanisms responsible for making decisions have, until recently, remained elusive. However, working from the premise that many of the basic mechanisms of sensory perception and movement generation are largely understood, a small but growing group of neurobiologists has begun to explore the possibility that the decision process can be investigated physiologically. These scientists have discovered that the deliberative process by which a single behavioral response is selected from several possible alternatives leaves a signature in the activity of single neurons in a variety of sensory and motor areas. Moreover, the resultant behavioral choice appears to be generated through the gradual accretion of signals favoring one alternative over another (Figure 2). This review briefly describes several studies in this field conducted over the past several years, with a focus on, but not limited to, the decision processes engaged when monkeys choose where to look.

Weighing the evidence: neural correlates of sensory judgements

In the ethological example described above, the mother monkey discriminated the acoustic cue as a distress call, determined the caller to be kin, and oriented in the direction of the loudspeaker rather than in the direction of the other females present. Orienting appropriately in response to a sensory cue thus depends on making accurate perceptual, as well as conceptual, judgements. Clearly, perceptual judgements involve the activation of primary and secondary sensory areas of the cerebral cortex, but, until recently, the neurophysiological mechanisms underlying these perceptual analyses remained largely unknown.

Figure 1



Example of decision-making in primates. The same acoustic stimulus elicits different behavioral responses from different individuals. (a) Two female monkeys sitting near each other are played the pre-recorded distress call of one of their infants (B') through a hidden loudspeaker. (b) The infant's mother (Monkey B) orients towards the loudspeaker, whereas the other female (Monkey A) orients towards the infant's mother. Drawing by John Watanabe.

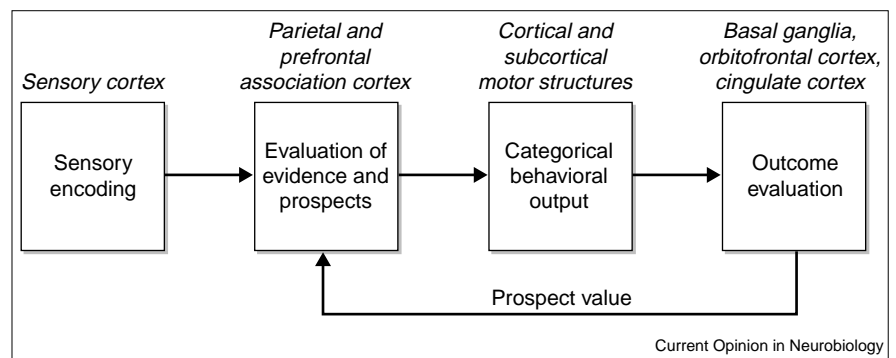
In the past decade, Newsome *et al.* [8,9] provided the first compelling neurophysiological evidence that neurons in extrastriate visual cortex actually form the percept of visual motion. In this now classic experiment, the authors presented trained rhesus macaques with a visual discrimination problem, while simultaneously recording the activity of single neurons in the middle temporal (MT) area. MT is an area of extrastriate visual cortex known, on the basis of neurophysiological evidence, to be activated specifically by visual motion [10,11]. On each trial, a monkey subject was required to indicate, with an eye movement, the direction in which a small number of dots were moving coherently, within a sea of identical dots flickering randomly, across a computer screen (Figure 3a). Across trials, changing the proportion of dots moving coherently in any one direction systematically varied the difficulty of the discrimination. The authors demonstrated that both the accuracy of perceptual judgements and the activity of motion-sensitive neurons in area MT was correlated with the fraction of coherently moving dots. Moreover, microstimulation of particular columns of neurons in MT, sensitive to a particular direction of motion, systematically biased the judgements made by monkeys in

favor of the direction signaled by the stimulated column [12]. Similar correlations between perceptual judgements and neuronal activation in primary and secondary somatosensory cortex have been found in monkeys trained to make vibrotactile discriminations [13•,14,15,16••].

These studies demonstrate that perceptual discrimination depends upon the activation of neurons within sensory areas of cortex, and that the accuracy of perceptual analysis depends on the strength of the sensory stimulus. They do not reveal, however, the mechanisms responsible for generating a single behavioral report of what was perceived. For judgements of visual motion, Shadlen *et al.* [17] proposed that pools of neurons in area MT signal the direction and coherence of motion in each direction, within a topographic map of visual space. Neurons in higher-order cortical areas compute the time integral, or sum, of neuronal activity in MT associated with each direction. They hypothesized that, when the experimenter requests a behavioral report from the monkey subject, a 'winner-take-all' mechanism computes the motion direction associated with the highest cumulative activity and this information is then used to select an appropriate eye movement for execution.

Figure 2

A simple decision circuit. Sensory inputs inform neurons in sensory–motor association areas of the cortex, which accumulate information favoring one alternative over another and weigh this evidence against the likely prospects of choosing each option. Neurons in downstream motor structures reflect the categorical output of the decision process and a single behavioral response is produced. Neurons in the basal ganglia and limbic structures encode the outcome of behavior, and relay this information to association cortex in order to inform future decisions.



This model suggests that neurons in areas of the brain that are involved in the decision process will show signs of temporal integration in their activity. In fact, these authors have found precisely such a pattern of neuronal activation in several areas of the brain that receive input from area MT and project, in turn, to principal areas of eye movement control, such as the frontal eye fields (FEFs) and superior colliculus (SC). In these experiments, monkeys were again asked to determine the direction in which small dots were moving on a computer screen, and changing the proportion of dots moving coherently in any one direction again systematically varied the difficulty of the discrimination. Shadlen and Newsome found that neuronal activity in both parietal cortex [18,19**] and prefrontal cortex [20*] gradually accrued as the monkey viewed the motion stimulus. More importantly, the average activity of neurons in these two cortical association areas increased more rapidly when the motion discrimination was easier than when it was more difficult (Figure 3b). The temporal profile of activity in parietal and prefrontal cortex is consistent with the integration of motion signals, such as those carried by neurons in area MT. Taken together, these studies suggest that judgements made on current sensory inputs occur through the gradual accumulation of signals favoring one sensory interpretation over others.

Remembrance of things past: neural correlates of decisions derived from prior knowledge

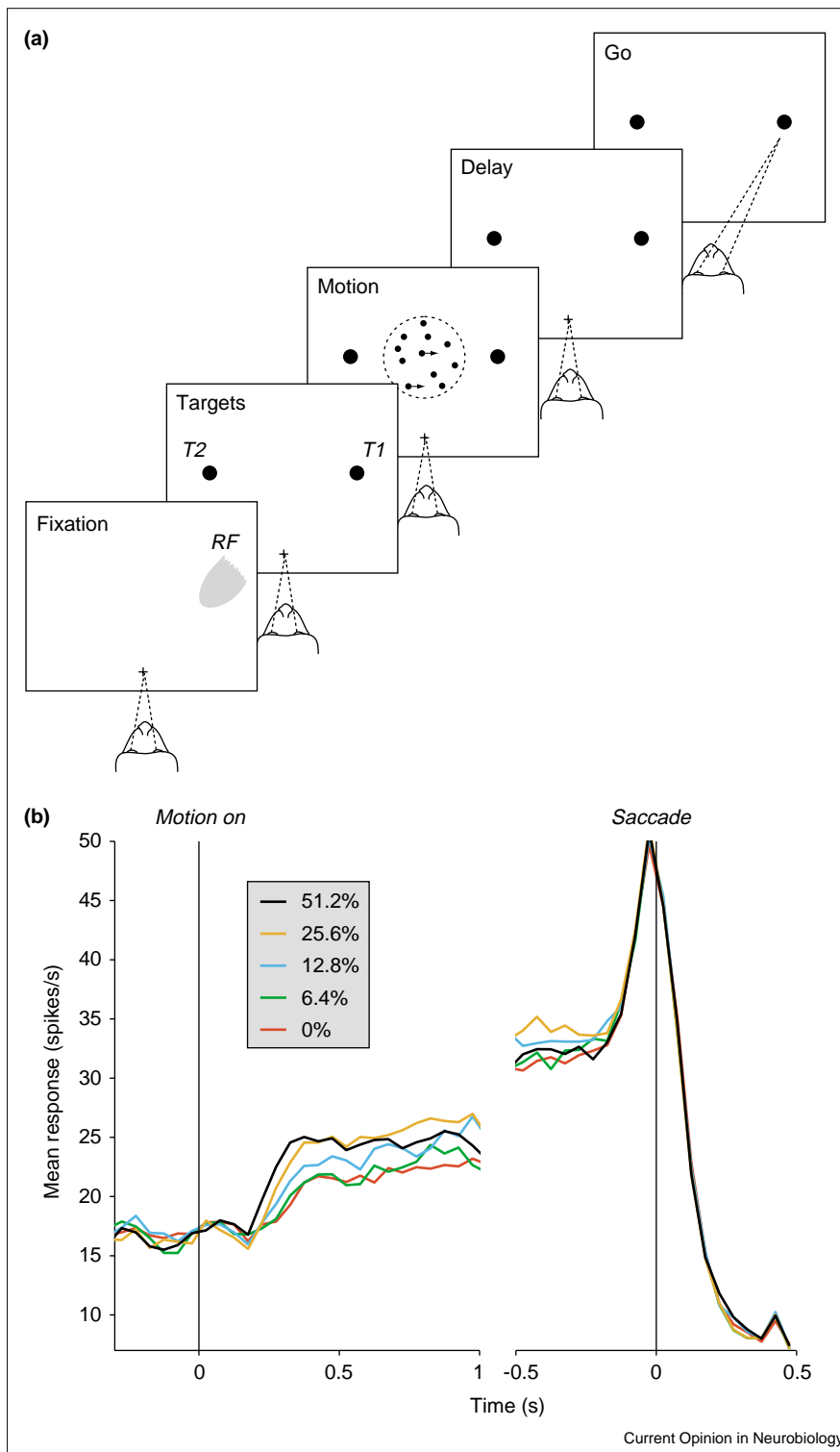
Although many decisions surely depend on making accurate sensory discriminations, such as determining the direction of an infant monkey's distress call or judging the color of a traffic light, numerous decisions are also informed by prior experience. In the behavioral example cited above, a monkey may come to the aid of another monkey if the two animals have cooperated in the past. In fact, many approaches to decision-making, within the social and behavioral sciences, begin from the premise that individuals choose between options, depending on the outcomes associated with each alternative in the past [21–23]. Normative theories of decision-making developed within economics [24] and mathematics [25] argue that individuals should choose the option with the highest

expected value or utility, which can be computed on the basis of the expected profits or losses associated with each alternative. In the absence of complete knowledge of the environment, these values can be estimated from the outcomes of choosing each option in the past. A wealth of behavioral data indicates that the choices made both by animals [26,27] and humans [28] in simple situations are often consistent with such models, although expected value and expected utility theories often fail to predict behavior in more complex situations [29,30]. These data suggest that many decisions do indeed incorporate estimates of behavioral value derived from prior experience, implicating the engagement of reward systems of the brain during decision-making (Figure 2).

Although behavioral theory and data strongly indicate that prior experience often guides behavioral choices, most neurobiological studies of decision-making have focused primarily on the processes that convert sensory discriminations into action, as described above. Recently, however, several groups of neurophysiologists have begun to explore the impact of prior experience on behavioral choice and the underlying decision processes that unfold in sensory–motor pathways. In a series of studies, Platt and Glimcher [31] explicitly probed the representation of behavioral value by neurons in the lateral intraparietal area (LIP). Shadlen and Newsome previously showed this same region of the brain to carry signals correlated with judgements of motion direction in the random dot eye movement task.

Platt and Glimcher [31] carried out two sets of experiments. In the first, monkeys were cued by the color of a fixation stimulus to shift gaze to one of two peripheral visual targets, while the activity of single LIP neurons was monitored electrophysiologically. Behavioral value was systematically varied by either delivering different amounts of fruit juice for correct gaze shifts to each of the targets, or by altering the probability that each of the possible gaze shifts would be cued across blocks of trials. In both cases, the authors found that, when cue color, target location, and movement metrics were held constant,

Figure 3



Neural correlates of a perceptual decision. **(a)** Motion discrimination task used to study neuronal activity in pathways linking visual inputs with eye movements. A monkey subject views a patch of randomly-moving dots and, after a delay, indicates its judgement of motion direction by shifting gaze to T1 or T2, one of which is positioned with the response field of the neuron under study. Task difficulty is controlled by varying the proportion of dots moving coherently in one direction or another. **(b)** Temporal integration of signals favoring a judgement of motion in one direction over another. Average neuronal activity in a population of 104 neurons in area LIP, plotted as a function of time during the motion task for different motion strengths (see inset), and aligned on either motion stimulus onset (left panel) or saccade onset (right panel). Similar signals have been found in prefrontal cortex and the SC using the same task. RF, neuron's preferred target, or response field. Adapted with permission from [19**].

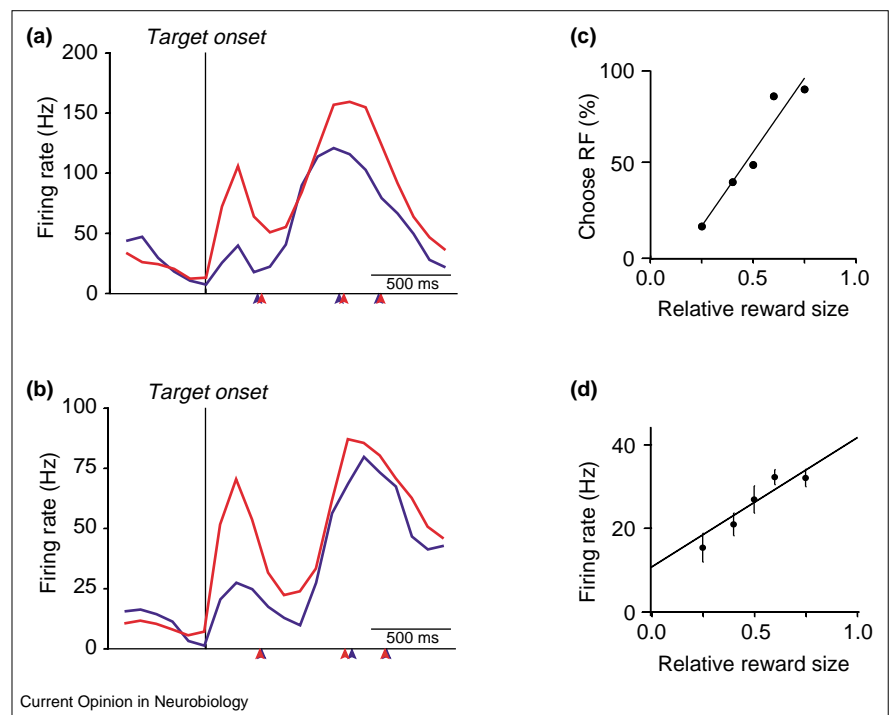
the activity of many neurons in area LIP was proportional to behavioral value (Figure 4a,b). Similar correlations between neuronal activity and the behavioral value of a particular eye movement (either movement probability or expected reward) have been found in prefrontal cortex [32], the caudate nucleus [33] and substantia nigra pars

reticulata (SNr) [34*] of the basal ganglia, and the SC [35,36]. In the second study, Platt and Glimcher [31] further demonstrated that, in the absence of an instructional cue, monkeys choose to shift gaze to the most rewarding target in the visual array and the activity of many LIP neurons parallels these value-based decisions (Figure 4b,c).

Figure 4

Neural correlates of behavioral value.

(a) Average firing rate of a single LIP neuron plotted as a function of time, on trials in which a saccade in the preferred direction (RF) of the neuron was cued. Neuronal activity was greater when a large reward was associated with the cued saccade (red curve) than when a small reward was associated with the same movement (blue curve). Arrows indicate, successively, mean times of instruction cue onset, central fixation stimulus offset, and saccade onset in high (red) and low (blue) reward blocks. **(b)** Neuronal activity for a second LIP neuron was greater when the cued movement was more probable (red curve) than when the same movement was less probable (blue curve). Conventions as in (a). **(c)** When free to choose, monkeys shift gaze to the target associated with the larger reward. Relative reward size reflects the volume of juice available for a saccade in the neuron's preferred direction, divided by the total volume of juice available from both possible saccades, within a block of trials. Data are from a single experiment. **(d)** Average activity (\pm standard error) of a single LIP neuron measured after target onset and plotted as a function of relative reward size, for trials in which the monkey shifted gaze in the neuron's preferred direction. Data are from the same experiment as in (c). Adapted with permission from [60]. RF, response field.



Taken together, the results of these studies indicate that brain areas implicated in the conversion of sensory judgements into behavioral reports also encode the behavioral outcome that can be expected from each available option on the basis of prior experience. This makes sense because even purely sensory discriminations require prior knowledge of the goal of behavior in any context. Thus, expectations, goals, and prior experience must, by necessity, be included in any adaptive decision process. From the viewpoint of optimal design [37,38], it seems reasonable that neurons involved in the decision process would adjudicate current sensory inputs in the context of past experience. Indeed, Gold and Shadlen [39**] recently proposed that neurons in parietal and prefrontal cortex compute a decision variable that combines current sensory evidence with estimates of behavioral value. The resultant value represents the logarithm of the likelihood ratio of one response over another, which is then compared to a criterion in order to decide upon a single behavioral response [40].

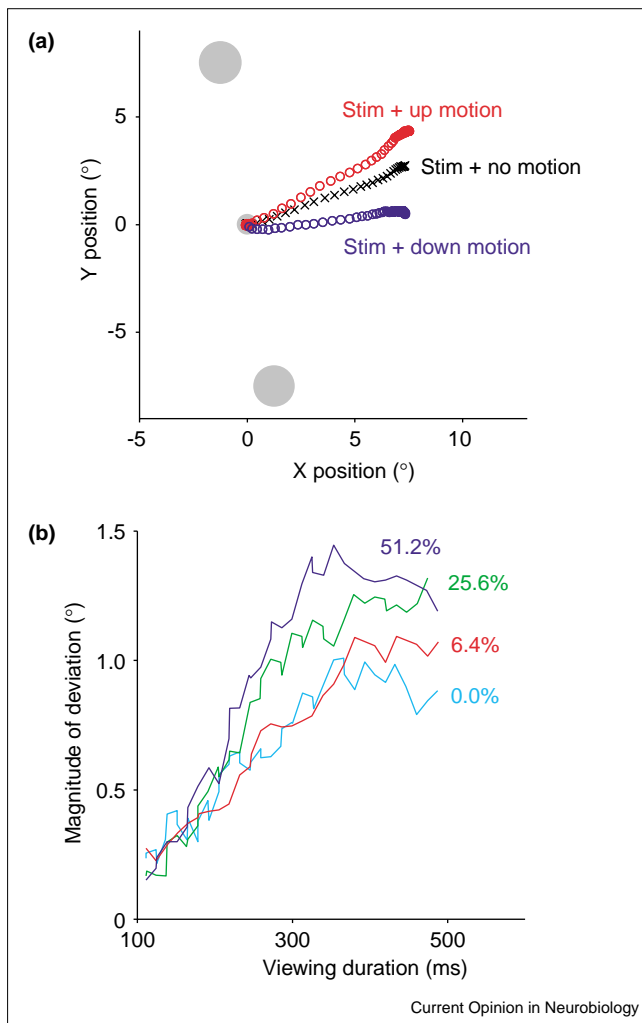
These studies also indicate that motivational systems of the brain are deployed when individuals make even simple choices. Indeed, adaptive decision-making requires encoding the outcome, either good or bad, of prior action. Signals correlated with the reward outcome of events have been found in the basal ganglia, including the activation of dopaminergic neurons of the substantia nigra pars compacta [41], and modulations in activity in the caudate

nucleus [42] and nucleus accumbens [43**,44*]. Such signals have also been uncovered in largely midline cortical areas such as the orbitofrontal cortex [45,46*,47**], cingulate cortex [48], and the supplementary eye fields [49**]. These areas presumably contribute to the extraction and maintenance of representations of behavioral value upon which future decisions may be informed (Figure 2).

Arbitration without a judge: conversion of analog decision signals into a categorical response

Recent studies suggest that decisions are made by combining gradually accumulating sensory evidence, favoring one alternative over others, with prior knowledge about the likely consequences of each action. This process leaves a signature in the activity of neurons at various stages in sensory-motor pathways. But where does the decision actually occur? Which regions of the brain convert neuronal activity favoring competing alternatives into a single behavioral response? A recent study by Gold and Shadlen [50**] directly tested this question by applying microstimulation to the FEF, while monkeys performed the random dot motion discrimination task. As previously observed [51], stimulation in the FEF during passive fixation evoked a saccade of fixed direction and amplitude (Figure 5a). Microstimulation applied while monkeys judged motion direction in the random dot stimulus, however, evoked saccades that deviated systematically in the direction reported by the monkey when no stimulation was delivered (Figure 5a). More importantly, the magnitude of

Figure 5



Gradual conversion of sensory evidence into an eye movement decision. **(a)** Microstimulation is delivered to the FEF while a monkey subject passively fixates (black crosses), views dots moving coherently upwards (red circles), or dots moving coherently downwards (blue circles). Saccade trajectory and endpoint deviate systematically in the direction of motion viewed during the random dot discrimination task. Small gray circle indicates fixation point; large gray circles indicate response targets for up and down motion. **(b)** Magnitude of deviation in stimulation-induced saccade evoked by viewing motion stimulus. Both motion strength and viewing time systematically influence movement deviation. Percentages indicate motion strength. Adapted with permission from [50**].

deviation depended on both the proportion of coherently moving dots and the amount of time the monkey had spent viewing the stimulus (Figure 5b). These data suggest that developing eye movement plans reflect the gradual accumulation of motion information, as if decision formation and movement preparation shared a common neural organization. However, once decision signals reach brain structures more closely associated with movement production — such as the FEFs [52] and SC [53,54], for eye movements, and the primary motor cortex, for skeletal-muscular movements [55] — the activity of many neurons

more closely reflects the categorical output of these decision processes and a single movement is produced.

Conclusions

Recent research is consistent with the view that decision signals evolving in higher sensory–motor areas gradually specify a particular movement. In speeded tasks, the rate at which these signals accrue determines the time it actually takes to unleash the movement [56,57]. At present, the contribution of prior experience and motivation to movement preparation and reaction time remains obscure [58]. Moreover, the overwhelming array of neurological and psychiatric disorders in which decision-making is compromised, such as schizophrenia, obsessive–compulsive disorder, and addiction, argues for the importance of particular brain areas, such as the frontal lobe, in making decisions. These syndromes may impact decision processes through the assignment of improper behavioral value to available options.

Neurobiological models of the decision process described in this review, derived from simple sensory discrimination and choice psychology, eschew executive control mechanisms. However, these mechanisms might be required for the deliberative and sometimes conscious process of making decisions that occurs within complex social and cultural situations. One intriguing possibility is that frontal cortical areas implement executive control mechanisms on gradually evolving decision signals in higher sensory–motor areas [59]. The decision-making process offers several challenges to neurobiologists. First, we need to determine whether particular brain areas contribute more specifically to decision processes than to sensory discrimination or motor preparation. Second, the mechanisms by which prior knowledge and expectations are combined with sensory data during ongoing decision processing need to be elucidated. Third, the processes that select the appropriate information upon which a decision should be informed in a particular context need clarification. In order to address these issues, neurophysiological approaches to decision-making must begin to study the process of behavioral selection in contexts that more closely approximate the complex and fluid situations in which decision mechanisms evolved. The combination of judgement and decision theory, neurophysiological techniques, and ethological approaches to behavior should provide a powerful paradigm for future explorations of the neurobiology of decision [60].

Acknowledgements

I would like to thank R Seyfarth and M Shadlen for graciously making figures available for this paper. In addition, E Brannon, J Crowley, R Deaner, D Fitzpatrick, and D Purves made helpful comments on the manuscript. I would also like to thank the editors for soliciting this review.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Cheney DL, Seyfarth RM: **Vocal recognition in free-ranging vervet monkeys.** *Anim Behav* 1980, **28**:362-367.

2. Cheney DL, Seyfarth RM: **Recognition of other individuals' social relationships by female baboons.** *Anim Behav* 1999, **58**:67-75.
3. Hastie R: **Problems for judgment and decision making.** *Annu Rev Psychol* 2001, **52**:653-683.
This excellent review summarizes developments during the last five years in the field of judgement and decision-making. Although brief, the review details 16 different research problems that lie at the core of current research, many of which will become important questions for neurobiological studies of decision-making. In fact, some of these current research problems are themselves motivated and informed by research work in neuroscience, particularly the neurobiology of emotion.
4. Plous S: *The Psychology of Judgment and Decision Making.* New York: McGraw-Hill, Inc.; 1993.
5. Stephens DW, Krebs JR: *Foraging Theory.* Princeton: Princeton University Press; 1986.
6. Herrnstein RJ: **Relative and absolute strength of response as a function of frequency of reinforcement.** *J Exp Anal Behav* 1961, **4**:267-272.
7. Kahneman D, Tversky A: **Prospect theory: an analysis of decision under risk.** *Econometrica* 1979, **47**:263-291.
8. Newsome WT, Britten KH, Movshon JA: **Neuronal correlates of a perceptual decision.** *Nature* 1989, **7**:52-54.
9. Salzman CD, Britten KH, Newsome WT: **Cortical microstimulation influences perceptual judgments of motion direction.** *Nature* 1990, **346**:174-177.
10. Dubner R, Zeki S: **Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey.** *Brain Res* 1971, **35**:528-532.
11. Zeki S: **Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey.** *J Physiol* 1974, **236**:549-573.
12. Salzman CD, Britten KH, Newsome WT: **Cortical microstimulation influences perceptual judgments of motion direction.** *Nature* 1990, **346**:174-177.
13. Hernandez A, Zainos A, Romo R: **Neuronal correlates of sensory discrimination in the somatosensory cortex.** *Proc Natl Acad Sci USA* 2000, **97**:6191-6196.
The authors of this paper describe an important extension of techniques used to link perceptual performance and neuronal responses for visual motion discrimination to somatosensory processing. In this study, monkeys discriminated frequency differences in two vibrotactile stimuli applied sequentially to the fingertips, while neuronal responses in S1 were recorded. The authors find that changes in neuronal firing rate closely matched psychophysical performance, but changes in the periodicity of neuronal firing did not. These data suggest that the activity of neurons in primary somatosensory cortex (S1) underlies tactile perception.
14. Salinas E, Hernandez H, Zainos A, Romo R: **Periodicity and firing rate as candidate neural codes for the frequency of vibro-tactile stimuli.** *J Neurosci* 2000, **20**:5503-5515.
15. Romo R, Hernandez A, Zainos A, Salinas E: **Somatosensory discrimination based on cortical microstimulation.** *Nature* 1998, **392**:387-390.
16. Romo R, Hernandez A, Zainos A, Brody CD, Lemus L: **Sensing without touching: psychophysical performance based on cortical microstimulation.** *Neuron* 2000, **26**:273-278.
This elegant study demonstrates that the activation of pools of neurons in S1 directly contributes to tactile perception. Following up on their prior studies linking perceptual performance to the firing rate of neurons in S1 [15], the authors addressed the functional consequences of S1 activation for perception, by applying microstimulation to S1, while monkeys performed a sequential vibrotactile frequency discrimination task. When microstimulation was substituted for one of the vibrotactile stimuli, monkeys treated the artificial activation of S1 as if it were the consequence of a real vibrotactile stimulus. Psychophysical performance on stimulation and non-stimulation trials was nearly identical, suggesting that direct stimulation of S1 can trigger perceptual experiences that can be stored in memory and used to make a decision.
17. Shadlen MN, Britten KH, Newsome WT, Movshon JA: **A computational analysis of the relationship between neuronal and behavioral responses to visual motion.** *J Neurosci* 1996, **15**:3870-3896.
18. Shadlen MN, Newsome WT: **Motion perception: seeing and deciding.** *Proc Natl Acad Sci USA* 1996, **93**:628-633.
19. Shadlen MN, Newsome WT: **Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey.** *J Neurophysiol* 2001, **86**:1916-1936.
In this follow-up to a preliminary report [18], the neural correlates of visual motion judgements were investigated in parietal cortex (area LIP). The activity of single LIP neurons was studied while monkeys judged motion direction in a stochastic random dot display, and indicated their decision with an eye movement. The authors find that not only did neuronal activity predict the monkey's eye movement response, but also that neuronal activity increased more rapidly over time for stimuli with stronger motion. The time course of the neuronal response suggests that LIP neurons accumulate sensory evidence in favor of one target for an eye movement over another. LIP thus appears to play an important role in the decision process that results in a gaze shift from one object to another in the visual environment.
20. Kim JN, Shadlen MN: **Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque.** *Nat Neurosci* 1999, **2**:176-184.
21. Herrnstein RJ: **Relative and absolute strength of response as a function of frequency of reinforcement.** *J Exp Anal Behav* 1961, **4**:267-272.
22. MacArthur RH, Pianka ER: **On optimal use of a patchy environment.** *Am Nat* 1966, **100**:603-609.
23. Pyke GH, Pulliam HR, Charnov EL: **Optimal foraging: a selective review of theory and tests.** *Q Rev Biol* 1977, **52**:137-154.
24. von Neumann J, Morgenstern O: *The Theory of Games and Economic Behavior.* Princeton: Princeton University Press; 1944.
25. Bernoulli D: *The Works.* Boston: Birkhauser; 1982.
26. DeVilliers PA, Herrnstein RJ: **Toward a law of response strength.** *Psychol Bull* 1976, **83**:1131-1153.
27. Stephens DW, Krebs JR: *Foraging Theory.* Princeton: Princeton University Press; 1986.
28. Winterhalder B: **Foraging strategies in the boreal forest: an analysis of Cree hunting and gathering.** In *Hunter-Gather Foraging Strategies.* Edited by Winterhalder B, Smith E. Chicago: University of Chicago Press; 1981.
29. Caraco T: **Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*).** *Behav Ecol Sociobiol* 1981, **8**:820-830.
30. Kahneman D, Tversky A: **Prospect theory: an analysis of decision under risk.** *Econometrica* 1979, **47**:263-291.
31. Platt ML, Glimcher PW: **Neural correlates of decision variables in parietal cortex.** *Nature* 1999, **400**:233-238.
32. Leon MI, Shadlen MN: **Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque.** *Neuron* 1999, **24**:415-425.
33. Kawagoe R, Takikawa Y, Hikosaka O: **Expectation of reward modulates cognitive signals in the basal ganglia.** *Nat Neurosci* 1998, **1**:411-416.
34. Handel A, Glimcher PW: **Contextual modulation of substantia nigra pars reticulata neurons.** *J Neurophysiol* 2000, **83**:3042-3048.
Handel and Glimcher examine modulations in the activity of tonically-active neurons in the SNr of the basal ganglia, a nucleus interposed between the FEFs and the SC and thought to be involved in the control of saccadic eye movements, during both spontaneous and task-related eye movements. They find that the activity of many neurons in the SNr are modulated by context; movements followed by reward produced greater modulations in neuronal activity than movements made to either initiate a trial or to spontaneously scan the visual scene. These data suggest that the SNr might be sensitive to learned reinforcement contingencies associated with eye movements and might therefore play a role in eye movement decisions.
35. Basso MA, Wurtz RH: **Modulation of neuronal activity by target uncertainty.** *Nature* 1997, **389**:66-69.
36. Dorris MC, Munoz DP: **Saccadic probability influences motor preparation signals and time to saccadic initiation.** *J Neurosci* 1998, **18**:7015-7026.
37. Gallistel CR: **Foraging for brain stimulation: toward a neurobiology of computation.** *Cognition* 1994, **50**:151-170.
38. Shizgall P: **Neural basis of utility estimation.** *Curr Opin Neurobiol* 1997, **7**:198-208.

39. Gold JI, Shadlen MN: **Neural computations that underlie decisions about sensory stimuli.** *Trends Cogn Sci* 2001, **5**:10-16.
This opinion paper formalizes the proposal that decisions arise through the temporal integration of sensory signals favoring one alternative over others. These signals are combined with signals encoding the behavioral value of each option in order to compute a metric of response likelihood. The log likelihood ratio associated with each possible behavioral response can be used to determine the optimal course of action in any context and provides a natural currency for decision-making, because information from a variety of sources can be combined together and in time. The authors describe possible neural correlates of this model in the activation of neurons in parietal and prefrontal cortex. By providing a formal, mathematical description of a neurobiological decision process that combines sensory information with estimates of behavioral value, on the basis of prior experience, this model should prove to be a valuable tool for future investigations of the neurobiology of decision-making.
40. Carpenter R, Williams M: **Neural computation of log likelihood in control of saccadic eye movements.** *Nature* 1995, **377**:59-62.
41. Schultz W: **Predictive reward signal of dopamine neurons.** *J Neurophysiol* 1998, **80**:1-27.
42. Shimo Y, Hikosaka O: **Role of tonically active neurons in primate caudate in reward-oriented saccadic eye movement.** *J Neurosci* 2001, **21**:7804-7814.
43. Berns GS, McClure SM, Pagnoni G, Montague PR: **Predictability modulates human brain response to reward.** *J Neurosci* 2001, **21**:2793-2798.
Berns *et al.* examine the activation of areas of the human brain in response to both predictable and unpredictable rewards using functional magnetic resonance imaging (fMRI). Human subjects underwent fMRI scanning while small amounts of either fruit juice or water were delivered into the mouth, in either predictable or unpredictable sequences. The authors find that the nucleus accumbens, medial orbitofrontal cortex, and a large area of parietal cortex were selectively activated by unpredictable sequences of fluid delivery, and that these activations were independent of subjective preference for fruit juice or water. These regions have also been implicated in reward processing, from neurophysiological data gathered in animals. These data provide support for learning and decision models derived from reward prediction error, and extend these models directly to human neurophysiology.
44. Knutson B, Adams CM, Fong GW, Hommer D: **Anticipation of increasing monetary reward selectively recruits nucleus accumbens.** *J Neurosci* 2001, **21**:RC159.
In this study, activation of the human nucleus accumbens by anticipation of either reward or punishment was investigated. During fMRI scanning, subjects viewed a series of cues indicating whether they had won money or lost money on the previous trial, and their cumulative monetary total at that point. On some trials, subjects could win money or avoid losing money by actively pushing a button during cue presentation. The authors found that the nucleus accumbens was systematically activated during anticipation of increasing monetary rewards, but not losses, and that this activation was associated with reports of positive happiness in subjects. Activation of the medial caudate, in contrast, was associated with anticipation of both monetary rewards and losses. These data suggest a functional segregation in the representation of incentive value and positive incentive value in the ventral striatum.
45. Tremblay L, Schultz W: **Relative reward preference in primate orbitofrontal cortex.** *Nature* 1999, **398**:704-708.
46. Tremblay L, Schultz W: **Reward-related neuronal activity during go-nogo task performance in primate orbitofrontal cortex.** *J Neurophysiol* 2000, **83**:1864-1876.
These authors present evidence that neurons in Brodmann's areas 11, 13, and 14 of primate orbitofrontal cortex encode rewards and stimuli that predict rewards, but do not selectively encode the actions required for obtaining rewards. Monkey subjects performed a Go-NoGo task, in which one cue instructed them to make one of two possible arm movements, and a second cue indicated whether a liquid reward or a sound would follow successful completion of the cued movement. The activity of many neurons was modulated by cues predicting liquid reward and by rewards themselves, but not movement cues or cues predicting an auditory stimulus. Many of these neurons began firing after the reward cue and fired at increasingly higher rates until just after reward delivery. The reward expectation signals reported in this study may be involved in the computation of reward prediction error.
47. O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C: **Abstract reward and punishment representations in the human orbitofrontal cortex.** *Nat Neurosci* 2001, **4**:95-102.
This intriguing fMRI study demonstrates that the human orbitofrontal cortex is activated proportionately by the magnitude of abstract rewards and punishments. Subjects were scanned while they performed a visual choice task for monetary rewards. Two visual stimuli were presented on each trial, and subjects were required to learn which stimulus was associated with monetary gain and which was associated with loss. The authors find that the lateral orbitofrontal cortex is activated following a punishing outcome, and that the medial orbitofrontal cortex is activated following a rewarding outcome. Moreover, the magnitude of activation in each of these two areas, as measured using fMRI, was proportional to positive and negative value, respectively. These data are consistent with neurophysiological studies demonstrating that rewarding and punishing stimuli activate neurons in the orbitofrontal cortex in nonhuman primates. These data are also consistent with the hypothesis that impaired social behavior and decision-making, observed in patients with damage to orbitofrontal and prefrontal cortex, results from deficits in processing rewards and punishments.
48. Shima K, Tanji J: **Role for cingulate motor area cells in voluntary movement selection based on reward.** *Science* 1998, **282**:1335-1338.
49. Stuphorn V, Taylor TL, Schall JD: **Performance monitoring by the supplementary eye field.** *Nature* 2000, **408**:857-860.
The authors of this recent study investigate signals carried by neurons in the supplementary eye field (SEF) of dorsomedial prefrontal cortex. Neuronal activity was monitored in monkeys performing an eye-movement countermanding task, in which monkeys were instructed to shift gaze to a visual target; on some trials, a cue instructed the monkey to cancel the planned saccade. Some neurons were modulated when monkeys failed to cancel the planned movement, some neurons were modulated when monkeys successfully cancelled the planned movement, and some neurons were active before and after the delivery of fluid reward. These data suggest a supervisory role for the SEF, in which neurons signal errors, reinforcement, or response conflict. If so, the SEF might be part of a frontal cortical system that implements executive control over other elements in the decision process.
50. Gold JI, Shadlen MN: **Representation of a decision in developing oculomotor commands.** *Nature* 2000, **404**:390-394.
This elegant study demonstrates that decision formation and movement preparation may share a common neural organization. In this study, microstimulation was delivered to FEFs in monkeys either passively fixating or making judgements of motion direction, in a stochastic random dot display. On fixation trials, FEF stimulation evoked a movement of fixed direction and amplitude. On motion discrimination trials, the saccade evoked by microstimulation deviated in the direction of the monkey's judgement. The magnitude of this deviation was systematically related to the strength of the motion stimulus and viewing time. These data are consistent with the temporal integration of visual motion signals favoring one alternative over another and suggest that sensory decisions occur through the gradual transformation of accumulating sensory information into motor plans.
51. Bruce CJ, Goldberg ME, Bushnell MC, Stanton GB: **Primate frontal eye fields. II. Physiological and anatomical correlates of electrically evoked eye movements.** *J Neurophysiol* 1985, **54**:714-734.
52. Bruce CJ, Goldberg ME: **Primate frontal eye fields. I. Single neurons discharging before saccades.** *J Neurophysiol* 1985, **53**:603-635.
53. Munoz DP, Wurtz RH: **Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells.** *J Neurophysiol* 1995, **73**:2313-2333.
54. Glimcher PW, Sparks DW: **Movement selection in advance of action in the superior colliculus.** *Nature* 1992, **355**:542-545.
55. Salinas E, Romo R: **Conversion of sensory signals into motor commands in primary motor cortex.** *J Neurosci* 1998, **18**:499-511.
56. Hanes DP, Schall JD: **Neural control of voluntary movement initiation.** *Science* 1996, **274**:427-430.
57. Roitman JD, Shadlen MN: **Response of neurons in area LIP during a reaction-time direction discrimination task.** *Soc Neurosci Abstr* 1998, **24**:262.
58. Leon MI, Shadlen MN: **Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque.** *Neuron* 1999, **24**:415-425.
59. Stuphorn V, Taylor TL, Schall JD: **Performance monitoring by the supplementary eye field.** *Nature* 2000, **408**:857-860.
60. Platt ML, Glimcher PW: **Neural correlates of decision variables in parietal cortex.** *Nature* 1999, **400**:233-238.