

# Neural computations that underlie decisions about sensory stimuli

Joshua I. Gold and Michael N. Shadlen

**Decision-making behavior has been studied extensively, but the neurophysiological mechanisms responsible for this remarkable cognitive ability are just beginning to be understood. Here we propose neural computations that can account for the formation of categorical decisions about sensory stimuli by accumulating information over time into a single quantity: the logarithm of the likelihood ratio favoring one alternative over another. We also review electrophysiological studies that have identified brain structures that may be involved in computing this sort of decision variable. The ideas presented constitute a framework for understanding how and where perceptual decisions are formed in the brain.**

The brain is a powerful decision-maker, able to form judgments about issues as simple as whether a sensory stimulus is present to those as complex as what career to choose or whom to marry. How are these judgments formed? Decision analysis in such diverse fields as biology, computer science, economics, political science and psychology has provided valuable insights into which factors are taken into account and how those factors are combined to form a decision<sup>1-3</sup>. However, because these insights are derived from behavior, they are inherently limited in terms of their ability to reveal the inner workings of the brain during decision formation. To achieve this level of understanding, investigators have begun to measure neural activity in subjects, usually monkeys, performing perceptual tasks that require decision formation (see Fig. 1 for an example of this kind of task). The aim of this article is to synthesize from these results a framework for understanding the neural basis of the decision process.

We develop this framework in three stages. First, we discuss the likelihood ratio (LR), a simple quantity that expresses the relative probability that a particular hypothesis is favored over the alternatives. We show why the logarithm of the likelihood ratio (logLR) provides a natural currency for trading off sensory information, prior probability and expected value to form a perceptual decision. Second, we describe how neurons can compute the logLR from the representation of sensory information in the brain. Third, we propose that this neural computation, representing the formation of a perceptual decision, occurs in structures in the brain that are involved in the preparation for action.

## The likelihood ratio

Consider the following problem. You are given a single measurement from a light detector, which you must use

to decide whether a dim light is on or off at a specified location. Unfortunately, the detector does not indicate with certainty whether or not light is present. Instead, it indicates a value from 0 to 9 in the presence or absence of light, with some values being more likely than others when light is present (see Box 1). How do you use the value from the detector to decide if the light was present?

This problem consists of deciding which hypothesis – light is present ( $h_1$ ) or light is absent ( $h_2$ ) – is most likely to be true given the evidence in the form of the value indicated on the detector. The evidence ( $e$ ) bears on the *likelihood* of each of the hypotheses. Likelihood is defined as the conditional probability of obtaining  $e$ , given that a particular hypothesis is true. Likelihood is considered a function of the given hypothesis, but it is worth noting that the likelihood for a hypothesis is not the same as the probability that it is true. For example, a low barometer reading might suggest that rain is more likely than not, but the probability of rain depends on other factors, like whether the reading was obtained from a desert or rain forest. Nevertheless, likelihood is useful because a decision does not require knowledge of the probability of  $h_1$ , but merely whether  $h_1$  is more likely than  $h_2$ .

The decision can be made by computing the LR, which describes the likelihood that  $e$  would be obtained if  $h_1$  were true relative to the likelihood that  $e$  would be obtained if  $h_2$  were true:

$$LR_{1,2|e} \equiv \frac{\Pr(e|h_1)}{\Pr(e|h_2)} \quad [1]$$

A reasonable decision rule is as follows: for a given  $e$ , if  $LR > 1$  then  $h_1$  is more likely than  $h_2$ , so decide  $h_1$ ; otherwise, decide  $h_2$ . As shown in Box 1,  $LR > 1$  when  $e \geq 5$ , so an effective use of the detector is to decide that light is present when the value indicated is  $\geq 5$ .

The rule is easily adjusted to incorporate a variety of factors. For example, suppose that there is only a one in ten chance that  $h_1$  is true (light is present), independent of the evidence from the detector. This ‘prior probability’ implies that more evidence is required to support a decision in favor of  $h_1$ . In fact, the optimal rule is to choose  $h_1$  when

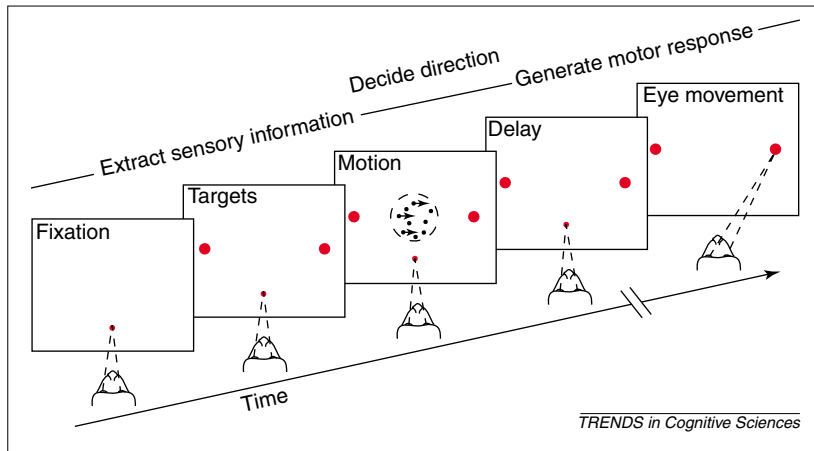
$$LR_{1,2|e_1} > \frac{\Pr(h_2)}{\Pr(h_1)} \quad [2]$$

that is, when  $LR > 9$  in this case. The rule also accommodates multiple observations ( $e_1, e_2$ , etc.). If the observations are independent, then the LR based on  $n$  observations is the product of the LRs:

$$LR_{1,2|e_1, e_2, \dots, e_n} = LR_{1,2|e_1} \cdot LR_{1,2|e_2} \cdots LR_{1,2|e_n} \quad [3]$$

For example, if the light is equally likely to be on or off and sequential readings from the detector are 4 and 3, then the decision should be  $h_2$  because LR is 0.4 (see Box 1), which is less than 1. Finally, the rule can be used to factor in the anticipated costs and benefits associated with the various outcomes, which can strongly affect many forms of decision-making<sup>1</sup>. When the hypotheses are equally likely, the decision

Joshua I. Gold  
Michael N. Shadlen\*  
Department of Physiology and Biophysics, HHMI and Regional Primate Research Center, University of Washington Medical School, Box 357290, Seattle, WA 98195-7290, USA.  
\*e-mail: shadlen@u.washington.edu



**Fig. 1.** Direction-discrimination task used in studies considered in this review. In most versions of the task, the subject (often a monkey) fixates for a few hundred milliseconds. Two targets then appear, indicating the two possible directions of motion. Next, dynamic random-dot motion<sup>10</sup> is presented between the two targets. The monkey is trained to decide the direction of motion and, after the fixation point is turned off, to indicate its decision by making an eye movement to one of the targets. The task is made difficult by controlling the fraction of random dots that move coherently at any moment (e.g. Ref. 10) and the length of time that the random dots are displayed (e.g. Ref. 20). In some experiments, the monkey must remember its decision through a delay period after the random dots are turned off.

rule that provides the most benefit on average is to choose  $h_1$  when

$$LR_{1,2|e_1} > \frac{(V_{22} - V_{21})}{(V_{11} - V_{12})} \quad [4]$$

where  $V_{ij}$  is the expected value (benefits are positive, costs are negative) associated with choosing hypothesis  $j$  when hypothesis  $i$  is true. Combining Eqns 2–4, we obtain a general decision rule (for an extensive treatment of this derivation, see Ref. 4, especially pp. 7–29):

$$LR_{1,2|e_1} \cdot LR_{1,2|e_2} \dots \cdot LR_{1,2|e_n} \cdot \frac{\Pr(h_1)}{\Pr(h_2)} \cdot \frac{(V_{11} - V_{12})}{(V_{22} - V_{21})} > 1 \quad [5]$$

The left side of Eqn 5 combines measurements from multiple sources – or multiple measurements from the same source over time – with knowledge of prior probabilities and anticipated costs and benefits into a single quantity, called a decision variable.

A notable property of this kind of decision rule is that it can accommodate more than two alternatives, because multiple LRs can be computed and compared<sup>4</sup>. In principle, even a single LR can be used to decide whether the evidence supports one hypothesis ( $h_1$ ) versus a set of multiple alternatives ( $h_2 = \text{'not } h_1$ '). Another interesting property is that any quantity that is monotonically related to the decision variable can be used to generate an equivalent rule (given an appropriate criterion value)<sup>4</sup>. For example, the monotonic relationship between the output of the light detector and the associated LRs implies that equivalent decision rules can be found using either quantity. Similarly, taking the logarithms of the two sides of the inequality in Eqn 5 yields an equivalent decision rule, in which  $h_1$  is chosen when

$$\log LR_{1,2|e_1} + \log LR_{1,2|e_2} \dots + \log LR_{1,2|e_n} + \log \left[ \frac{\Pr(h_1)}{\Pr(h_2)} \right] + \log \left[ \frac{V_{11} - V_{12}}{V_{22} - V_{21}} \right] > 0 \quad [6]$$

This rule is interesting because it demonstrates that simple addition can be used to accumulate information towards a decision. Moreover, this accumulating information is easily interpreted: a positive value indicates support for  $h_1$ , a negative value indicates support for the alternative(s),  $h_2$ .

In short, the logLR (or, equivalently, the LR) could provide a currency that allows information from a variety of sources to be combined together and over time. Accumulation of this currency over time represents an evolving decision variable that can be compared with a criterion value in order to reach a perceptual judgment<sup>5</sup>.

### The difference between two opposing sensors is proportional to the logLR

Having discussed the usefulness of the logLR, we will now demonstrate that neurons can compute an approximation to this quantity. Consider the light-detection problem, but instead of a mechanical device you are given the output of a light-sensitive neuron (measured in spikes per second). Like the device, the neural response can vary considerably but tends to be higher when the light is present. As shown in Fig. 2a, the neuron's output in the presence and absence of light can be characterized with a probability density function (PDF) for each condition, which we will refer to as  $f(e|h_1)$  and  $f(e|h_2)$ , respectively.

Given a particular output of this neuron ( $e_k$ ), it is possible to decide whether light is likely present ( $h_1$ ) or absent ( $h_2$ ) by computing the LR from the two PDFs. The likelihood of obtaining  $e_k$  in the presence of light is the height of the 'light present' PDF, corresponding to  $f(e|h_1)$ , at the value  $e_k$ . Similarly, the likelihood of obtaining  $e_k$  in the absence of light is the height of the PDF corresponding to  $f(e|h_2)$ , at the value  $e_k$ . As with the device, a decision can then be made by determining whether the ratio of these likelihoods is greater or less than 1.

The problem with evaluating the LR in this manner is that the brain would need to know the information represented by the PDFs. In other words, the brain would need to store the information that allows it to infer the likelihood that a neuron (or ensemble of neurons) responds in a certain way under the two hypotheses under consideration. Moreover, the brain would need to take into account a potentially large range of conditions that can affect the neural responses, including changes in both excitability and stimulus conditions. For example, a neuron that responds to light in its receptive field might respond more or less depending on the light's color or direction of motion. Depending on these factors, the distributions of the neuron's responses with light present or absent could vary considerably.

### Equivalent decision rules

A simpler approach is to implement an equivalent decision rule that does not depend on an evaluation of the LR from a representation of the PDFs. Recall that equivalent rules can be found using quantities that are monotonically related to the LR, as we showed for

### Box 1. Using the likelihood ratio

A hypothetical light detector can indicate a value ( $e$ ) of 0 to 9 in the presence or absence of light. As indicated in Table I, the detector tends to indicate higher values in the presence of light. Columns 2 and 3 indicate the number of trials in which each value  $e$  was indicated in a block of 450 'light-present' trials and 450 'light-absent' trials, respectively. Columns 4 and 5 convert these counts into conditional probabilities, or likelihoods. The ratio of these likelihoods ( $LR_{1,2|e}$ ) indicates whether it was more likely to be true that light was present or that light was absent for each given  $e$ . Specifically, when  $LR_{1,2|e} > 1$ , 'present' was more likely. Therefore, to use the detector, read the value  $e$  and then decide 'present' if  $LR_{1,2|e} > 1$ . This is equivalent to deciding 'present' if the value  $e \geq 5$ .

**Table I. Calculating the light likelihood for a hypothetical light detector**

Detector value ( $e$ )	No. light-present trials ( $h_1$ )	No. light-absent trials ( $h_2$ )	$Pr(e h_1)$	$Pr(e h_2)$	$LR_{1,2 e}$
0	0	90	0.00	0.20	0.0
1	10	80	0.02	0.17	0.1
2	20	70	0.04	0.15	0.3
3	30	60	0.06	0.13	0.5
4	40	50	0.08	0.11	0.8
5	50	40	0.11	0.08	1.3
6	60	30	0.13	0.06	2.0
7	70	20	0.15	0.04	3.5
8	80	10	0.17	0.02	8.0
9	90	0	0.20	0.00	inf

the output of the light-detection device (Box 1). We next develop the idea that the brain can easily approximate such a quantity – the logLR – from the activity (measured as a rate, in spikes per second) of certain sensory neurons.

Consider a single sensory neuron (or pool of neurons) that responds with variable discharge under two conditions,  $h_1$  and  $h_2$ . Assume that the responses under the two conditions are described by normal distributions with means  $\mu_1 > \mu_2$  and standard deviations  $\sigma_1 = \sigma_2$  (denoted as  $\sigma$ ). Accordingly,

$$LR_{1,2|x} = \frac{\exp\left[-\frac{1}{2\sigma^2}(x - \mu_1)^2\right]}{\exp\left[-\frac{1}{2\sigma^2}(x - \mu_2)^2\right]} \quad [7]$$

and

$$\begin{aligned} \log LR_{1,2|x} &= -\frac{1}{2\sigma^2}[(x - \mu_1)^2 - (x - \mu_2)^2] \quad [8] \\ &= -\frac{1}{2\sigma^2}[2x(\mu_2 - \mu_1) + \mu_1^2 - \mu_2^2] \end{aligned}$$

where  $x$  is the neuron's response in spikes/s. Notice that the logLR is a linear function of  $x$ , so  $x$  and the LR are monotonically related (Fig. 2a). This relationship indicates that an optimal decision rule based on  $x$  is possible: when  $x > (\mu_1 + \mu_2)/2$  (i.e. when  $\log LR > 0$ ), decide  $h_1$ ; otherwise decide  $h_2$ .

According to this formulation, a decision is made by comparing the neural response  $x$  with a criterion value. There is some experimental evidence that the brain uses this kind of decision rule. For example, a

criterion level of responses from neurons involved in the generation of eye movements appears to signal a decision to make a particular, visually guided movement<sup>6</sup>. However, the rule derived from Eqn 8 has a familiar problem: the criterion,  $(\mu_1 + \mu_2)/2$ , like the PDFs, must take into account anything that affects  $\mu_1$  or  $\mu_2$ , including changes in neuronal excitability or different stimulus conditions. In other words, to interpret the evidence  $x$  as favoring  $h_1$  or  $h_2$ , the brain must know how the sensory neuron would be expected to respond, on average, under the given conditions.

### Neurons and antineurons

This problem can be solved by incorporating a second neuron or group of neurons whose responses ( $y$ ) are in opposition to those of the first ( $x$ ). Specifically, these 'antineurons'<sup>7</sup> respond, on average, with a rate of  $\mu_2$  when  $h_1$  is true and with a rate of  $\mu_1$  when  $h_2$  is true (see Eqn 7). For the light-detector example, an antineuron would be more likely to give a larger response in the absence than in the presence of light. Another example is a motion-sensitive neuron that tends to respond best to rightward motion, paired with an antineuron that tends to respond best to leftward motion. The logLR in favor of  $h_1$  versus  $h_2$  for the antineuron is (see Eqn 8)

$$\log LR_{1,2|y} = -\frac{1}{2\sigma^2}[2y(\mu_1 - \mu_2) + \mu_2^2 - \mu_1^2] \quad [9]$$

Note that Eqn 9, in contrast to Eqn 8, predicts a smaller response when  $h_1$  is true than when  $h_2$  is true.

The logLR now depends on both observations,  $x$  and  $y$ , from this neuron/antineuron pair:

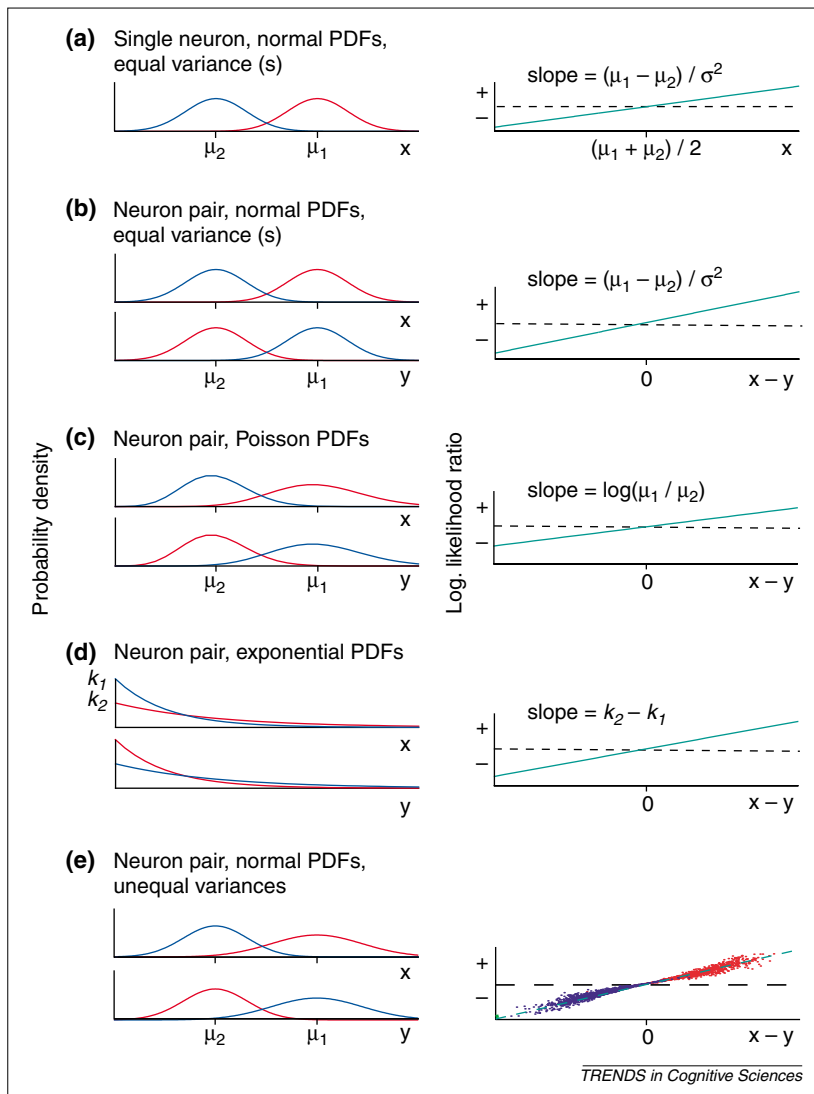
$$\log LR_{1,2|x,y} = \log LR_{1,2|x} + \log LR_{1,2|y} \quad [10a]$$

By combining Eqns 8 and 9, this becomes:

$$\log LR_{1,2|x,y} = \frac{\mu_1 - \mu_2}{\sigma^2}(x - y) \quad [10b]$$

According to this formulation, to interpret the sensory evidence as favoring  $h_1$  or  $h_2$ , the brain does not need to know how the sensory neurons would be expected to respond under a variety of conditions. Instead, the brain needs to know only the sign of the difference  $(x - y)$ : a positive difference implies that  $h_1$  is more likely, whereas a negative difference implies that  $h_2$  is more likely. In short, a simple difference in neural activity, measured in spikes per second, comprises a decision variable that is proportional to the logLR.

At first glance, this neuron/antineuron formulation appears to suffer from the same problems as previous expressions, because Eqn 10b depends on  $\mu_1$ ,  $\mu_2$  and  $\sigma$ . However, these factors affect only a scaling term,  $(\mu_1 - \mu_2)/\sigma^2$ . This term would influence how the sensory evidence is weighed when combined with other sources of information, like knowledge of prior probabilities (see Eqn 6), but not whether the evidence supports one hypothesis or another. It should also be noted that the scaling depends on a difference,  $\mu_1 - \mu_2$ , and would therefore tend to be insensitive to factors



**Fig. 2.** Theoretical relationship between neuronal response and log likelihood ratio (logLR). The graphs illustrate that the difference in spike rates from two appropriately chosen neurons (or neural ensembles) can approximate the logLR favoring one hypothesis over another. **(a)** Calculation of the logLR using the response from a single neuron. The red and blue curves are probability density functions (PDFs) that describe the hypothetical distributions of responses from a sensory neuron when either hypothesis  $h_1$  or  $h_2$  respectively, is true. For example, these curves could represent the PDFs from a direction-selective neuron that prefers rightward motion when the stimulus motion is rightward (red) or leftward (blue). The green curve represents the logLR computed from a single observation,  $x$ , as the log of the ratio of heights of the PDFs at  $x$ . Note that knowledge of the PDFs is required to determine whether the response  $x$  favors  $h_1$  ( $\log\text{LR} > 0$ ) or  $h_2$  ( $\log\text{LR} < 0$ ). **(b-e)** Calculation of the logLR using the responses from two neurons assuming a variety of forms of the PDFs, as indicated. In each case, the PDF from a second neuron is shown below the first. This 'antineuron' responds best when  $h_2$  is true (blue curves). The green curves represent the logLR computed from two observations,  $x$  and  $y$ , from the neuron/antineuron pair. In (b-d), the logLR is proportional to the difference ( $x - y$ ). Note that knowledge of the PDFs is not required to interpret this difference: a positive value indicates support for  $h_1$ , a negative value indicates support for  $h_2$ . In (e), the relationship between the logLR and the difference ( $x - y$ ) is not linear (the red and blue points indicate this relationship for 1000 random samples of  $x$  and  $y$  from the distributions shown when  $h_1$  or  $h_2$  was true, respectively, and the green curve is a linear fit to these points). Nevertheless, in nearly all cases the difference can be interpreted correctly as favoring  $h_1$  or  $h_2$ .

that affect the neuron and antineuron equivalently, such as the overall excitability of the cortical network.

The principle that a difference in spike rates is proportional to the logLR is valid under a variety of assumptions. Expressions similar to the one in Eqn 10b follow if the responses of the neuron and antineuron are described by normal distributions with equal variances (Eqns 7 – 10; Fig. 2b), Poisson

distributions (Fig. 2c) or exponential distributions (Fig. 2d). Even when the principle does not hold exactly, it may be a useful approximation (e.g. normal distributions with unequal variances; Fig. 2e).

### Where in the brain are decisions formed?

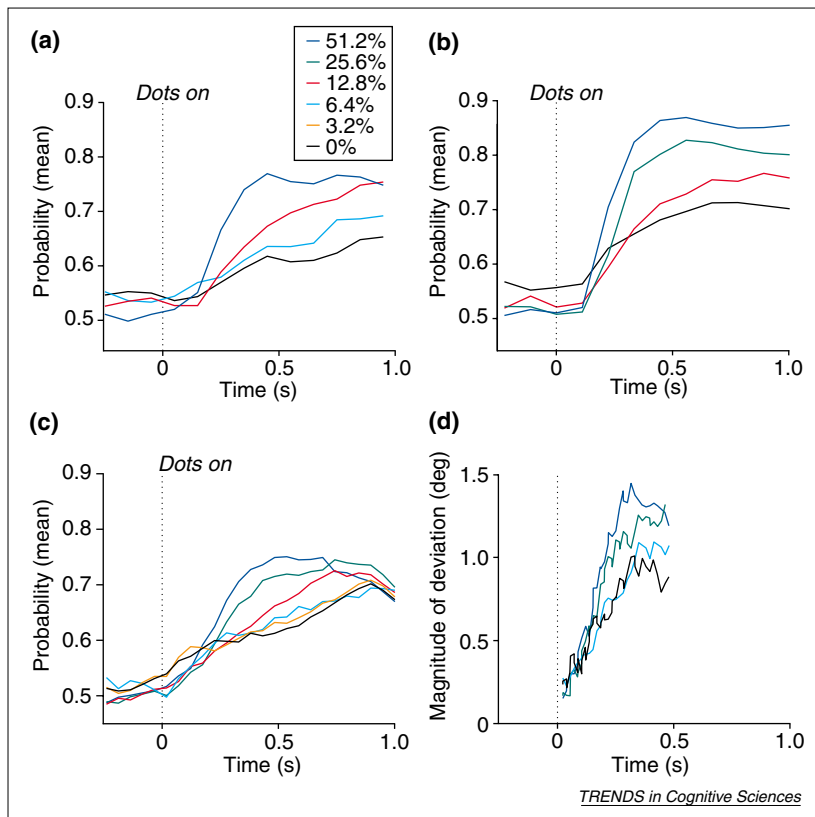
According to our computational framework, neurons form decisions by calculating the difference in spike rates from appropriately chosen neurons. This difference approximates the logLR, a quantity that allows sensory information, prior probabilities and reward expectation to be combined into a single decision variable. Below, we review experimental evidence that the neurons that compute this kind of decision variable are found in brain structures involved in planning for action. First, we show that neural responses in these structures represent the sensory information that is required for decision formation. Second, we discuss evidence that responses in these circuits are also affected by knowledge of prior probabilities and expectation of reward in decision-making.

### Representation of sensory signals that contribute to decision formation

Perceptual-decision formation requires at least two stages of neural processing: first, sensory neurons to represent features of the stimulus, and second, neurons to calculate the decision variable from responses of neurons in the first stage<sup>8</sup>. Neurons in sensory cortex appear to fulfill the role of the first stage. For example, motion-sensitive neurons in extrastriate visual cortex have been shown via physiological, lesion and microstimulation studies to encode the information needed to discriminate the direction of random-dot motion (see Fig. 1)<sup>9-13</sup>. Likewise, neurons in somatosensory cortex encode the frequency of vibration of a tactile stimulus and have been shown to play a role in solving a vibrotactile-discrimination task<sup>14-16</sup>.

However, sensory neurons respond to stimuli in a moment-by-moment manner (e.g. Refs 17,18), whereas decisions often depend on more persistent neural activity. For example, the variable responses from sensory neurons must be accumulated in time to explain performance accuracy in motion-discrimination tasks<sup>13,19,20</sup>. Moreover, a sustained representation of sensory evidence is required for the discrimination or interpretation of sequentially presented stimuli<sup>21-23</sup>. These observations support the idea that to form decisions, an additional stage of processing is necessary to accumulate sensory responses from pools of neurons and over time<sup>19,24-29</sup>.

Anatomical and physiological evidence indicates that neurons in the parietal and frontal 'association cortex' are well positioned to provide this second stage of processing. These neurons have been shown to carry signals that reflect sensory qualities, such as visual saliency<sup>30,31</sup>, and involvement in motor planning<sup>32,33</sup>. For example, in monkeys trained to shift their gaze to a visual target defined by a conjunction of shape and color, responses of single neurons in the frontal eye field (FEF) both



**Fig. 3.** Neural representation of a decision variable in brain structures devoted to eye movements. The data are from four experiments that measured neural signals related to the accumulation of information about random-dot motion during the direction-discrimination task (see Fig. 1). 'Dots on' refers to the onset of dynamic random-dot motion. **(a–c)** Ideal observer analysis on pooled data from direction-selective neurons, plotted as a function of viewing duration and separated by motion strength (the percentage of coherently moving dots; see key). The ordinate represents the probability of correctly predicting the monkey's decision from 100–250 ms of spike discharge. **(a)** Area LIP,  $n = 47$  (adapted from Ref. 49). **(b)** Superior colliculus,  $n = 44$  (adapted from Ref. 51). **(c)** Prefrontal cortex,  $n = 53$  (adapted from Ref. 50). **(d)** The effect of motion strength and viewing duration on eye movements evoked with electrical microstimulation of the FEF (adapted from Ref. 20). The evolving decision variable was evident in the magnitude of deviation, defined as the dot product between the vector defined by the endpoint of the electrically evoked eye movement and the unit vector in the direction of the subsequently selected target. Data are from trials in which correct responses were made.

discriminate the target from distractors and indicate the impending eye-movement response<sup>34</sup>. In addition, neurons in these association areas are active through instructed delays and appear to carry the sustained signals needed to link sensation to action for some perceptual tasks<sup>33,35</sup>. We propose that this persistent activity represents information from sensory cortex that has been accumulated into a decision variable that guides behavior.

#### Preparation for potential actions

An interesting characteristic of this kind of decision-related activity in association cortex is that it tends to involve neurons that are linked to a specific behavioral response. For example, neurons in frontal and parietal oculomotor regions that signal visual saliency also respond selectively in anticipation of an impending eye movement with a particular trajectory<sup>33,36–38</sup>. Similarly selective neurons in predominantly motor structures, like primary motor cortex, also appear to represent the sensory signals used to select the motor response<sup>39–42</sup>. These results suggest that the formation of decisions about sensory information may involve both

association and motor structures that are involved in planning bodily action, an idea reminiscent of a cognitive theory referred to as embodiment<sup>43</sup>.

We wish to emphasize that this idea about brain organization does not require decision formation to be coupled with an overt behavioral response. The identification of persistent activity in motor-planning structures suggests that sensory information may be interpreted in a 'pragmatic' framework that includes representations of potential or deferred actions<sup>44,45</sup>. For example, areas of the prefrontal cortex appear to play important roles in tasks involving sensory-motor integration with delayed action<sup>22,46,47</sup> and the linkage of a perceptual judgment with different behavioral responses<sup>48</sup>. Thus, neural circuits involved in preparation for potential action may play a general role in perceptual-decision formation.

A series of recent experiments using a direction-discrimination task (see Fig. 1) illustrates this principle. For this task, a monkey is trained to make a decision about the net direction of random dots that appear on a video monitor. The task is easy when a large fraction of the dots are moving coherently at any moment, and the monkey can decide correctly in a short time. By contrast, when only a small fraction are moving coherently, the monkey requires more time and makes more errors<sup>20</sup>. This relationship between motion strength, viewing duration and performance accuracy suggests that the monkey's decision forms gradually as the sensory evidence accumulates over time. As illustrated in Fig. 3a–c, neural correlates of this accumulation have been found in sensorimotor-integration areas that contain persistent activity related to planning eye movements<sup>49–51</sup>.

Based on these results, we reasoned that the accumulating sensory evidence might be detected in commands to generate the eye-movement response. To test this idea, we evoked eye movements by interrupting the motion-viewing period with electrical microstimulation of the FEF (Fig. 3d)<sup>20</sup>. The trajectories of these evoked eye movements indicated that formation of the monkey's decision corresponded to the development of commands to move the eyes to the appropriate choice target (see Fig. 1). These commands reflected an accumulation of the difference in responses between pools of motion-sensitive neurons in extrastriate visual cortex that represent the two possible directions of motion. Thus, for this task, an evolving decision variable based on the logLR appears to be represented in structures that play a role in guiding the eye-movement response.

#### Representation of psychological factors that contribute to decision formation

An advantage of forming decisions by calculating the logLR is the ability to incorporate information from numerous sources. Simple addition can be used to accumulate both sensory information and psychological factors like prior probability and anticipated value (Eqn 6). This idea predicts that the action-oriented

circuits thought to be involved in interpreting sensory information toward a perceptual decision also reflect psychological factors that influence decision formation.

For tasks involving visually guided eye movements, neural correlates of prior probability have been found in circuits involved in generating the oculomotor response. In these experiments, the probability that a saccade to a particular target would be required was varied systematically, by changing either the number of possible target locations<sup>52,53</sup> or the relative probabilities of the target appearing at particular locations within blocks of trials<sup>54,55</sup>. In addition to affecting saccadic metrics and response times, these probabilities caused an offset in the responses of neurons in both the superior colliculus<sup>52–54</sup> and LIP<sup>55</sup> before and during presentation of the saccade target.

Likewise, anticipated reward has been shown to affect the responses of neurons thought to be involved in decision formation. For example, varying the size of a juice reward associated with each outcome of a visual task has been shown to modulate the activity of neurons in area LIP<sup>55</sup>. Similar reward-related activity has been

observed in lateral prefrontal and orbitofrontal cortex<sup>56–60</sup>. This kind of activity is thought to reflect an ongoing assessment of the difference between actual and predicted reward, which, analogous to the ‘anticipated value’ term in our formulation (Eqns 4–6), may be used to modulate signals involved in forming decisions that guide actions<sup>61</sup>.

### Conclusion

We have presented a framework that describes how the brain makes decisions about simple perceptual stimuli. A categorical decision arises through the evaluation of a decision variable that approximates the log of the likelihood ratio favoring one hypothesis over another. We noted that the logLR is a natural currency for combining sensory evidence obtained from multiple sources – or from multiple samples in time – with prior probability and anticipated costs and benefits. We showed that under a variety of assumptions, the logLR can be easily computed by comparing the spike rates from two groups of sensory neurons, one that responds more strongly under one hypothesis and the other that responds more strongly under the alternative.

Recent experiments have suggested that the logLR is accumulated and represented in neural structures that are involved in planning actions. Because these structures lie at the nexus of sensory and motor processing, it is perhaps not surprising that they play a role in transforming sensory information into a decision that guides behavior. What may be more surprising is that activity in these structures can be influenced by psychological factors that can bias decisions.

It is hoped that these ideas can guide a more general understanding of how the brain forms decisions. However, it is worth noting that many aspects of this framework remain unproven, even for simple perceptual tasks. Moreover, their relevance to the myriad other decisions that the brain is capable of making is unclear. These and other outstanding questions are currently motivating this active area of research.

### Acknowledgements

The authors thank Matt Leon, Mark Mazurek, John Palmer and Fred Rieke for helpful comments on the manuscript.

### Outstanding questions

- Where are perceptual decisions formed in the brain?
- How does the brain learn to route the information about a particular stimulus to the response process appropriate for the given task? Does attention affect this routing?
- How are psychological factors such as prior probability and reward expectation incorporated into the decision process?
- How and when does a signal representing the accumulation of information used to reach a decision actually indicate the decision?
- What neural computations are responsible for decisions that involve more than two hypotheses?
- Which neural circuits are responsible for decisions that are not linked to a particular action?
- Which neural circuits are responsible for decisions that are not based on sensory perception?

### References

- 1 von Neumann, J. and Morgenstern, O. (1944) *The Theory of Games and Economic Behavior*, Princeton University Press
- 2 Savage, L.J. (1972) *The Foundations of Statistics (2nd revised edn)*, Dover
- 3 Goldstein, W.M. and Hogarth, R.M., eds (1997) *Research on Judgment and Decision Making: Currents, Connections, and Controversies*, Cambridge University Press
- 4 Green, D.M. and Swets, J.A. (1966) *Signal Detection Theory and Psychophysics*, John Wiley & Sons
- 5 Carpenter, R. and Williams, M. (1995) Neural computation of log likelihood in control of saccadic eye movements. *Nature* 377, 59–62
- 6 Hanes, D.P. and Schall, J.D. (1996) Neural control of voluntary movement initiation. *Science* 274, 427–430
- 7 Newsome, W.T. et al. (1989) Neuronal correlates of a perceptual decision. *Nature* 341, 52–54
- 8 Graham, N.V.S. (1989) *Visual Pattern Analysers*, Oxford University Press
- 9 Newsome, W.T. and Paré, E.B. (1988) A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J. Neurosci.* 8, 2201–2211
- 10 Britten, K.H. et al. (1992) The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.* 12, 4745–4765
- 11 Salzman, C.D. et al. (1992) Microstimulation in visual area MT: effects on direction discrimination performance. *J. Neurosci.* 12, 2331–2355
- 12 Albright, T.D. (1993) Cortical processing of visual motion. In *Visual Motion and Its Role in the Stabilization of Gaze* (Miles, F.A. and Wallman, J., eds), pp. 177–201, Elsevier
- 13 Parker, A.J. and Newsome, W.T. (1998) Sense and the single neuron: probing the physiology of perception. *Annu. Rev. Neurosci.* 21, 227–277
- 14 Mountcastle, V.B. et al. (1969) Cortical neuronal mechanisms in flutter-vibration studied in unanesthetized monkeys: neuronal periodicity and frequency discrimination. *J. Neurophysiol.* 32, 452–484
- 15 Romo, R. et al. (1998) Somatosensory discrimination based on cortical microstimulation. *Nature* 392, 387–390
- 16 Romo, R. et al. (2000) Sensing without touching: psychophysical performance based on cortical microstimulation. *Neuron* 26, 273–278
- 17 Seidemann, E. et al. (1998) Temporal gating of neural signals during performance of a visual discrimination task. *Nature* 394, 72–75
- 18 Hernandez, A. et al. (2000) Neuronal correlates of sensory discrimination in the somatosensory cortex. *Proc. Natl. Acad. Sci. U. S. A.* 97, 6191–6196
- 19 Shadlen, M.N. et al. (1996) A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *J. Neurosci.* 16, 1486–1510
- 20 Gold, J.I. and Shadlen, M.N. (2000) Representation of a perceptual decision in developing oculomotor commands. *Nature* 404, 390–394
- 21 Boussaoud, D. and Wise, S.P. (1993) Primate frontal cortex: neuronal activity following attentional versus intentional cues. *Exp. Brain Res.* 95, 15–27
- 22 Miller, E.K. et al. (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.* 16, 5154–5167
- 23 Romo, R. et al. (1999) Neuronal correlates of parametric working memory in the prefrontal cortex. *Nature* 399, 470–473
- 24 Johnson, K.O. (1980) Sensory discrimination: decision process. *J. Neurophysiol.* 43, 1771–1792
- 25 Johnson, K.O. (1980) Sensory discrimination: neural processes preceding discrimination decision. *J. Neurophysiol.* 43, 1793–1815
- 26 Seung, H.S. and Sompolinsky, H. (1993) Simple models for reading neuronal population codes. *Proc.*

- Natl. Acad. Sci. U. S. A.* 90, 10749–10753
- 27 Deneve, S. *et al.* (1999) Reading population codes: a neural implementation of ideal observers. *Nat. Neurosci.* 2, 740–745
- 28 Prince, S.J. *et al.* (2000) The precision of single neuron responses in cortical area V1 during stereoscopic depth judgments. *J. Neurosci.* 20, 3387–3400
- 29 Recanzone, G.H. *et al.* (2000) Correlation between the activity of single auditory cortical neurons and sound-localization behavior in the macaque monkey. *J. Neurophysiol.* 83, 2723–2739
- 30 Schall, J.D. and Bichot, N.P. (1998) Neural correlates of visual and motor decision processes. *Curr. Opin. Neurobiol.* 8, 211–217
- 31 Colby, C.L. and Goldberg, M.E. (1999) Space and attention in parietal cortex. *Annu. Rev. Neurosci.* 22, 319–349
- 32 Bruce, C.J. and Goldberg, M.E. (1985) Primate frontal eye fields: I. Single neurons discharging before saccades. *J. Neurophysiol.* 53, 603–635
- 33 Snyder, L.H. *et al.* (2000) Intention-related activity in the posterior parietal cortex: a review. *Vis. Res.* 40, 1433–1442
- 34 Bichot, N.P. and Schall, J.D. (1999) Effects of similarity and history on neural mechanisms of visual selection. *Nat. Neurosci.* 2, 549–554
- 35 Quintana, J. and Fuster, J. (1999) From perception to action: temporal integrative functions of prefrontal and parietal neurons. *Cereb. Cortex.* 9, 213–221
- 36 Colby, C.L. and Goldberg, M.E. (1999) Space and attention in parietal cortex. *Annu. Rev. Neurosci.* 22, 319–349
- 37 Platt, M.L. and Glimcher, P.W. (1997) Response of intraparietal neurons to saccade targets and visual distractors. *J. Neurophysiol.* 78, 1574–1589
- 38 Schall, J. and Thompson, K. (1999) Neural selection and control of visually guided eye movements. *Annu. Rev. Neurosci.* 22, 241–259
- 39 Shen, L. and Alexander, G.E. (1997) Neural correlates of a spatial sensory-to-motor transformation in primary motor cortex. *J. Neurophysiol.* 77, 1171–1194
- 40 Zhang, J. *et al.* (1997) Dynamics of single neuron activity in monkey primary motor cortex related to sensorimotor transformation. *J. Neurosci.* 17, 2227–2246
- 41 Salinas, E. and Romo, R. (1998) Conversion of sensory signals into motor commands in primary motor cortex. *J. Neurosci.* 18, 499–511
- 42 Fadiga, L. *et al.* (2000) Visuomotor neurons: ambiguity of the discharge or 'motor' perception? *Int. J. Psychophysiol.* 35, 165–177
- 43 Thelen, E. *et al.* The dynamics of embodiment: a field theory of infant perseverative reaching. *Behav. Brain Sci.* (in press)
- 44 Jeannerod, M. (1994) The representing brain: Neural correlates of motor intention and imagery. *Behav. Brain Sci.* 17, 187–245
- 45 Rizzolatti, G. *et al.* (1994) Space and selective attention. In *Attention and Performance XV: Conscious and Unconscious Information Processing* (Umiltà, C. and Moscovitch, M., eds), pp. 231–265, MIT Press
- 46 Fuster, J. (1989) *The Prefrontal Cortex*. Raven Press
- 47 Funahashi, S. *et al.* (1993) Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature* 365, 753–756
- 48 di Pellegrino, G. and Wise, S. (1993) Visuospatial versus visuomotor activity in the premotor and prefrontal cortex of a primate. *J. Neurosci.* 13, 1227–1243
- 49 Shadlen, M.N. and Newsome, W.T. (1996) Motion perception: seeing and deciding. *Proc. Natl. Acad. Sci. U. S. A.* 93, 628–633
- 50 Kim, J.-N. and Shadlen, M.N. (1999) Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat. Neurosci.* 2, 176–185
- 51 Horwitz, G.D. and Newsome, W.T. (1999) Separate signals for target selection and movement specification in the superior colliculus. *Science* 284, 1158–1161
- 52 Basso, M.A. and Wurtz, R.H. (1997) Modulation of neuronal activity by target uncertainty. *Nature* 389, 66–69
- 53 Basso, M.A. and Wurtz, R.H. (1998) Modulation of neuronal activity in superior colliculus by changes in target probability. *J. Neurosci.* 18, 7519–7534
- 54 Dorris, M.C. and Munoz, D.P. (1998) Saccadic probability influences motor preparation signals and time to saccadic initiation. *J. Neurosci.* 18, 7015–7026
- 55 Platt, M.L. and Glimcher, P.W. (1999) Neural correlates of decision variables in parietal cortex. *Nature* 400, 233–238
- 56 Watanabe, M. (1996) Reward expectancy in primate prefrontal neurons. *Nature* 382, 629–632
- 57 Leon, M.I. and Shadlen, M.N. (1999) Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron* 24, 415–425
- 58 Tremblay, L. and Schultz, W. (1999) Relative reward preference in primate orbitofrontal cortex. *Nature* 398, 704–708
- 59 Hikosaka, K. and Watanabe, M. (2000) Delay activity of orbital and lateral prefrontal neurons of the monkey varying with different rewards. *Cereb. Cortex* 10, 263–271
- 60 Tremblay, L. and Schultz, W. (2000) Reward-related neuronal activity during go–nogo task performance in primate orbitofrontal cortex. *J. Neurophysiol.* 83, 1864–1876
- 61 Schultz, W. *et al.* (1997) A neural substrate of prediction and reward. *Science* 275, 1593–1599

# Temporal binding and the neural correlates of sensory awareness

Andreas K. Engel and Wolf Singer

**Theories of binding have recently come into the focus of the consciousness debate. In this review, we discuss the potential relevance of temporal binding mechanisms for sensory awareness. Specifically, we suggest that neural synchrony with a precision in the millisecond range may be crucial for conscious processing, and may be involved in arousal, perceptual integration, attentional selection and working memory. Recent evidence from both animal and human studies demonstrates that specific changes in neuronal synchrony occur during all of these processes and that they are distinguished by the emergence of fast oscillations with frequencies in the gamma-range.**

The goal of the present article is to consider the relevance of binding mechanisms for sensory awareness. A large body of neuropsychological and physiological evidence suggests that consciousness has

to be understood as a function of numerous interacting systems, such as sensory areas, memory structures, centres for executive control as well as circuits mediating emotion and motivation<sup>1,2</sup>. Thus, any theory about the neural correlates of consciousness (NCC) must explain how multiple component processes can be integrated and how large-scale coherence can emerge within distributed neural activity patterns. Furthermore, such a theory must specify mechanisms for the dynamic selection of subsets of neuronal responses, because only a fraction of all available information gains access to consciousness. In this article, we suggest that achieving both, cross-systems coherence and dynamic response selection, requires mechanisms for binding of distributed information<sup>3,4</sup>.

Our discussion of the relationship between binding and conscious states will be restricted to one particular aspect of consciousness, namely, sensory awareness. With many authors, we share the view that sensory awareness is one of those facets of consciousness that is (probably) most easily accessible both in terms of experimental quantification and theoretical explanation<sup>5</sup>. There seems to be wide agreement<sup>1,2,5–7</sup> that the physiological prerequisites of awareness include: (1) *arousal*: the 'waking up' of the brain by non-specific modulatory systems; (2) *sensory segmentation*: the basic step in sensory processing,