

Psychology and neurobiology of simple decisions

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Patterns of neural firing linked to eye movement decisions show that behavioral decisions are predicted by the differential firing rates of cells coding selected and nonselected stimulus alternatives. These results can be interpreted using models developed in mathematical psychology to model behavioral decisions. Current models assume that decisions are made by accumulating noisy stimulus information until sufficient information for a response is obtained. Here, the models, and the techniques used to test them against response-time distribution and accuracy data, are described. Such models provide a quantitative link between the time-course of behavioral decisions and the growth of stimulus information in neural firing data.

The question of how two-alternative decisions are made is an important one for neuroscience and psychology alike because of the pivotal role played by decision making in translating perception and cognition into action. This translation brings encoded stimulus information into contact with the behavioral intention of the decision maker to produce a goal-directed act. Psychology has a long history of decision-making research that has resulted in detailed mathematical models of underlying processes [1,2] but only recently has it become possible to observe the neural correlates of these processes directly in awake behaving monkeys.

To study processes involved in simple two-choice decisions, neuroscientists have used an analog of the two-choice response-time (RT) task from psychology, in which monkeys make saccadic eye movements to indicate their decisions about visual stimuli. Recordings from cells in premotor areas of the frontal lobe and the posterior parietal cortex have shown that the time-course of activity in these cells corresponds well with that of behavioral eye movement decisions [3–7]. This article describes how these developments are leading psychologists and neuroscientists to converge at a common view of the underlying mechanisms. As a result, it could soon be possible to explain behavioral data and single-cell firing data with the same class of mathematical models.

Neural correlates of simple two-choice decisions

Neural activity linked to eye movement decisions has been recorded in several visual tasks (Figure 1) from oculomotor

areas including the middle temporal area (MT), the lateral intraparietal area (LIP) in extrastriate cortex [8], the frontal eye field (FEF) [9–11], and the superior colliculus (SC) [12–14]. These structures are part of the circuit that controls saccadic eye movements to behaviorally salient targets [3]. For example, in the oddball discrimination task, monkeys are trained to make eye movements to a distinctively colored target element in an array of distractor elements. Activity has been recorded from FEF sensory cells whose receptive fields contain either the target or a distractor. Initially, activity in target and distractor cells increases similarly and nonselectively, but at longer delays the firing rates reflect discriminative information: activity in the target cell increases or is maintained while that in the distractor decreases. Similar results have been obtained from MT cells and LIP cells in a coherent motion task (Figure 1c) [8] and from SC prelude or buildup cells [12,13] in a dot separation task [15].

The view that neural firing rate can be understood as a correlate of the behavioral decision process [3,4,15] is supported by several pieces of evidence. First, the build-up of information occurs irrespective of whether a saccade is ultimately made [10,11] (Figure 1) or of whether it is made to the correct location [16,17]. This suggests that the firing rate is not merely an antecedent of the eye movement itself but reflects a more central process of target selection. Second, the growth in firing rate predicts decision time: fast responses are associated with a rapid rise in activity whereas slow responses are associated with a slow rise [8,18]. Third, behavioral decision time is predicted from the time taken for the firing rate to reach a threshold value. This has been shown for FEF motor neurons [18] and for direction-sensitive cells in LIP [8] and SC [15]. Fourth, the rate of growth of discriminative information depends on the difficulty of the decision; the difference in firing rates between cells responding to selected and nonselected stimuli increases more slowly when the decision is difficult than when it is easy. Finally, the build-up of information is sensitive to the prior probabilities of the response alternatives and to the likelihood the response will be rewarded. Information favoring a particular response builds up more quickly when the response is highly probable or more likely to be rewarded [13,19,20].

From neurons to sequential-sampling models

The picture that emerges from these findings is strikingly consistent with statistical decision models that have been

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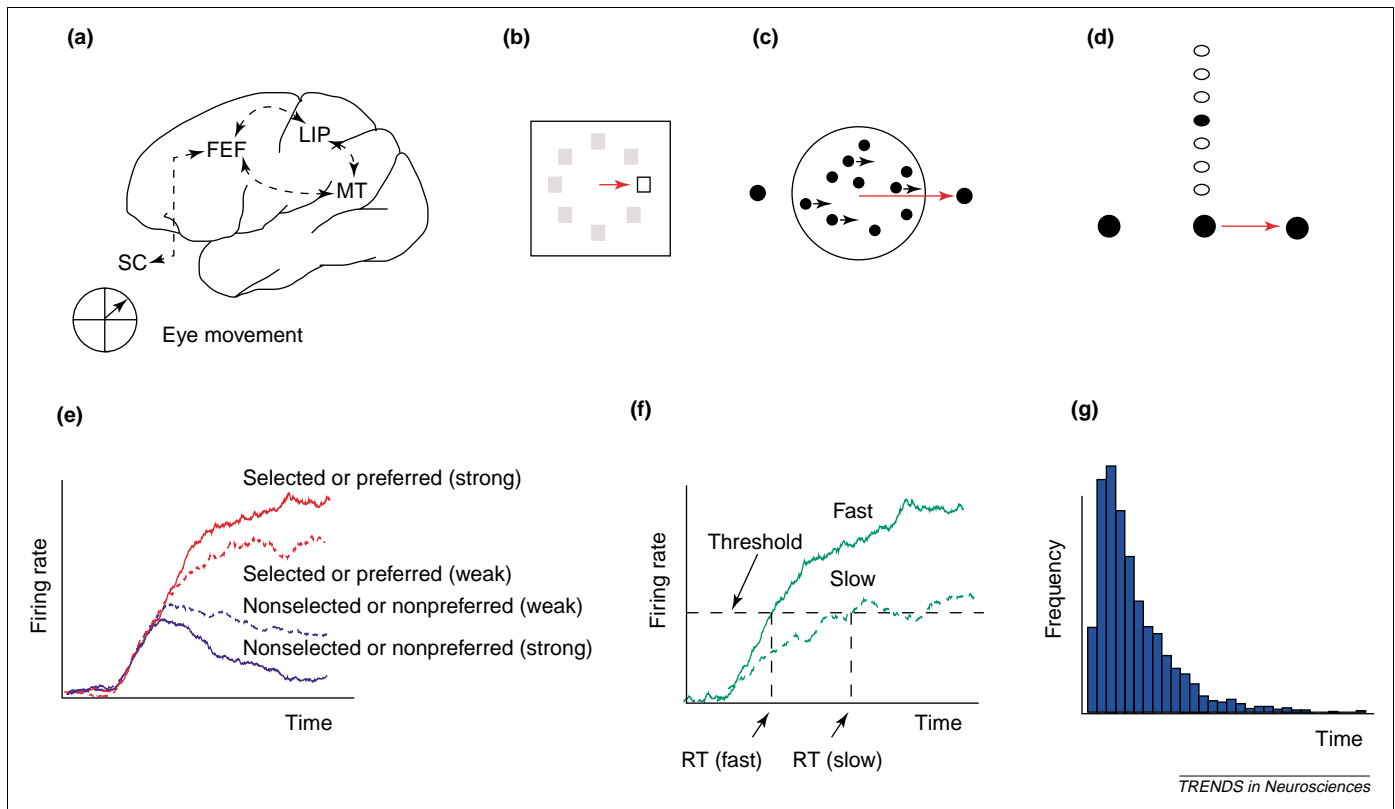


Figure 1. Neural and behavioral correlates of eye movement disorders. **(a)** Some neural sites from which decision-related activity has been recorded. Patterns of neural firing that predict the time-course of behavioral decisions have been recorded in the frontal eye field (FEF), lateral intraparietal area (LIP), middle temporal area (MT) and superior colliculus (SC). **(b–d)** Some tasks used to study perceptual decisions. **(b)** Oddball task. Eight colored stimulus patches are illuminated in a circle around the fixation point: the monkey makes a saccade (red arrow) to the odd-colored patch. Task difficulty is manipulated by varying the similarity of the colors of the odd element and the distractors. **(c)** Coherent-motion detection task. An array of moving dots, some moving in random directions and some moving to the left or to the right, is presented centrally: the monkey makes a saccade to a left or right target to indicate the direction of motion. Task difficulty is manipulated by varying the proportion of coherently moving dots. **(d)** Dot separation task. One of a set of stimulus lights arranged vertically above a fixation light is illuminated. The monkey makes a saccade to the left or right to indicate a large or small distance between the stimulus light and fixation. Task difficulty is manipulated by varying the position of the stimulus light relative to the middle of the set of stimulus lights. **(e)** Neural activity associated with stimulus selection has been recorded in LIP, from sensory neurons in FEF, and from prelude or buildup neurons in SC. Early stimulus-linked activity does not discriminate between decision alternatives. Later, cells associated with the selected stimulus or the preferred direction of motion show an increased or maintained level of firing. Cells associated with the nonselected stimulus or the nonpreferred direction show a decreased level of firing. The growth of discriminative information represented by the difference in firing rates occurs more rapidly for easily discriminated stimuli (strong) than for less easily discriminated stimuli (weak). **(f)** Response time (RT) is predicted by the time at which activity in LIP or in FEF motor neurons reaches a threshold. Rapid activity growth is associated with fast responses; slow activity growth is associated with slow responses. The distribution of RT **(g)** is a reflection of variability in the time taken for the activity to reach threshold.

developed during the past 40 years in mathematical psychology. Two broad classes of model have been developed that apply to different kinds of decisions. One class, of sequential-sampling models, applies to speeded decisions in perceptual and memory tasks [1,21]. These decisions are typically made within a second or so. A second class, based on economic concepts of expected utility, applies to complex decisions among differently valued alternatives [2]. Both have been linked to recent neurobiological findings but only the former is discussed here. The link between neurobiology and utility-based decision theories is discussed in Refs [7,22].

Figure 2 summarizes the main sequential-sampling models and shows two successful models of this kind. The models both assume that decisions are based on accumulated noisy information about the stimulus but they differ in how the accumulation is assumed to occur. In random-walk models, the information is accumulated as a single total: information in favor of one response is evidence against the other [23,24]. In accumulator models and counter models, information favoring the two responses is accumulated separately [25–29]. The Wiener diffusion

and Ornstein–Uhlenbeck diffusion models on the left of Figure 2a are continuous time counterparts of random walks [30–32].

The Wiener diffusion model, shown in Figure 2b, has successfully accounted for RT and accuracy data from a variety of behavioral paradigms [33–39]. It assumes that a decision is the result of continuously accumulating noisy stimulus information until one of two response criteria is reached. Because of moment-by-moment fluctuations in noise in the decision process (the irregular sample paths in the figure) and trial-to-trial variability in the quality of information about the stimulus, the process sometimes terminates at the wrong criterion, resulting in an error. If the information quality is low, the rate of accumulation is slower and errors are more likely than if the information quality is high. RT distributions are predicted to be right-skewed because of the geometry of diffusion process paths: equal size differences in accumulation rate between pairs of sample paths are projected as unequal size differences on the decision boundary (Figure 2b). The Ornstein–Uhlenbeck model is similar to the Wiener model but assumes decay or ‘leakage’ in the accumulation

process. Mathematically, the predicted decision times for the models are obtained by solving the so-called first-passage time problem for the accumulation process. This solution gives the distributions of correct and error decision times as a function of accumulation rate and decision criteria [30,32,37].

Accumulator models, such as that shown in Figure 2c, model the decision process as a race between two competing evidence totals, with the response determined by the first total to reach criterion. Accumulator models predict many of the same behavioral data as random-walk and diffusion models, although most accumulator models cannot correctly predict shapes of RT distributions or account for error responses being sometimes faster than correct responses [37]. An accumulator model in which the evidence totals are modeled as independent diffusion processes with leakage correctly predicts distribution shape but not fast errors [37,38]. If the evidence totals are mutually inhibitory instead of independent, and the starting points of the accumulation processes vary, the model also predicts fast errors. The leaky competing accumulator model of Usher and McClelland [40] (see also Ref. [41]) predicts the same range of behavioral data as does the Wiener diffusion model because the addition of mutual inhibition between the accumulators means that evidence for one response is evidence against the other, as in the diffusion model [37]. A related, neurally motivated model was proposed by Shadlen *et al.* [42].

For both the diffusion and accumulator models, the decision criteria that determine the amount of information needed for a response are under the control of the decision maker. Criteria are reduced with instructions to respond rapidly and increased with instructions to respond accurately. Criteria can also be set independently of each other. If one response in an experiment is more probable than another or has a higher reward, the criterion for the more probable or more rewarded response can be decreased and the criterion for the other response increased. Through such changes, the models predict the regular ways in which accuracy rates and RTs vary with instructions and with changes in the relative probabilities of the two responses. Empirically, a shift from speed to accuracy instructions results in slower and more accurate responses, whereas a shift from accuracy to speed instructions results in the converse (a phenomenon known as 'speed-accuracy tradeoff'). In addition, when relative response probabilities are varied experimentally, high-probability responses are faster than low-probability responses, but are more likely to be made in error. In both cases, more of the change in RT comes from an increase in the skew of the distribution than from a shift in its location. These characteristics of the speed and accuracy of simple decisions are among the most frequently replicated findings in experimental psychology [23,43].

A crucial feature of current successful diffusion and accumulator models is the assumption that the rate of information accumulation, the starting values of the accumulation process (or, equivalently, the response criteria) and the duration of nondecision components of RT all vary randomly from trial to trial [23,28,30,35,37]. Without such variability, the models are unable to predict

some characteristics of the data, such as the ordering of mean RTs for correct responses and errors, or the shapes of the leading edges of RT distributions.

Sequential-sampling models contrast with signal detection theory [44], which typically assumes that a decision is based on a single sample of information. In sequential-sampling models, noisy information is accumulated over time under the assumption that multiple samples will improve reliability and minimize the effects of internal noise. In this assumption, they resemble the classical sequential probability test of mathematical statistics [45] and, indeed, some models have assumed that decisions are made by computing a direct behavioral or neural analog of this test [4,23,46,47]. Mathematically, this test is based on likelihood and requires knowledge of distributions of evidence that could only be estimated from thousands of observations of a stimulus. It is therefore more plausible that the nervous system implements an easily computable approximation to this statistical ideal. When the distributions of evidence are normal, a model that accumulates samples of evidence directly is statistically equivalent to one that accumulates their log-likelihood ratios [4,23]. However, in neither case can the orderings of mean RTs for correct responses and errors be predicted without the addition of further sources of variability.

Testing behavioral models

Behavioral research in psychology has identified several key patterns of data that must be explained by any plausible model for two-choice tasks. First, there are systematic relationships between RT and accuracy; explanation of these relationships requires a model capable of producing errors [48,49]. Second, a model must account for the ordering of mean RTs for correct responses and errors across experimental conditions – that is, across the values of manipulated variables and across levels of accuracy ranging from chance to near-perfect performance. The model must explain the characteristic right-skewed shape of RT distributions and the changes in shape that occur across conditions. Third, a model must account for the patterns of error versus correct RTs that occur empirically. Correct responses are typically faster than errors in easy, speed-stress conditions and typically slower in difficult, accuracy-stress conditions [1,36,37]. All of these patterns of data need to be explained together in a theoretically principled way, through systematic and interpretable changes in model parameters – that is, changes in the means or variances of the components of processing embodied in the model.

Figure 3 shows a fit of the Wiener diffusion model to typical human data from an experiment in which the discriminability of the stimuli and instructions to respond rapidly or accurately were varied. The fits are shown in a compact form that presents all of the RT distribution and accuracy information in a single plot. The plot illustrates graphically how RT distribution shape and response accuracy vary as a function of experimental condition. Decreasing stimulus discriminability increases error rates and increases the means, standard deviations and skew of the RT distributions. RTs are longer under accuracy than speed instructions and the effects of

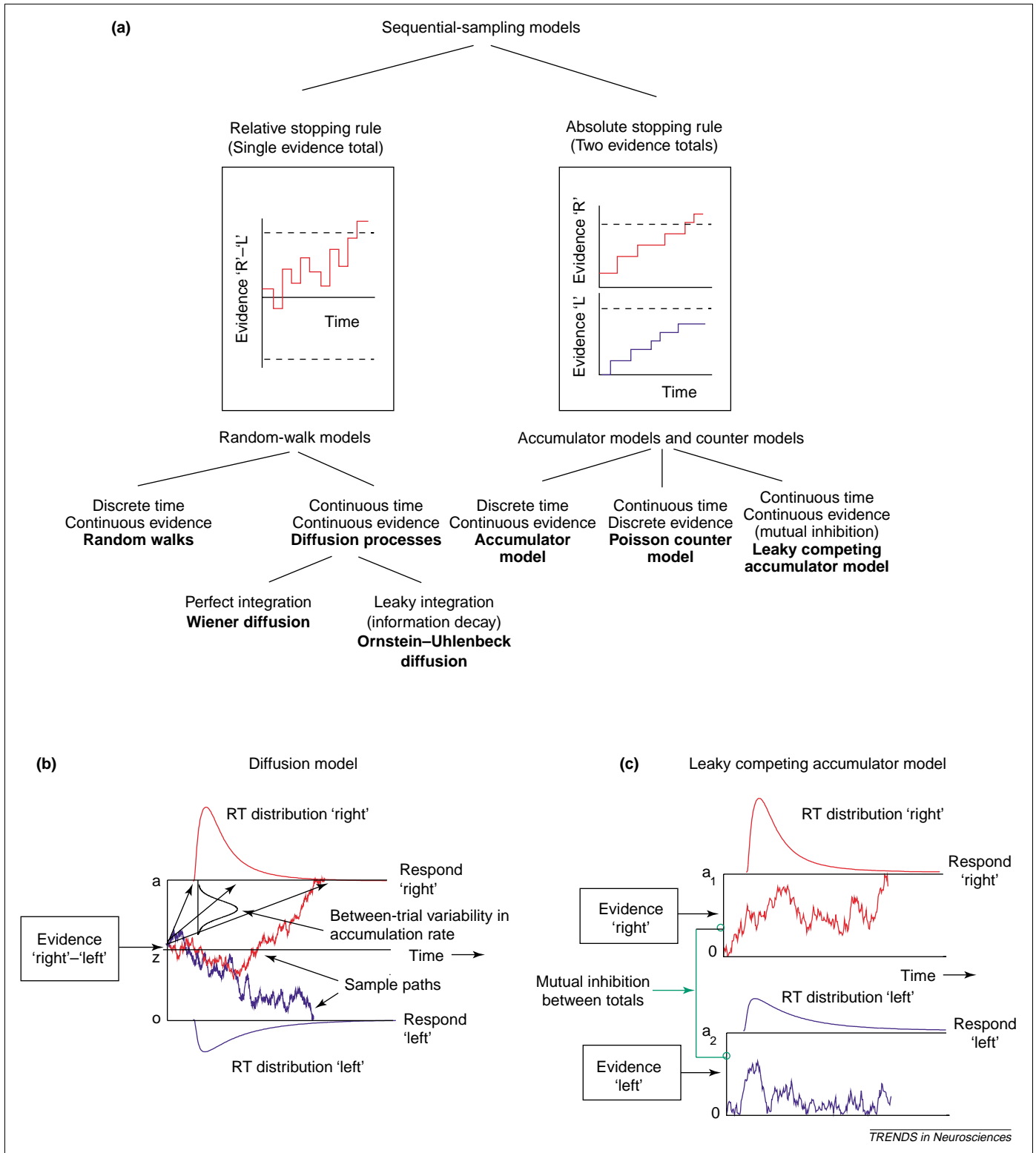


Figure 2. Sequential-sampling models for two-choice decisions. **(a)** Taxonomy of the main model classes. The models assume that decisions are made by integrating noisy stimulus information over time until a criterion amount of evidence needed for a response is obtained. In random walks, evidence is accumulated as a single total. Evidence for a right response ('R') increases the total; evidence for a left response ('L') decreases it. A response is made when the evidence for one response exceeds the evidence for the other by a criterion amount (a relative stopping rule). In accumulator models and counter models, evidence for the two responses is accumulated as separate totals. The response is determined by the first total to reach a criterion (an absolute stopping rule). Models are classified according to whether evidence accumulates continuously or at discrete time points, and whether the increments to the evidence totals are of variable size (continuously distributed) or occur in discrete units (e.g. counts). Random walks in continuous time are diffusion processes. **(b)** Diffusion model. The sample paths represent moment-by-moment fluctuations in the evidence favoring right and left responses. The process starts at z and accumulates evidence until it reaches one of two criteria, 0 and a . If the upper criterion is reached first, a 'right' response is made; if the lower is reached first, a 'left' response is made. The moment-by-moment fluctuations in the sample paths reflect noise in the decision process. The mean rate of accumulation varies randomly from trial to trial because of variability in the quality of the stimulus information. This variability allows the model to predict errors that are slower than correct responses. Other behaviorally important sources of variability are the location of the starting point of the accumulation process and the duration of the nondecision component of times for stimulus encoding and response execution (RT). The first of these sources of variability allows the model to predict errors that are

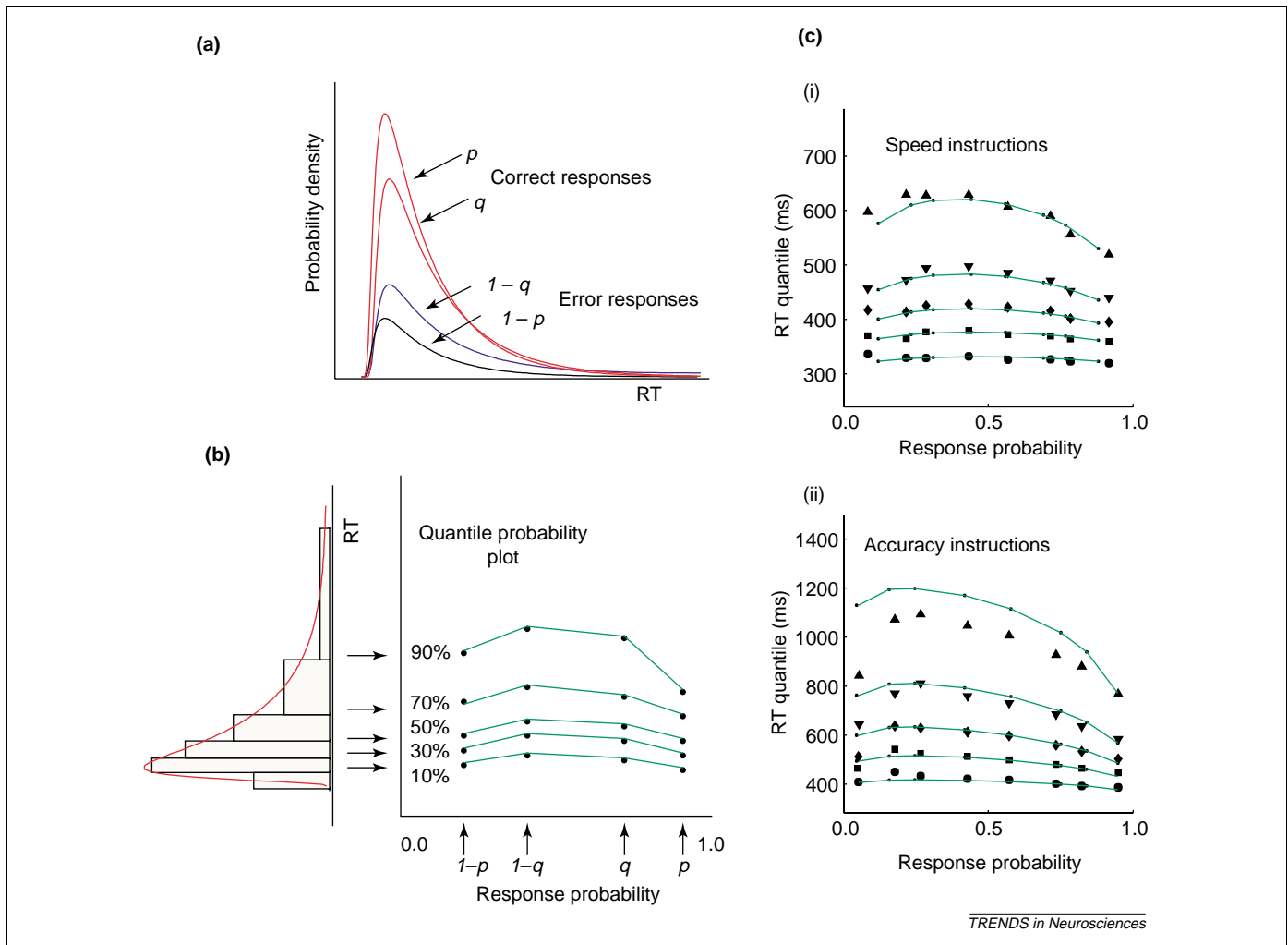


Figure 3. Summary of response time (RT) and accuracy data from behavioral experiments. **(a)** Typically the mean, standard deviation and shape of the RT distribution all vary with the experimental condition, as does the proportion of the two responses. With two stimuli, for the easy condition the proportion of correct responses is p and the proportion of error responses is $1 - p$. For the more difficult condition, the proportions are q and $1 - q$. **(b)** Quantile probability plot of RT and accuracy data for two conditions. Selected quantiles of the RT distribution are plotted against the probability of the response. The five quantiles used to construct the plots are the values of RT that cut off 10%, 30%, 50%, 70% and 90% of the area under the RT density function. The quantiles provide a summary of the shape of the RT distributions and show how the shape varies with stimulus difficulty. **(c)** Fits of the diffusion model to human data from the dot separation task (Figure 1d) for speed instructions (i) and accuracy instructions (ii). The plotted symbols are the empirical data; the continuous curves are fits of the model. The only model parameter that varies with dot separation is the accumulation rate for near versus far responses; the only parameters that vary between instruction conditions are the decision criteria. The parameters of the model used to obtain these fits are given in Ref. [37]. Model parameters estimated from data averaged over subjects show reasonable agreement with the average of parameters estimated from individual subjects [39]. The leaky competing accumulator model (Figure 2) fits these data similarly well; other models do appreciably worse [37]. The pattern of stimulus and instruction dependencies shown in (c) is representative of results from a variety of behavioral paradigms.

changing discriminability on RT are larger. The model provides a good account of the data, although it underestimates the range of accuracy values in the speed conditions and overestimates the RT skew (tail quantiles) in the accuracy conditions. The tail quantiles are estimated with low accuracy empirically, especially for errors, because of the sparseness of the data in the distribution tails [50]. The model accounts for the data by allowing only the rate of accumulation of information to vary with stimulus discriminability, and only the response criteria to vary with speed-accuracy instructions – a natural correspondence of experimental effects and components

of processing for the model [30,37]. The leaky competing accumulator model [40] provides a similarly good account of these data and a similar correspondence of components of processing to experimental effects [37].

Linking neurobiology and psychology

A model that seeks to link neurobiology and behavior needs to relate three levels of analysis: the spike trains of individual neurons, the statistical properties of the neural ensemble, and behavioral data. A successful model would simultaneously account for data on all three levels. Whether decisions are based on single cells, small groups

faster than correct responses; the latter allows it to describe the shape of the leading edge of RT distributions. **(c)** Leaky competing accumulator model. Evidence for 'right' and 'left' responses is accumulated in separate totals, each modeled as a diffusion process, towards criteria a_1 and a_2 . The two evidence totals decay in proportion to the amount of evidence accumulated and they also mutually inhibit each other. The response with the greatest accumulated evidence inhibits the other response more strongly than it itself is inhibited. If inhibition is removed, the model still predicts the shape of RT distributions correctly but is unable to predict fast errors unless variability in the starting point is large or the starting points are variable and negatively correlated across trials. The latter provides an alternative to the within-trial inhibition between accumulators required by the leaky competing accumulator model.

of cells or populations of cells is an open question. Some authors have reported that individual neurons predict responses that match the accuracy of behavioral decisions [51]. Others have computed that 7–14 neurons are required [52] and others have suggested that behavior depends on entire populations [53,54]. If the number involved is of the order of a few hundred, then one might expect the effects of noise within the system to be negligible and neural processing to be essentially deterministic. Models that assume deterministic information accumulation have been proposed in both the neurobiological and the psychological literatures [1,48,55] and it has been proved mathematically that models of this kind can be constructed *post hoc* that exactly predict any given pair of correct and error RT distributions [56]. Whether such models can account for the full set of RT distributions and accuracy data from a range of experimental conditions using a single set of parameters is not known. By contrast, the Wiener diffusion and the leaky competing accumulator models can account for the effects of changing stimuli or instructions using a single parameter for each.

However, deterministic or near-deterministic processing is not a necessary consequence of large populations of neurons. The firing rates of individual neurons in the same cortical region are weakly correlated ($r \approx 0.15\text{--}0.2$ [57,58]). Consequently, they do not function as statistically independent sources of information and so variations in individual firing rates are not eliminated by ensemble averaging, which they would be in populations of independent neurons [53,57]. Thus, population averages of even several hundred neurons can contain significant levels of noise, suggesting that stochastic models of the decision process might be more appropriate than deterministic ones.

Beyond questions about the number of cells on which decisions are based are questions about how firing rates combine. For example, to predict behavioral data, if the decision is based on the aggregate difference between two populations of neurons coding evidence for two response alternatives, the accumulating evidence would be most appropriately modeled as a diffusion process. Alternatively, if the decision is based directly on the most active of two populations, with some inhibitory interactions between them, then it might be more appropriately modeled as a leaky competing accumulator model [40].

Both these possibilities have been investigated in recent attempts to model neural firing rates and behavioral data jointly. Mazurek *et al.* [59] described a model for the coherent-motion task (Figure 1d) in which evidence from direction-sensitive neurons in MT is accumulated by two pools of mutually inhibitory neurons in LIP. A decision is made, as in the leaky competing accumulator model, by the first of the accumulating totals to reach a response criterion. This model was able to predict the LIP response, mean RT for correct responses, and accuracy, but has not yet been shown to predict RT distributions and error RTs.

In a similar vein, Ratcliff *et al.* [15] showed that the diffusion model could account for behavioral RTs, accuracy and activity in SC buildup neurons in the dot separation task (Figure 1d). For decisions in the most difficult stimulus condition, firing rates were divided into those

corresponding to the fastest, middle and slowest thirds of the behavioral responses. The difference between firing rates for movements to the receptive field of the target response and the nontarget response (Figure 4) showed delayed onset of discriminative information as a function of the behavioral RTs. Ratcliff *et al.* fitted the diffusion model (Figure 2b) to the behavioral data and then used the parameters of the fitted model to generate 2000 simulated decision paths. The means over simulations for the paths of the fastest, middle, and slowest thirds of the responses showed the same delayed onset of discrimination as the firing-rate data. An alternative, accumulator, model could not predict delayed discrimination in this way. In addition, with an added assumption about decay of the decision process back to its starting point after reaching a decision criterion, the diffusion model predicted the entire time-course of the discrimination functions in the firing-rate

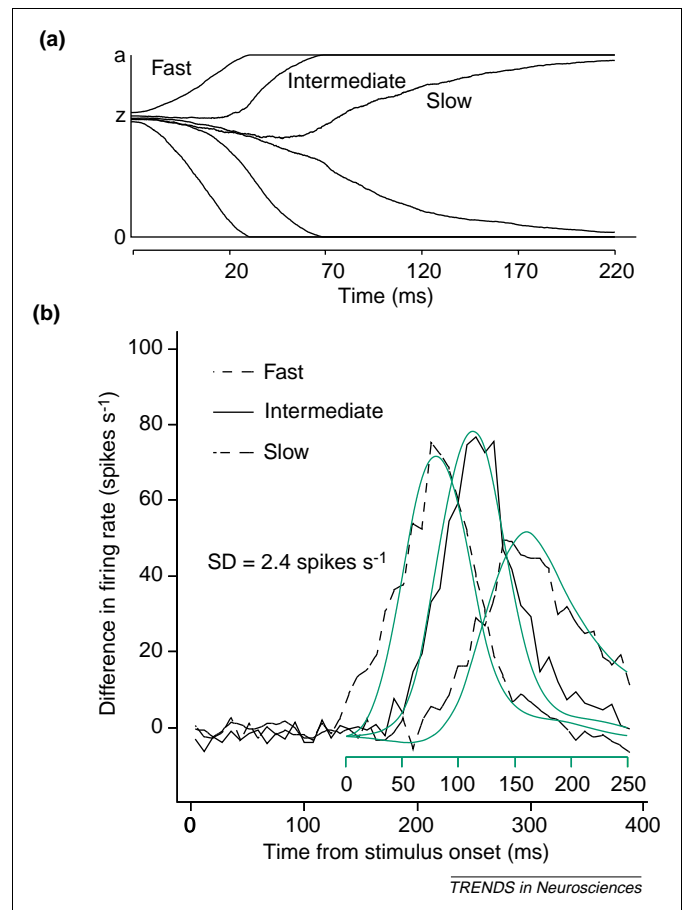


Figure 4. Comparison of diffusion model predictions with differences in firing rates for selected and nonselected stimuli. The monkey made a saccade to the left or to the right in response to small or large vertical displacements of a central target light (Figure 1d). (a) Average sample paths for the diffusion process for fast, intermediate and slow responses to difficult stimuli, aligned on stimulus onset. The paths were generated using the parameters of the diffusion model (Figure 2b) that gave the best fits to the response time distributions and response probabilities in the behavioral data. (b) Neural firing data. The black firing-rate functions are the differences between cell activity when a saccade was made to the stimulus in the receptive field of a cell and when a saccade was made to the alternative stimulus, which was not in the receptive field. The green lines are the differences in position between the paths for 'large' and 'small' responses obtained from (a). It was assumed that once a process reached one of the decision criteria, it decayed exponentially back to its starting point with a decay constant of 20 ms. Reproduced, with permission, from Ref. [15] © (2003) by the American Physiological Society.

data (Figure 4), but not individual target or nontarget firing rates.

Concluding remarks

The picture that emerges from recent single-cell studies of decision making in neuroscience is strikingly consistent with the picture that emerges from behavioral studies of decision making in psychology. In both, decisions are made by mechanisms that accumulate noisy information to a response criterion. Such mechanisms have been inferred from the results of behavioral experiments, but recent single-cell studies have begun to provide complementary evidence. Future theoretical progress in this area will come from quantitative models that link RT distribution and accuracy data in the behavioral domain to firing-rate data in the neural domain, providing a step towards a unified theory of the psychology and neurobiology of simple decisions.

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