

Optimal decision-making theories: linking neurobiology with behaviour

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This article reviews recently proposed theories postulating that, during simple choices, the brain performs statistically optimal decision making. These theories are ecologically motivated by evolutionary pressures to optimize the speed and accuracy of decisions and to maximize the rate of receiving rewards for correct choices. This article suggests that the models of decision making that are proposed on different levels of abstraction can be linked by virtue of the same optimal computation. Also reviewed here are recent observations that many aspects of the circuit that involves the cortex and basal ganglia are the same as those that are required to perform statistically optimal choice. This review illustrates how optimal-decision theories elucidate current data and provide experimental predictions that concern both neurobiology and behaviour.

Introduction

Neurophysiological and psychological data suggest that during decision making driven by perceptual events, our brains integrate the sensory evidence that supports available alternatives before making a choice [1–7]. This integration process is required because the sensory evidence, at any given point in time, might not be entirely reliable due to noise in the sensory system or in the environment itself [8–10]. Because the process of decision making involves integration of noisy evidence, it can be formulated as a statistical problem [9,10]. Several recently proposed theories assume that the brain implements statistical tests to optimize decision making. These statistical tests define decision rules that are the best solutions to tasks that subjects face during experiments that aim to model tasks that animals face on a daily basis. These tests optimize the speed and accuracy of decisions and the rate of obtaining rewards for correct choices, thus providing a clear evolutionary advantage to the animals that use them.

This article reviews optimal-decision theories and shows that they enable neurobiology and behaviour to be linked in two ways: first, they enable the identification of correspondences between models of decision making that have been proposed on different levels of abstraction [3,6,7,11–16] by showing that they can implement the same optimal test; and second, they enable a better understanding of current data and provide predictions for (i) the neurobiology of decision circuitry, including the basal ganglia, whose architecture can be mapped onto the

equation that describes an optimal test, and (ii) behaviour in terms of speed–accuracy trade-offs.

Neurobiology of decision

The neural bases of decision making are typically studied in experiments by presenting a subject with a stimulus that comprises moving dots [8]. A fraction of these dots move coherently in one direction, while the rest move randomly. The subject must identify the direction of coherent movement of the majority of dots and make an eye movement in this direction.

On the basis of single-unit recordings from monkeys performing this task [4–6,8], it has been proposed that such perceptual decisions involve three process [17] (Figure 1). First, the neurons in sensory areas that are responsive to critical aspects of the stimulus (in this task, motion-sensitive neurons in the medial temporal area) represent evidence in support of their preferred alternatives in their firing rate [8]. The goal of the decision process has been formulated as choosing the alternative for which the sensory evidence has the highest mean [9,10]. However, because the incoming evidence is noisy, a second process is required. The neurons in cortical areas that are associated with alternative actions (in this task, neurons that control eye movements in the lateral intraparietal area and the frontal eye field) integrate the sensory evidence over time [5,6]. This integration effectively removes the noise that is present in the sensory evidence and thereby facilitates more accurate decisions. Finally, a third process checks whether a certain criterion (e.g. confidence level) has been satisfied: if it is, the relevant behavioural output is engaged; if it is not, the integration continues. Two neural mechanisms have been proposed to underlie the criterion satisfaction: some authors assume that the choice is made when the firing rate of the cortical integrators that correspond to one of the alternatives reaches a threshold [5,6,17]; others assume that criterion satisfaction is determined through a set of interconnected subcortical nuclei, namely the basal ganglia [14–16,18].

Linking models of decision

The models that have been proposed to describe the decision process [3,6,7,11–16] range from detailed models of neural circuits to abstract psychological models of behaviour; this is because different models were designed to capture experimental data from different domains. Nevertheless, this section shows that, in the case of a choice between two alternatives (multiple alternatives will be discussed in the next section), the majority of these models

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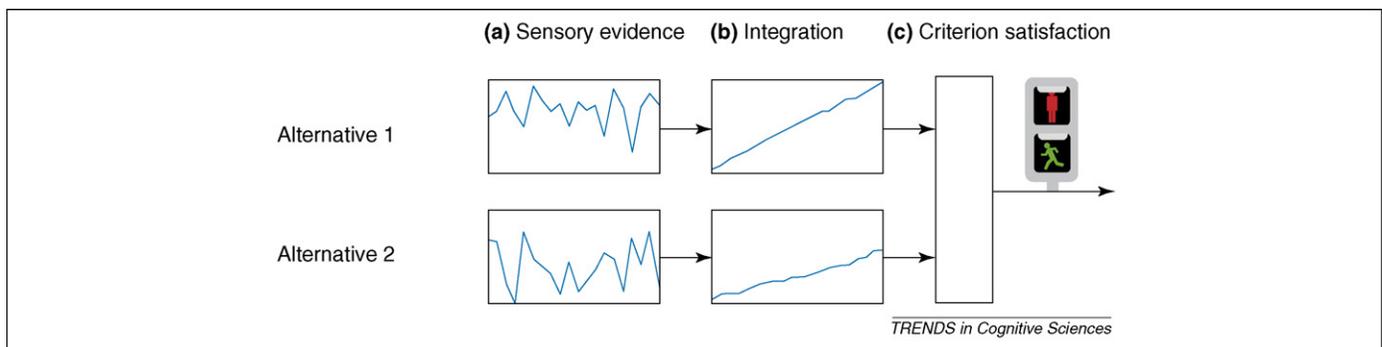


Figure 1. Schematic representation of three processes of decision making [17]. (a) The first process provides sensory evidence to support the alternatives. Blue lines show schematically hypothetical firing rates of two populations of sensory neurons as functions of time. Note that the mean amount of evidence that supports the first alternative is higher than the mean of the second, but the sensory evidence is noisy and at two first points the actual level of evidence is higher for the second alternative. (b) The second process integrates sensory evidence over time. Note that, after a certain amount of time, the integrated evidence in support of the first alternative is clearly higher than evidence in support of the second. (c) The third process checks whether a certain criterion has been satisfied. Its output can be compared to a traffic light: it will indicate if the action that is connected with a choice can be executed or if it is better to wait and continue the integration process.

can be parameterized to implement an optimal test called the sequential probability ratio test (SPRT) [19], and then they predict exactly the same error rate (ER) and reaction time (RT) distributions. Thus, if one model that implements SPRT fits behavioural data, all other models (including those on the neural level) can be parameterized to do so equally well (of course, fitting the data does not imply that the model is correct, but discrepancy of the predictions made by the model with the data can be used to discard the model).

Psychological models

Let us consider two criteria that have been proposed for terminating the process of deciding between two alternatives. According to the simplest criterion, a choice should be made as soon as the integrated evidence in support of one of the alternatives exceeds a threshold – this criterion is implemented in the ‘race’ model [7]. According to the second criterion, a choice should be made as soon as the difference between the evidence supporting the winning alternative and the evidence supporting the losing alternative exceeds a threshold – this criterion is implemented in the ‘diffusion’ model [1,3,20].

The diffusion model is usually formulated in a simpler way (equivalent to the description of above): instead of two integrators, the model includes just one abstract integrator that accumulates the difference between the evidence for the two alternatives; the choice is made when the level of the activity of this integrator exceeds a positive or a negative threshold (see first paragraph in Box 1). Recent versions of the diffusion model include additional parameters that describe the variability in the decision process between trials and improve the fit to behavioural data [21].

Optimality

The diffusion model implements SPRT [19]. SPRT optimizes the speed of decisions for a required accuracy [19]; this property can be illustrated using examples of the race and the diffusion models. In both models, the speed and the accuracy depend on the decision threshold, and there is always a speed–accuracy trade-off (the higher the threshold, the greater the accuracy but the slower the speed of the decision). However, if the thresholds in the two models are

chosen to give the same accuracy (e.g. 10%), then the optimal property of SPRT implies that the diffusion model, on average, will be faster than the race model. Intuitively, the advantage of the diffusion model comes from its ability to react adaptively to the levels of evidence supporting the losing alternative: the diffusion model will integrate for a shorter time if the evidence supporting the losing alternative is weak relative to the winning alternative, and for a longer time if the levels of evidence for each alternative are similar – that is, there is a conflict between alternatives (because, in this case, it will take longer for the accumulated difference in evidence to cross the threshold). This adaptive ability is not present in the race model. As will be explained later (in the section ‘Optimal threshold’), the diffusion model also has the ecologically important property of optimizing the amount of reward that is acquired as a consequence of choices.

If decision making by the brain is optimal, the analysis described above predicts that the diffusion model should provide a better explanation of observed experimental data than the race model. The diffusion model has been used successfully by Ratcliff and colleagues to describe behavioural outcomes in a wide range of choice-related tasks and paradigms (e.g. Refs [22–24]). Careful analyses of RTs from choice tasks have established that the diffusion model can indeed fit the distributions of RTs better than the race model [21,25–27]. Moreover, Ratcliff *et al.* [26] showed that, in the superior colliculus (the subcortical eye-movement control nucleus that receives input from cortical integrators), the growth of discriminative information is also better described by the diffusion model than by the race model.

Models of decision processes in the cerebral cortex

Three models have been proposed, by Shadlen and Newsome [6], Usher and McClelland [12] and Wang [13], to describe the cortical processes that underlie decision making. The cortical models have the ability to describe both the firing rate of cortical neurons and the behavioural data [6,12,13,17]. Each of these cortical models includes two neural integrators that correspond to the two alternatives and assumes that a choice is made as soon as the activity level in one of the integrators exceeds a threshold. In this aspect, the cortical models are related to the race

Box 1. Relationships among models

Figure 1 in this box illustrates the relationship among the models of decision making, whose architectures are presented in a form of diagrams. To clarify these diagrams, the race model includes two integrators that independently accumulate evidence; hence, the corresponding diagram includes two circles (which denote integrators) receiving input (denoted by triangles). In the diffusion model, one integrator receives the difference between the evidence in support of the two alternatives.

An arrow between two models indicates that there is a set of parameters of the first model for which the first model reduces to the second. For example, in the Shadlen and Newsome [6] (SN) model (as in all cortical models), the choice is made when the activity of any of the integrators exceeds a threshold. If the weights of inhibitory connections are set to 0, then the SN model reduces to the race

model. If the weights of inhibitory connections are equal to the weights of excitatory connections, then each integrator accumulates the difference between evidence in support of the two alternatives (1st – 2nd and 2nd – 1st) and, hence, the SN model is computationally equivalent to the diffusion model.

The reduction of the Usher and McClelland [12] (UM) model to the diffusion model requires the analysis of its dynamics; this was first reported by Usher and McClelland [12] and later developed by Bogacz *et al.* [28]. The model proposed by Wang [13] is a detailed spiking neuron model. Wong and Wang have recently shown that, for certain parameters, the model can closely approximate the diffusion model [64]. Bogacz *et al.* [28] analyzed a population-level model using the architecture of the Wang [13] model, and identified parameters for which it can be reduced to the UM model and to the diffusion model.

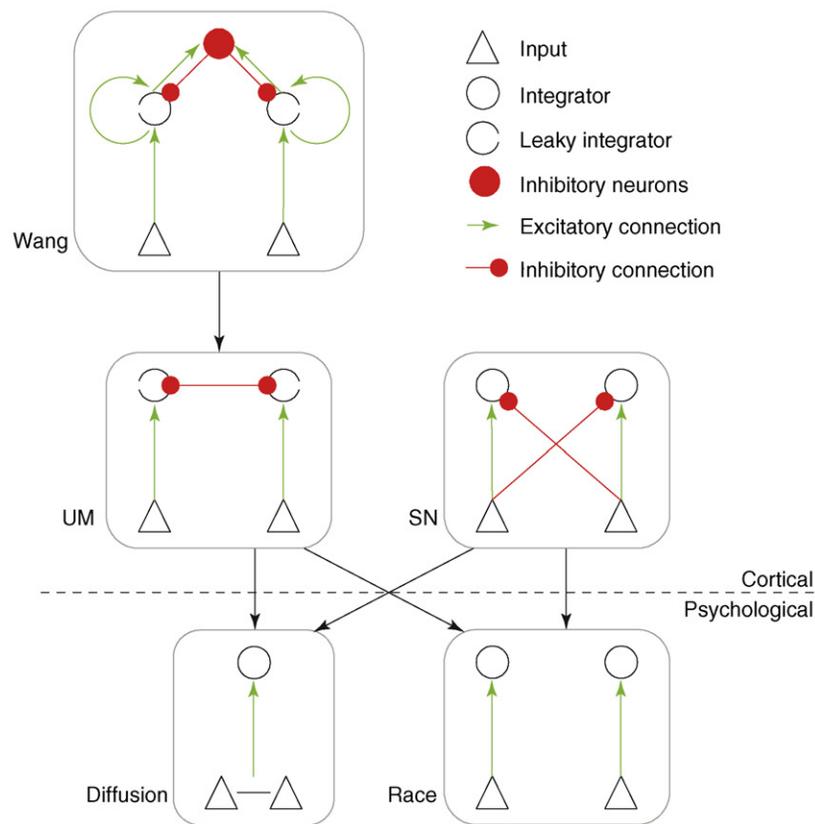


Figure 1. Relationships among the models of decision making. Each box with rounded edges contains a diagram that shows the architecture of one model. The elements of the diagrams are explained in the key. The following models are shown: Wang [13], Usher and McClelland [12] (UM), Shadlen and Newsome [6] (SN), the diffusion model [1,3,20] and the race model [7]. Arrows between two models indicate that parameters of the first model reduce to the second model. The horizontal dashed line separates the cortical models from the models that are proposed in psychological context.

model. However, each of the cortical models also includes inhibitory connections that, for certain parameter values, enable the integrators to accumulate the difference between evidence in support of the two alternatives (Box 1). Therefore, for these optimal parameter values, all the cortical models become computationally equivalent to the diffusion model and, thus, achieve optimal performance.

Consequently, the cortical models predict exactly the same behavioural data as the diffusion model if they are appropriately parameterized [28]. However, if they are not appropriately parameterized, the models might produce different behavioural predictions [12,21,29]. Importantly, different cortical models make slightly different predictions

regarding neuronal firing rates of integrators. For example, the models that have inhibitory connections from inputs to integrators [6,17] predict that the firing rate of cortical integrators depends only on the difference between the inputs, whereas the models that have mutual inhibitory connections between integrators (direct [12] or indirect [13]) predict that their firing rate will also depend on the total input to integrators [28]. Therefore, although all cortical models can be parameterized to perform the same computation, it is of interest to discover which model best describes the integration process at the neuronal level.

In summary, all three cortical models become computationally equivalent to the diffusion model for

parameter values that optimize their performance. Because the diffusion model can describe behavioural data from choice tasks [22–24], this equivalence implies that the cortical models that can describe neurophysiological data can also be parameterized to fit behavioural data [6,12,13,17].

Models of decision processes in the basal ganglia

This section reviews recent hypotheses that the basal ganglia perform the third process of decision making shown in Figure 1: the criterion satisfaction. In this section, I review the theory that the basal ganglia evaluate the criterion satisfaction in an optimal way [14] – namely, that they implement the multihypothesis SPRT (MSPRT) statistical test, which is a generalization of SPRT, to the choice between multiple alternatives [30]. This section first reviews how the basal ganglia interact with the functional

systems of the brain; it then shows how they might implement MSPRT and how this theory relates to the theories of reinforcement learning in the basal ganglia.

Redgrave *et al.* [18] and others [31–33] have proposed that the basal ganglia resolve competition between parallel-processing cortical and sub-cortical functional systems that are vying for behavioural expression. Redgrave *et al.* [18] pointed out that the resolution of competition by a ‘central switch’ (i.e. the basal ganglia), rather than by mutual communication between cortical and subcortical regions in competition, dramatically reduces the amount of connections and information transmission that is required and conforms to the observed anatomical organization of the brain.

Alexander *et al.* [34] proposed that the basal ganglia are divided into channels that correspond to individual actions and traverse all nuclei (because all basal nuclei include

Box 2. Mapping MSPRT onto the basal ganglia

The goal of decision making between N alternatives is to choose the alternative with the most evidence supporting it. Hence, the decision process can be formalized as a choice between N hypotheses H_i , each stating that the sensory evidence that supports alternative i has the highest mean [9,14]. In MSPRT [30], at each moment in time and for each alternative i , one computes the probability P_i of hypothesis H_i given the evidence that has been observed so far, and the decision is made as soon as any P_i exceeds a threshold. Bogacz and Gurney [14] proposed that the activity of channel i of the output nuclei of the basal ganglia is proportional to $OUT_i = -\log P_i$ (note that $-\log P_i > 0$ because $P_i < 1$). Thus, to implement MSPRT, the decision is made in the model as soon as any OUT_i decreases below a threshold, which is consistent with the selection by disinhibition by the basal ganglia (see ‘Models of decision processes in the basal ganglia’). Computing $-\log P_i$ from the Bayes theorem gives Equation 1, where y_i denotes the integrated evidence that supports alternative i :

$$OUT_i = -y_i + \ln \sum_{k=1}^N \exp(y_k) \quad (1)$$

Equation 1 includes two terms: the first expresses the integrated evidence for alternative i ; the second involves summation over all chan-

nels, so it expresses the amount of conflict between alternatives. Thus, according to Equation 1, the more conflict between alternatives, the higher the integrated evidence for the winning alternative needs to be for OUT_i to decrease below the threshold.

Figure 1 in this box shows the proposed mapping of Equation 1 onto the nuclei that comprise the basal ganglia [14]. y_i is computed by cortical integrators. The output nuclei receive two inputs that correspond to the two terms in Equation 1: term $-y_i$ is provided by the inhibitory projections of the striatum, whereas the conflict term is computed by the network of subthalamic nucleus (STN) and globus pallidus (GP). Bogacz and Gurney [14] proved that the required form of the conflict term can be computed by this network if the activity of STN neurons is proportional to the exponent of their input. Here, an intuition for the computation of the conflict term is provided. The conflict term in Equation 1 includes three operations that are implemented in the model in the following way: first, exponentiation of cortical input is performed by the STN; second, the summation over channels is achieved due to the diffused projections of the STN (Figure 1), so that each output channel receives input from many STN channels [65]; third, the logarithm is achieved due to interactions of the STN with inhibitory GP, which compresses the range of STN activity.

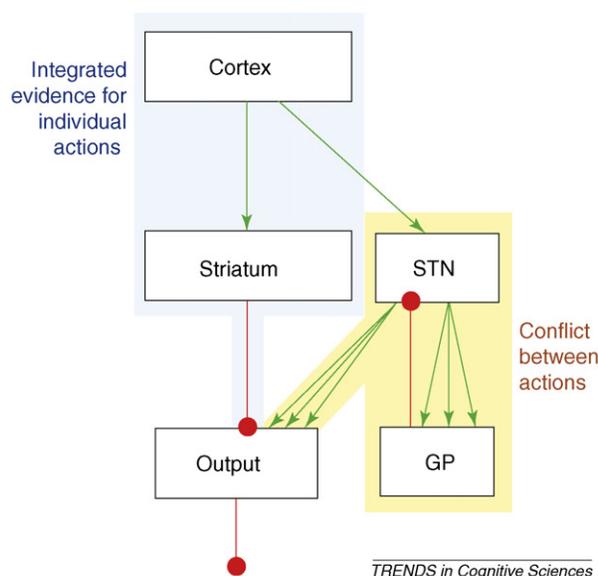


Figure 1. The pathways within the basal ganglia that are required for MSPRT. The top box denotes the cortex; other boxes denote basal nuclei: the striatum, subthalamic nucleus (STN), output nuclei (including substantia nigra pars reticulata and entopeduncular nucleus) and globus pallidus (GP). The arrows denote excitatory connections and the lines with circles denote inhibitory connections. Single lines denote connections within channels and multiple lines (i.e. those originating from STN) denote diffused projections across channels.

neurons that are selective for the movements of particular body parts [35,36]). In the default state, the output nuclei of the basal ganglia send tonic inhibition to all input structures in the cortex (via the thalamus) and the brain stem, thereby blocking the execution of any action [37,38]. The actions prescribed by the winning competitors are selected by disinhibition: when the basal ganglia inputs that represent a particular action are sufficiently active, a series of selective processes within the basal ganglia nuclei lead to the selective inhibition of the relevant channels in the output nuclei. In turn, this output inhibition releases the ‘winning system’ from the inhibition that enables execution of its prescribed action [37,38].

Several simulation studies have demonstrated the capacity of the basal ganglia to underlie decision making [15,16,39]. Recently, Bogacz and Gurney [14] showed that the equation that describes MSPRT maps onto a subset of anatomy of the basal ganglia (Box 2). This theory gives an analytic description of the computations in the basal ganglia, thus providing a new framework for understanding why the basal ganglia are organized as they are [14]. In agreement with previous simulation studies [15,16,40,41], this theory postulates that one of the basal nuclei, the subthalamic nucleus, has a role in modulating the decision process proportionally to the conflict between evidence for various alternatives. Additionally, the work of Bogacz and Gurney [14] specifies how the conflict should be computed to yield optimal performance, enabling quantitative predictions. In particular, the equation for the MSPRT criterion includes exponentiation, and the mapping between the equation and the architecture predicts that the firing rate of subthalamic neurons should be equal to

an exponent of their inputs (Box 2). Such input–output relationship is highly unusual (reported before only in the visual system of locusts [42]). Figure 2 compares this prediction with existing biological data. For all subthalamic neurons that have been measured [43,44], the relationship between input and firing rate follows precisely an exponential function [14].

Much experimental and theoretical evidence suggests that the basal ganglia are also involved in learning from rewards and punishments. It has been observed that a particular signal computed by reinforcement learning algorithms [45] (the reward prediction errors) describes certain aspects of the activity of dopaminergic neurons that project to striatum [46–48] (cf. [49,50]). Moreover, recently Frank *et al.* [51] provided compelling evidence that the direct pathway from the striatum to the output nuclei is involved in learning from rewards, whereas the indirect pathway via globus pallidus (not shown in Figure I in Box 2) is involved in learning from punishments.

The theories of decision making and reinforcement learning should not be viewed as contradictory but rather as complementary: Bogacz and Gurney [14] propose that the reinforcement learning models describe the computations of the basal ganglia during task acquisition, whereas decision-making models describe the computations of the basal ganglia when subjects are proficient in the task. Furthermore, they have shown that when the connections that are involved in learning from punishments (see above) are added to their model of decision making, the network continues to implement MSPRT [14].

In summary, in the case of choice between multiple alternatives, a model with sophisticated architecture of

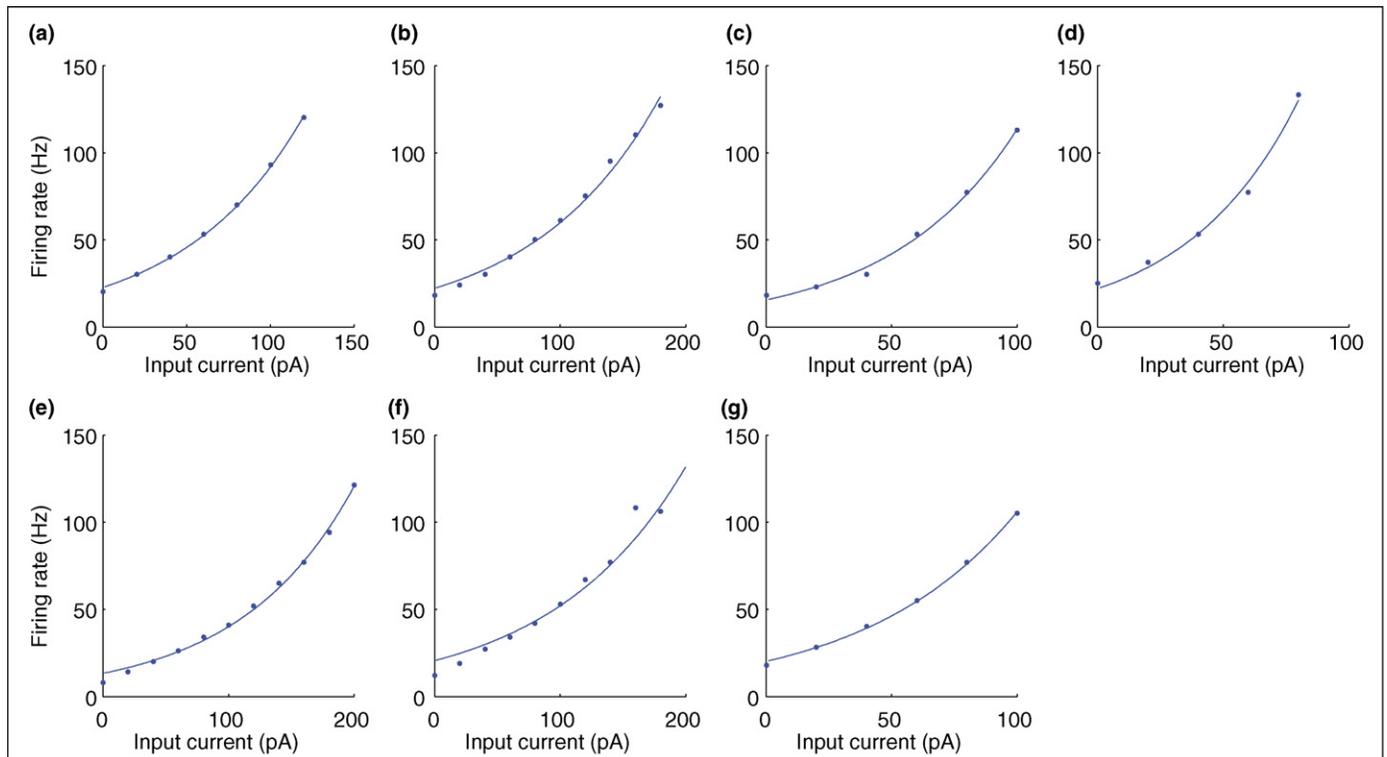


Figure 2. Firing rates f of subthalamic neurons as a function of input current I . (a–d) Re-plotted data on the firing rate of subthalamic neurons presented in Hallworth *et al.* [43] [Figure 4b, 4f, 12d and 13d respectively (control condition)]. (e–g) Re-plotted data from subthalamic neurons presented in Wilson *et al.* [44] [Figure 1c, 2c and 2f respectively (control condition)]. Only firing rates below 135 Hz are shown. Lines show best fit of the function $f = a \exp(bI)$. Reproduced, with permission, from Ref. [14].

the basal ganglia implements optimally the third process of Figure 1 (i.e. the criterion satisfaction), enabling faster decisions than would be possible using simpler cortical models [14,52]. Nevertheless, the cortical models provide a good description for the first two processes of Figure 1 (i.e. the integration of sensory evidence).

Optimal threshold

As mentioned earlier in this review, the speed–accuracy trade-off is controlled by the height of the decision threshold (e.g. in the diffusion model, the higher the threshold, the slower but more accurate the decisions). Gold and Shadlen [10] proposed that subjects in decision-making experiments choose a threshold that

maximizes the reward rate, which is defined as the number of rewards per unit of time. The expression for the reward rate and, therefore, the optimal threshold is task specific. Gold and Shadlen [10] considered a sequential choice task – at the beginning of each trial, a stimulus is presented, after which the subject is allowed to respond at any time, and there is a fixed delay between the response and the next stimulus. In the simplest version of this task, the subject receives a reward if the choice is correct and there is no penalty for errors. In this version, there is a unique value of the decision threshold that maximizes the reward rate [28]. (If the threshold is too low, the subject is not accurate, so the reward rate is low; but if the threshold is too high, the subject is too slow and the trials are so long

Box 3. Predictions of the optimal threshold

Here, I describe the relationship between decision time (DT) and error rate (ER) as predicted by the diffusion model with the optimal threshold in the sequential choice task of Gold and Shadlen [10]. DT is defined as a fraction of reaction time (RT) that is connected with decision processes; the remainder of RT that describes the duration of non-decision processes (e.g. visual and motor) is denoted by T_0 . The normalized DT (NDT) can be defined as the ratio of DT to the total time in the trial that is not connected with decision making, which includes T_0 and the delay D between the response and the next stimulus – that is, $NDT = DT / (T_0 + D)$. The thick curve in Figure 1 in this box shows the predicted relationship between NDT and ER.

The relationship shown in Figure 1 should be satisfied for any task parameter (i.e. for any task difficulty and delay D). The theory predicts that subjects should produce very low ER only during very easy tasks; hence, in this case, subjects should also be very fast, as indicated by the left end of the curve in Figure 1. Conversely, subjects should produce ER

close to 50% only for tasks so difficult that the optimal strategy is to guess; hence, in that case, the subjects should also be very fast, as indicated by the right end of the curve. The longest DT (for given D) should be obtained for $ER \approx 18\%$, in which case the mean DT should be equal to $\sim 19\%$ of the non-decision interval in the trial.

Histograms in Figure 1 show data from the sequential choice task presented by Holmes *et al.* [66]. They report that, when all subjects were considered, DT followed the theoretical predictions only qualitatively. However, when only 30% of subjects who earned the most reward in the experiment were considered, DT also followed the theoretical predictions quantitatively. The DT of other subjects was longer than optimal, which might suggest that they attempted to optimize a criterion that combined reward rate and accuracy [67]. Similar optimal performance curves have been derived for such combined criteria [28,66] and provide better fit to data from all subjects [66].

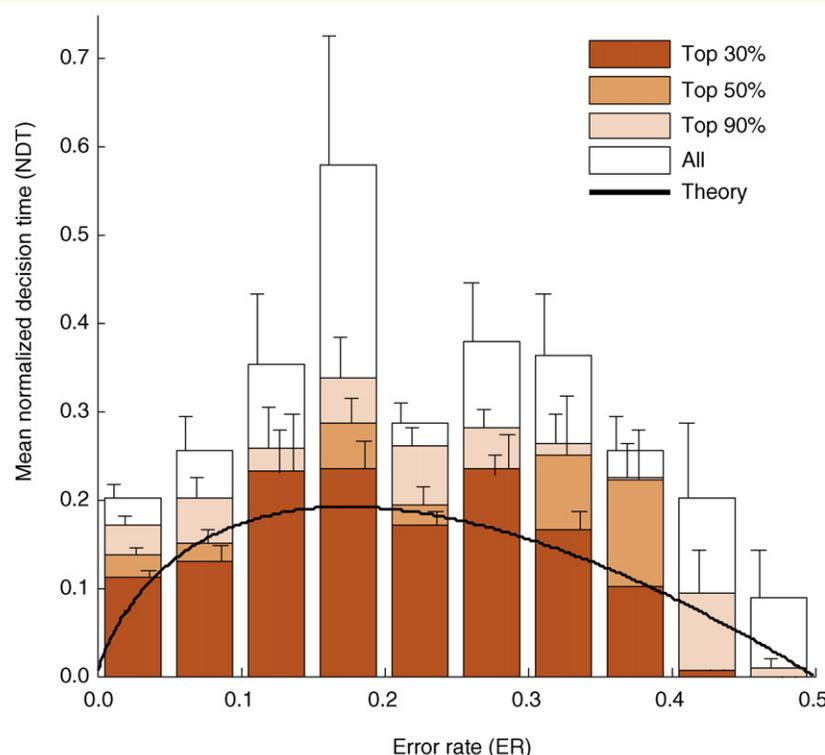


Figure 1. The relationship between the error rate (ER) and the normalized decision time (NDT). The thick curve shows the relationship that is predicted by the diffusion model with the optimal threshold. Histograms show data from an experiment in which 80 human subjects performed the sequential choice task, in which difficulty of choice and delay D varied between blocks of trials (D was 0.5 s, 1 s or 2 s). For each block, ER and NDT were computed. The blocks were grouped by ER in bins of 5%. For each group, the height of the histogram bar shows the average NDT and the error bar shows the standard error. White bars show the data from all subjects and coloured bars show the data from a selection of subjects who earned the highest reward rate in the experiment. Reproduced, with permission, from Ref. [66].

that the reward rate is also low). The assumption that subjects use the diffusion model with the optimal threshold permits quantitative predictions regarding the relationship between speed and accuracy, as discussed in [Box 3](#).

It was also proved mathematically that the diffusion model with the optimal threshold maximizes the reward rate in a wide range of tasks [28]. For example, the diffusion model with optimal threshold settings gives higher reward rates than the race model with its best threshold. This proof can be extended to the case of multiple alternatives to show that the MSPRT with the optimal threshold maximizes the reward rate. Thus, the diffusion model and the MSPRT optimize ecologically relevant criteria, expressing the expected reward.

Extensions of the theory

This review has focused on a theory that describes optimal decisions in simple choice. However, the theory has been extended to more complex scenarios including (i) biased choices in which one of the alternatives is more probable or more rewarded [2,28,53–56] than the other, (ii) multidimensional choices in which the alternatives need to be compared in several aspects [57–59], and (iii) tasks in which the information content of the stimulus varies within the trial [60]. How the height of the decision threshold is encoded in the cortico–basal ganglia circuit [40,41,61] and how its optimal value can be learnt [62,63] have also been modelled. Additionally, several studies have investigated how the introduction of biological constraints in cortical integrators (i.e. nonlinearities) affects decision performance [52,57,60].

Summary

This article has reviewed theories that make the ecologically motivated assumption that the brain implements decision algorithms that optimize the speed and accuracy of choices, and their trade-off. These algorithms have been implemented by models on different levels of abstraction, which implies that these models are computationally equivalent and, hence, produce the same behaviour. For example, in choices between two alternatives, a complicated network model of cortical integrators and the basal ganglia implements the same computation as the diffusion model, which implies that it can describe the same wide range of behavioural data. Furthermore, it has been demonstrated that the optimal-decision theories are effective tools in generating experimental predictions for both neurobiology and behaviour. I believe that the theoretical approaches assuming optimal performance will

answer further questions ([Box 4](#)) concerning the neural bases of decision making.

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Box 4. Outstanding questions

- Which of the cortical models best describes the mechanism of integration in the cortex?
- Can basal ganglia also implement MSPRT during task acquisition, when it has a key role in reinforcement learning?
- Can the algorithmic framework that describes decision making in basal ganglia in healthy people help in treating diseases that affect the basal ganglia (e.g. Parkinson's disease)?
- Does the brain allocate attentional resources or cognitive control [68,69] in an optimal way for different levels of the conflict that is present in the evidence supporting the alternatives?

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