

Probabilistic vs. non-probabilistic approaches to the neurobiology of perceptual decision-making

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Optimal binary perceptual decision making requires accumulation of evidence in the form of a probability distribution that specifies the probability of the choices being correct given the evidence so far. Reward rates can then be maximized by stopping the accumulation when the confidence about either option reaches a threshold. Behavioral and neuronal evidence suggests that humans and animals follow such a probabilistic decision strategy, although its neural implementation has yet to be fully characterized. Here we show that that diffusion decision models and attractor network models provide an approximation to the optimal strategy only under certain circumstances. In particular, neither model type is sufficiently flexible to encode the reliability of both the momentary and the accumulated evidence, which is a prerequisite to accumulate evidence of time-varying reliability. Probabilistic population codes, by contrast, can encode these quantities and, as a consequence, have the potential to implement the optimal strategy accurately.

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Introduction

Efficient decision-making requires inferring the state of the world from uncertain or ambiguous evidence [1]. Little evidence results in inaccurate decisions, such that it is in the decision maker's best interest to boost her confidence by accumulating evidence over time and, if possible, across cues before committing to a decision. Thus, it is essential for the decision maker to perform decisions in two stages: first, she accumulates evidence to reach a certain level of confidence, and – once this level is reached – commits to her decision (Figure 1). A hunting eagle, for example, needs to be fairly certain about the

presence of a rabbit before initiating its dive. Similarly, humans require certainty about the state of the surrounding traffic before crossing the street. In both of these cases a period of evidence accumulation is followed by acting upon this evidence.

We first give a short overview over the origins of statistically optimal, two-stage decision-making – which we will refer to as the *normative* strategy – as well as behavioral evidence that humans follow such a strategy. This provides us with a set of properties that decision-making models need to feature, and with respect to which we compare three types of models: diffusion models, models based on attractor dynamics, and probabilistic population codes. We show that the model based on probabilistic population codes provide a neural implementation of the normative model of decision making, while the other approaches provides various approximation to the normative approach.

Decision making under uncertainty

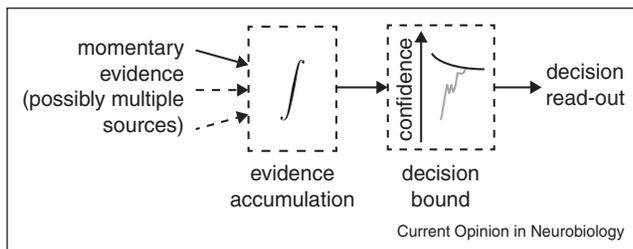
The realization that decision-making is essentially a task of probabilistic inference based on uncertain information was pioneered by Pascal in his famous wager on the benefits and losses involved in believing in God [2]. Gaining popular following, Pascal's approach was extended to all sorts of probabilistic decision problems, such as Bernoulli's well-known St. Petersburg paradox [3] that deals with wagering in games of chance. Finally, Laplace fully formalized general decision making under uncertainty [4] around 150 years after the efficacy of the probabilistic approach was first conceived.

The two-stage process of decision-making received particular attention in WW II, when Turing automatized breaking the Germans' Enigma code by first accumulating evidence in support of certain hypotheses, and committing to a decision once either hypothesis has reached a pre-set level of posterior probability [5,6]. Independently but at roughly the same time, Wald and colleagues [7,8] developed a similar approach, known as the Sequential Probability Ratio Test (SPRT), to initially determine which of two Navy firing procedures was to be preferred [9]. In both cases, the uncertain evidence supporting either option is accumulated until the belief about the correctness of either option reaches a pre-set level. At this point, the decision maker chooses according to this belief.

Optimal accumulation of evidence

Behavioral studies have confirmed that human observers do not only take uncertainty into account, but also do so close-to-optimally according to the two-stage procedure

Figure 1



Principles of optimal decision making. In order to perform optimal decision making, momentary evidence needs to be accumulated across time and, if available, across multiple cues, while monitoring ones confidence in the correctness of all available decisions. Once confidence in either option reaches a particular decision bound, a decision ought to be made.

outlined above. In the stage of evidence accumulation across time and cues, the decision maker needs to weight the momentary evidence in proportion to its reliability. Cue integration experiments that modulate the reliability of one of the cues have confirmed that humans indeed take this reliability into account [1,10,11], even if the cues' reliabilities change over time within single trials [12,13]. That they are able to do so on a trial-by-trial basis provides strong support for a direct neural representation of this reliability.

For evidence for optimal temporal accumulation of evidence we focus on experiments using the random-dot motion (RDM) task. In this task, the observer needs to decide for one of two opposing motion directions, based on a display of randomly moving dots, a fraction of which coherently moves towards the correct target [14,15]. The difficulty of this task, and as such the reliability of the evidence, is controlled by this fraction – referred to as coherence. If this coherence remains constant over time, subjects perform the task optimally by putting the same weight on the momentary evidence at each point in time during stimulus presentation. This has been confirmed behaviorally for short stimulus presentation times of up to 600 ms [16]. Further evidence comes from neural activity supporting the presence of neural integrators in the cortex [17,18^{*}], and from subjects being able to report or utilize confidence at decision time [19,20,21^{*},22,23]. Moreover, subjects performing a heading discrimination tasks have been shown to be able to accumulate momentary evidence optimally even if its reliability changes over time, by correctly weighting this evidence in proportion to its reliability (Drugowitsch *et al.*, abstract in Computational and Systems Neuroscience 2011, Salt Lake City, UT, February 2011).

Committing to a decision at the bound

The second stage of optimal decision-making under uncertainty is to commit to a decision once a pre-set

level of certainty, called the decision bound, has been reached. Setting this bound optimally is complex, as it depends on both factors internal to the decision maker and properties of the task at hand. Thus, we first consider evidence for the presence of such a bound, and then discuss its optimality.

In reaction time tasks, decision makers are able to trade-off their decision speed with the accuracy of this decision [19,24^{**},25–28], already hinting at the presence of a decision bound. This bound seems to find its neural correlate in parietal areas in monkeys performing the RDM task [16,17,29^{**},30–32]. There, neurons coding for particular saccade targets feature ramping activity with a slope proportional to the reliability of the momentary evidence [17,30]. Once this activity reaches a certain threshold, a decision seems to be triggered. Interestingly, the threshold seems to also be present when the experimenter determines the decision time [28,29^{**}], which implies that evidence late in the trial might be ignored, as confirmed behaviorally [16].

The optimal setting of the decision bound depends on multiple contingencies, such as the expected reward/loss for correct/incorrect decisions [33,34], the cost of accumulating evidence, the expected reliability of the evidence [35^{*}], the presence of stochastic deadlines [36], and the general timing of the task. For the simple case of a known reliability of the evidence and a constant cost of accumulating evidence, Wald and colleagues have shown that the best strategy corresponds to a constant bound on the belief of the correctness of either option [7,8,37]. Following this strategy leads to the fastest decisions for a pre-set level of correctness, or – when optimizing this level – to maximizing reward rate [17,33]. Observed behavior suggests on tasks with constant across-trial evidence reliability that humans seem to adjust their speed-accuracy trade-off to achieve close-to-optimal reward rates [38,39], with a slight bias towards overemphasizing decision accuracy [39]. If this reliability is allowed to vary across trials, the optimal strategy corresponds to a decision bound that collapses over time [35^{*}]. In this setting, it has been shown that humans and animals only follow this strategy if they feature a cost for accumulating evidence that rises over time [35^{*}].

In summary, there is sufficient evidence that humans and animals are able to perform optimal decision-making according to the two-stage strategy outlined above. We do not claim that all of their decisions are optimal in the senses described above [for example [40]]. However, observing optimality in some tasks already points to the existence of neural decision mechanisms that can feature this optimality. When discussing the different decision-making models we will this focus in particular on (i) the maintenance of reliability during evidence accumulation, and (ii) a measure of belief/confidence at the time of the decision.

Diffusion decision models for 2AFC decision-making

The dominant model of decision-making for two-alternative forced choice (2AFC) tasks in psychology is the diffusion decision model [DDM [24^{••},26,41,42]], in which a particle drifts and diffuses between two boundaries (Figure 2). Hitting either of these boundaries triggers a decision. A decision is correct if the particle hits the boundary corresponding to the mean drift rate. Incorrect choices occur due to the stochastic particle diffusion, and are less frequent for large drift rates. Thus, the magnitude of the drift is a representation of the reliability of the momentary evidence. Despite its simplicity, the DDM has been able to fit well a wide decisions and reaction times for a wide range of different tasks [for example [42]].

The position of the particle in the DDM is generally not interpreted as encoding a posterior probability [but see [35[•],37,41,43]], but rather as providing a purely mechanistic account of the decision-making process [for example [44]]. Nonetheless, it is possible to relate the particle position to a posterior probability, a particular useful exercise as it reveals when the DDM implements the ideal, normative strategy and when it does not. For binary decisions in which the drift rate remains constant within and across trials, the DDM implements the optimal strategy corresponding to SPRT [7,8]. When the drift rate varies within or across trials, which is to say when the reliability of the evidence changes over time, the DDM becomes suboptimal.

A further problem for the DDM is that it does not by itself have the ability to represent decision confidence, as all

that is known at decision time is that the particle has reached the bound. This is because, in a DDM, the bound is on particle location (as in Figure 2) rather than confidence (as in Figure 1), and mapping particle position to confidence might be time-dependent or not even one-to-one [35[•]]. A possible workaround for the case of a time-dependent mapping is to assume that, in addition to the particle location, the decision maker also keeps track of time. Then, the decision confidence becomes purely a function of time [21[•]]. This, however, is only possible with a separate neural representation of time, and is also only valid for binary decision in which the evidence reliability remains constant over time. Thus, DDMs are only able to meet our second requirement – a correct measure of belief at decision time – in very specific cases.

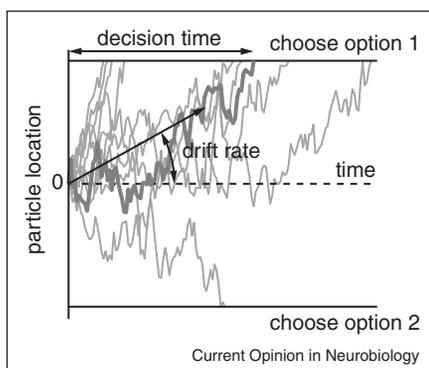
Another possibility for computing decision confidence involves using multiple accumulators, one for each possible choice. The race is stopped whenever one of the accumulators reaches the stopping bound. The state the losing integrator can then be used as a proxy for confidence. For instance, if the losing integrator is close to reaching the bound at decision time, the model assigns a low confidence to the decision [19,20]. As we will see later on, this idea can be formalized more precisely with a type of neural code known as probabilistic population codes [45^{••},46^{••}].

To summarize, the DDM falls short of the normative ideal, as its applicability is restricted to tasks in which the reliability of the momentary evidence is constant as a function of time. Furthermore, confidence at decision time can only be computed if one assumes a separate representation of time, and even then, the same restrictions on the evidence reliability applies. Still, the DDM performs remarkably well at describing behavior in tasks in which these restrictions are met, thus providing further evidence that decision-making is guided by a two-stage process, but most probably with an implementation that differs from the DDM.

Decision-making by attractor dynamics

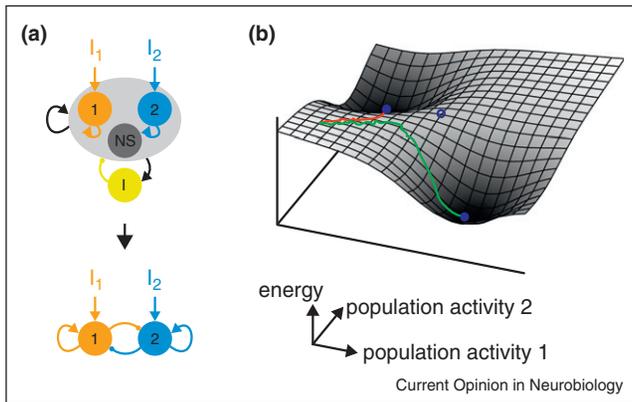
Many neural models of decision making are based on networks with attractor dynamics. As we will argue, these models only approximate diffusion decision models and, as such, might not be optimal even when decisions are binary and the evidence is of constant reliability. Nonetheless, these models have the advantage of incorporating many biological features, such as different types of neurotransmitter receptors and distinct classes of excitatory and inhibitory neurons [47]. Their dynamics is best imagined as the network's state being represented by a ball moving along an energy landscape (Figure 3b). The ball's motion is determined by the sensory inputs, the internal noise, and the landscape's topology. In Wang's model, the network connectivity is carefully tuned to achieve a flat landscape around the initial state, such that

Figure 2



Decision making in a diffusion model. In diffusion models, a particle drifts and diffuses between two absorbing boundaries. A decision is triggered as soon as the particle hits either boundary. The drift rate is proportional to the reliability of the mean of the momentary evidence, while the diffusion represents its fluctuation. A correct decision corresponds to hitting the boundary towards which the particle drifts – in this example the upper bound. The figure shows various example trajectories leading to different decision times, one of which causing the decision to be incorrect (i.e. hitting the lower boundary).

Figure 3



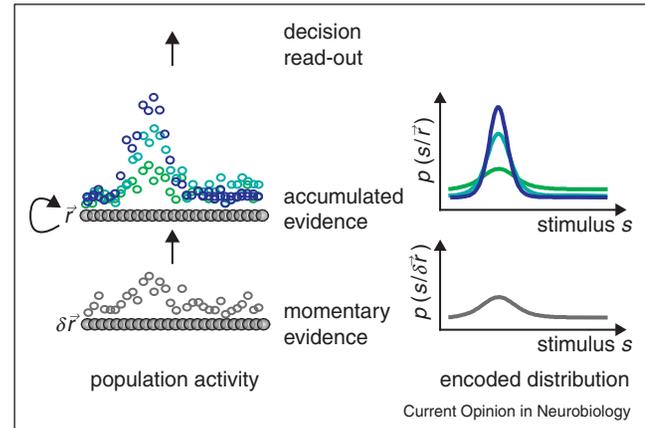
Attractor network models of decision-making. **(a)** The full model (top) contains one general (NS) and two input-dependent excitatory populations (1 and 2) and one inhibitory population (I) of neurons. This complex model is well approximated by a two-population model (bottom) that only tracks the average activity of the two input-dependent excitatory populations [49**]. **(b)** Schematic illustration of the energy landscape of the reduced model for balanced inputs. Initially, evidence is accumulated in the flat area of the energy landscape towards the unstable saddle point (blue empty dot), until the network state ‘drops’ into either of the two stable basins of attraction (blue solid dots), at which point a decision is made. The red and green traces provide two examples of network state trajectories, each leading to a different decision. An imbalanced input reshapes the energy landscape to make it more likely for the network state to reach the point attractor associated with the stronger input [49**].

the ball’s motion is initially mostly determined by the inputs – corresponding to the accumulation of evidence. Over time, the ball drops into either of two attractor states – valleys in this energy landscape that are hard to escape and correspond to the commitment of a decision [47,48,49**]. Thus, it also emphasizes a two-stage decision making process, but with less clear-cut boundaries between these two stages.

Mathematical analysis has shown that, in contrast to the one-dimensional state-space of the DDM, the network’s essential dynamics is captured by a two-dimensional state-space (Figure 3) [49**]. Thus, it is at least in principle possible to represent both decision and confidence simultaneously. However, using point attractors to commit to a decision implies that the network cannot take advantage of this property, as the network state at decision time are reduced to one of two possible states. Once the network adopts one of these states, the decision is known, but there is no other dimension available to encode the level of confidence.

In terms of evidence accumulation, the network implements a slow ‘integration’ phase by being tuned such as to avoid pre-mature convergence to committing point attractors, but without following principles of optimal accumulation of evidence. It is in fact unclear how

Figure 4



Probabilistic population codes for decision-making. The lower neural population encodes the momentary evidence, while the upper population represents the accumulated evidence. More specifically, both layers use probabilistic population codes to encode the probability distribution over the stimulus based either on the momentary evidence (in the input layer) or the evidence accumulated since the start of the trial (in the output layer). If the neural variability of the population encoding the momentary evidence follows the exponential family with linear sufficient statistics, then the upper layer only needs to sum the spikes from the input layer over time in order to encode the optimal posterior distribution over the choices given all the momentary evidence up to the present time [45**]. When the reliability of the momentary evidence only affects the gain, or height, of the input pattern of activity (with higher gain corresponding to more reliable data), this solution also works when the reliability of the momentary evidence changes during the course of the trial. This implies that the activity in the upper layer correctly encodes the decision maker’s confidence. Thus, the decision bound on confidence can be implemented via a bound on a function of this population activity.

effective the network is in capturing the information that is available in the input, particularly, as the majority of the noise comes from within the network rather than this input [47]. Furthermore, the use of attractor states causes a tilt in the energy surface towards the closer attractor, resulting in biases in evidence accumulation towards evidence supporting the decision associated with this attractor [50]. Thus, evidence accumulation overemphasizes early evidence rather than weighting all momentary evidence equally, as would be required in the simple RDM task in which all momentary evidence is equally reliable [16,18*].

Overall, while the network features higher neurobiological realism than the DDM, it lacks a clear probabilistic interpretation along with notions of belief and confidence – both of which are required to explain observed behavior and to model general-purpose decision-making. The same criticism applies to a recently proposed line-attractor variant for multiple-choice decision-making [51]. A further variant proposes slow learning of how reliably certain stimulus features are about predicting the correctness of either option through the modification of synaptic

weights [52]. The later is used to model a task in which symbols appearing consecutively on a screen each provide evidence of different reliability towards one or the other choice. Once presented on the screen, all symbols remain visible until the end of the trial. As a consequence, it remains unclear if the model is in fact accumulating evidence temporally within the network, or if this evidence is already combined before being fed into the network. More generally, it is difficult to see how this type approach could be used to implement the type of optimal filters, such as Kalman filters, that are needed to accumulate evidence optimally when the reliability of the evidence changes over time and when the value of the stimulus might also evolve over time [53].

Decision-making with probabilistic population codes

To recap, probabilistic decision-making requires the decision maker to at least maintain a representation of the certainty with which either option is correct throughout both stages of the decision process. Fortunately, neural population codes seem to be well suited to not only represent this certainty, but also full probability distributions over the stimulus [45^{••},54–56] (Figure 4). Furthermore, as long as the neural spike variability belongs to the exponential family with linear sufficient statistics (which include the independent Poisson distribution, but also allows for correlated variability and Fano Factors different from one) [45^{••}] – as observed in the cortex [57[•]] – optimal accumulation of evidence is achieved by a simple linear operation, even if the reliability of this evidence varies over time. Thus optimal decision making with probabilistic population codes (PPCs) corresponds to integrating neural population activity over time (and across cues), and committing to a decision once a weighted sum of this integrated activity crosses a certain threshold [46^{••}]. Neurally, all that is required is a PPC-based representation of the momentary evidence, and an integrator of neural activity – as observed in the cortex [18[•]] (Figure 4). A further advantage of this approach is that – once the decision boundary has been crossed – the most likely stimulus value can be decoded optimally with a separate line attractor network [46^{••},58,59]. Such architecture has been shown to explain well both behavioral and neurophysiological data of monkeys performing the RDM task [18[•],46^{••}].

In summary, PPCs are able to satisfy all previously outlined requirements for the normative ideal of decision-making [see also [53]]. Furthermore, they provide a potential explanation for some of the properties of these data, such as, for example, why it might be advantages to have the spike variability follow the exponential distribution. Future challenges include how to perform close-to-optimal inference even if the neural encoding deviates from the exponential family with linear sufficient statistics, as, for example, observed in MT [29^{••},46^{••},60] or

MSTd [61]. Also, the theory predicts that the decision bound ought to be on a linear combination of the neural population activity of areas that act as integrators of the momentary evidence (Drugowitsch, Moreno-Bote, and Pouget, abstract I-43, Computational and Systems Neuroscience 2011, Salt Lake City, UT, February 2011), whereas the data seem to suggest that – at least in LIP – the bound is on the activity of the pooled activity of neurons coding for evidence towards the correctness of single decisions [16,17,29^{••},30–32]. It remains to be seen how the theory can be updated in the light of these observations.

Conclusions

Based on behavioral and neural data of humans and animals, we have argued for following a normative approach to the modeling of decision-making. To this respect, we have pointed out weaknesses of both diffusion models as well as decision models based on attractor networks, in particular with respect to the representation of reliability and confidence. Probabilistic population codes, on the contrary satisfy requirements posed by the normative approach, and can explain both behavioral and neural observations, but on the downside feature less biological detail than attractor network models. Although models based on probabilistic population codes can in principle handle very general type of decisions, it remains to be seen how well the theory is able to predict the neural activity that arises from more complex life-like experimental setups, with changing reliability and additional flexibility in setting the decision bound. Without doubt, these questions will be addressed in the coming years, as several laboratories have started to test humans and animals in tasks with time-varying evidence reliability. The results of these experiments should provide valuable insights into whether decision making can be described within the probabilistic framework even in such complex, increasingly realistic situations.

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