



Bridging Neural and Computational Viewpoints on Perceptual Decision-Making

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Trends in Neurosciences

Bridging Neural and Computational Viewpoints on Perceptual Decision Making

--Manuscript Draft--

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Abstract:	<p>Sequential sampling models have provided the dominant theoretical framework guiding computational and neurophysiological investigations of perceptual decision making. While these models share the basic principle that decisions are formed by accumulating sensory evidence to a bound, they come in many forms which can make highly similar predictions of choice behaviour despite invoking fundamentally different mechanisms. The identification of neural signals that reflect the core computations underpinning decision formation offers new avenues for empirically testing and refining major model assumptions. The goal of this review is to highlight recent efforts to explore these avenues and, in so doing, to consider the conceptual and methodological challenges that arise when seeking to infer decision computations from complex neural data.</p>

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23rd January, 2018

Dear Professor Furman,

We wish to submit the revisions to our paper titled '***Bridging Neural and Computational Viewpoints on Perceptual Decision Making***'.

We are very grateful to you and to the two reviewers for all of the helpful comments which we believe have led to a considerably improved manuscript. We hope you will agree and look forward to hearing your decision in due course.

Kind regards

Redmond O'Connell, Michael Shadlen, Kongfatt Wong-Lin & Simon Kelly

Response to Reviewer Comments

We are most grateful to the editor and reviewers for their excellent comments which we feel have resulted in a much improved manuscript. We have responded to each of the reviewer comments in turn below. Amendments to the manuscript have been highlighted in blue font.

In general, I liked reading the manuscript. It's well written and important topics are highlighted and discussed from a fair perspective. I pretty much agreed with the all of the perspectives within, and so I have little to add for the review process.

I'm not sure if there is a limit on the references or what, but I did feel like the paper could connect to efforts coming from mathematical psychology, and not only neuroscience, to link these two streams of evidence. There are also already many reviews on strategies for linking, as well as whether the general philosophy is even warranted. For example, Schall (2003; Annual Reviews of Psychology) discusses the linking proposition at length, and Turner et al. (2017; Journal of Math. Psych.) discuss different statistical and mathematical strategies for relating the two measures.

We thank the reviewer for highlighting these excellent and highly relevant reviews which we have now cited repeatedly in the revised manuscript. The comments of both reviewers have highlighted to us that the opening sections of the original manuscript were somewhat ambiguous regarding the specific aims of our review and may have given the impression that we were intending to provide a comprehensive evaluation of the different approaches to integrating mathematical models with neural data. In reality our goal was to focus more specifically on two key emerging themes in the recent literature on perceptual decision making: A) the use of neural activity measurements to directly inform abstract mathematical models and hence resolve important theoretical debates in the literature and B) the increasing evidence that even elementary perceptual decisions involve numerous processing stages and the challenge this poses when seeking to infer decision computations from neural data. We now make our intentions much clearer in our revised title, abstract and opening paragraphs.

The authors also have a very narrow focus on the urgency interpretation of neural data based on their own work, but there are other mathematical models that explain the asymptotic properties of accuracy based on lateral inhibition and leakage, and recently the dynamics of lateral inhibition have been shown to correlate with frontal areas often engaged in cognitive control in humans (Turner et al., 2018; Cerebral Cortex).

Indeed, the inclusion of lateral inhibition and leakage in the leaky competing accumulator (LCA) model can account for the fact that accuracy reaches asymptotic levels as stimulus durations increase. However, we are not aware of any work in which it has been shown that the LCA can account for a decline in choice accuracy with increasing reaction time for a fixed stimulus duration - the key behavioural feature at play in the debate concerning the role of dynamic bound adjustments. Moreover, it is not clear to us how lateral inhibition and leakage could account for the evidence-independent component of build-up in motor preparation circuits observed in recent monkey (e.g. Hanks et al 2014) and human (Murphy et al 2016) studies. To provide a broader coverage of the literature, we have added additional discussion of Heitz and Schall's (2012) investigation of neural adjustments to speed/accuracy emphasis in the context of visual search (pages 9 and 10) which highlighted a distinct pattern of adjustments to those observed by Hanks et al (2014) and necessitated the development of a new biophysically-inspired model in order to reconcile the behavioural and neural data within a sequential sampling framework.

There is also a paper at Psych. Review by Purcell et al (2010) that uses single unit data as direct input to suites of accumulator models, and another one at Journal of Neuroscience in 2012. These explanations use gating as the main force, but one can imagine that predictions from gating models could look a lot like an urgency signal if the gate were not discrete but instead allowed for a gradual build up through time. Finally, there are some connections they could make to an optimal model of decision making that explains why bounds should collapse (Malhotra et al. 2017; PB&R), and another neuroimaging study that further identifies other neural bases of a time-varying boundary policy (van Maanen et al. 2016; NeuroImage).

Again we thank the reviewer for orienting us to these excellent papers which are clearly relevant to our discussion and which we have now cited in the revised manuscript. With respect to Purcell et al's work, these authors have demonstrated that visual search performance is well explained by a model in which the onset of evidence accumulation is regulated via gated inhibition. Increasing the level of the 'gate' is beneficial for choice accuracy in this context because it ensures that sensory evidence signals (salience encoding visual FEF neurons) are at a higher resolution by the time they begin to drive the accumulation process. In their 2012 J Neurosci paper, Purcell et al further showed that systematic adjustments to this gating parameter yielded speed-accuracy tradeoffs in choice behaviour that are analogous to those associated with static bound adjustments i.e. increased gating (or bound) leads to slower RT and higher accuracy. As far as we can deduce, a gradual opening of the gate would lead to the prediction of a progressive increase in the influence of sensory evidence on decision signal build-up over time, yet the urgency components identified in neurophysiological studies to date have been demonstrably evidence-independent. Thus, we cannot quite conceive of how a dynamic

gate adjustment could account for diminishing accuracy as a function of RT or the observation of time-dependent urgency signals in motor-preparation circuits.

We thank the reviewer for orienting us to Malhotra et al's paper which indeed provides an important demonstration that the optimality of dynamic bound adjustments varies as a function of task demands (page 3).

Reviewer 2

1. The title of the review is somewhat misleading, as it suggests that the authors will present a broad perspective on decision making. In fact, they restrict themselves to the consideration of sequential sampling models. There is nothing wrong with this, but as things stand, the more specific focus of the article should be clearly flagged up.

In retrospect we agree that our original title was too general and should have made specific reference to our focus on 'perceptual' decisions. Given this theme it is logical that we focus almost entirely on sequential sampling models since these are by some distance the most commonly implemented and most influential models in the field of perceptual decision making.

2. Similarly, there is an ambiguity in the purpose of the article. Are the authors aiming to specifically discuss work on sequential sampling models, or just use sequential sampling models as an example for broader points. If the former, I would expect to see more discussion of sequential sampling models, in particular, how plausible they are as psychological process theories. If the latter, then I would suggest that the paper includes more discussion of broad conceptual points, and the specific details of the literature on sequential sampling are reserved to illustrate specific points.

We have now made changes throughout the manuscript, including completely rewriting the Abstract, to make it clear that the focus of this review is on efforts to leverage neural data in resolving major theoretical debates that have arisen in the recent literature on *perceptual* decision making. While our review certainly touches on themes that are relevant to many domains of cognitive neuroscience, sequential sampling models have provided the dominant theoretical framework guiding research on perceptual decision making and therefore take center stage in the most prominent studies and debates in this field. As the reviewer alludes to here and in the next comment, our review brings up important questions about how we compare data across distinct levels of analysis i.e. refining psychological process models by testing the unique predictions they make for the neural implementation of those processes. We have added more discussion of these considerations to the revised manuscript (e.g. pages 4 and 5). We have also oriented the reader to recent reviews that comprehensively examine sequential sampling models and

their plausibility as psychological process theories (Ratcliff et al 2016, TICS; Forstmann et al 2016, Ann Revs Psychol).

3. A key point, which the authors mention but don't further explore, is the status of the models being used. Sequential sampling models could be considered a 'process theory' at a psychological level, but it is far from clear how they would be instantiated neurally. This motivates the search for neural correlates of aspects of this model, which the authors describe, but it also necessitates the search for neurobiological process models that implement sequential sampling. (This point could also be framed in terms of Marrian levels) I am surprised to see this second point given relatively little prominence in the article, being largely relegated to Box 4. This isn't a trivial point, without candidate neural process models, it can be difficult to confidently interpret the significance of the neural correlates of (for example) urgency signals. (I would recommend looking at Laurence Hunt's thoughtful 2014 TICS piece) None of these concerns are fatal to the points the authors are trying to make, but they do provide an important context.

We are grateful to the reviewer for raising this very important point. We have now made several changes to the main text in order to highlight the pivotal role that biophysically-grounded neural process models have played in establishing the plausible circuit configurations and settings that can support computations such as temporal integration and in interpreting empirical observations of decision-relevant neural dynamics (e.g. pages 9 and 10). We have also highlighted the importance of bridging between abstract models and these biophysically grounded neural models (pages 4, 5, 9 and 10).

4. I was surprised not to see discussion of recent work by Jonathan Pillow, Carlos Brody, and others that have called into question the LIP-as-evidence-accumulation story. It is essential that the authors cover this challenging recent material and how it relates to their contentions. Chris Summerfield's work looking at EEG correlates of evidence accumulation might also be relevant here.

Box 3 of the original submission was intended to highlight the recent LIP inactivation studies by Pillow, Huk and others and to examine the claim that they present a challenge to previous work linking activity in this region with evidence accumulation. However, we failed to cite the relevant rodent work of Brody et al and the reviewer's comment has highlighted to us that we may not have communicated our ideas with sufficient clarity. We have therefore amended the text of Box 3 and included the missing citations. Although these recent inactivation studies have drawn a considerable amount of attention, we point out that the notion that since LIP activity reflects the dynamics of sensory evidence accumulation, it must thus represent LIP's core function was always misguided. Numerous earlier studies had already indicated that LIP inactivation has at

best a weak impact on choice behaviour and that decision-related activity in this region is highly task-dependent. Nevertheless, we believe it has been convincingly demonstrated that, under carefully contrived circumstances, LIP neurons can provide a valuable window onto the neural decision process which can inform the construction of mathematical models.

It is not clear to us whether the reviewer also has in mind Latimer/Pillow et al's recent study (Latimer et al, 2015, Science) suggesting that single-trial LIP spike trains are better described by a statistical model involving discrete instantaneous steps and that the previously reported ramp-to-threshold dynamics are a byproduct of trial averaging. The methods employed in this study and the interpretation of results are the subject of a vigorous and very detailed debate (Shadlen et al 2016, Science; Latimer et al 2016, Science; Zylberberg et al 2016, BiorXiv; Latimer et al 2017, BiorXiv) including follow-up analyses that have yielded conflicting results (Zhao & Konrad, 2018, BiorXiv). However, Latimer et al themselves argue that their findings should not be taken as a rejection of the larger LIP accumulation-to-bound model but, rather, serve to highlight the gaps in our understanding of the relations between the functional properties of individual cells and the resulting circuit dynamics (Latimer et al 2017, BioRxiv). Even if correct, the idea that individual neurons might step instead of ramping is not at odds with the view that the brain implements evidence accumulation processes for making perceptual decisions or that trial- and population-averaged LIP activity can offer a window onto these processes. Thus, while highly interesting, Latimer et al's findings do not pose any obvious challenges to the overarching message of our review that decision-related neural activity measurements - not just from LIP but potentially from any recording established to reflect dynamics of decision formation - can be fruitfully used to inform abstract cognitive models. For this reason, due to space restrictions and because Latimer et al's study has already been extensively discussed and reviewed (Hanks & Summerfield, 2017) elsewhere, we have opted not to cover this particular study/debate in our revision.

We thank the reviewer for highlighting the EEG work of Summerfield et al, which we have cited in Box 2.

5. In places there is too much focus on the details of particular studies for a TiNS article (e.g. the paragraph from L123 - 140)

We have made amendments to the text in order to reduce the time spent on any single study. We understand that, having given the impression that our intention was to provide broad coverage of the literature on decision making, we appeared to spend an excessive amount of text discussing the paper by Hawkins et al. However, as we hope we have clarified in our responses above and in our changes to the manuscript, our focus is very

much on perceptual decision making and efforts to draw correspondences between sequential sampling models and neural activity measurements. This highly influential paper by Hawkins et al provides an excellent illustration of the limitations of developing models based purely on fits to behavioural data and we feel this can only be conveyed to the general reader by laying out the details of the study and, most importantly, how the model comparisons were conducted. We have sought to articulate this more clearly through amendments to the text.

6. The discussion of model comparison in the text is somewhat unclear. By definition, Bayesian model comparison gives us our best guess about the model (and therefore the mechanisms) that generated the data. Clearly there are limitations to this - we may not have the right models, the right priors, the right (or enough) data, but these are limitations of our knowledge and experiments, not model comparison as such. If the point that the authors want to make here is (as I take it to be) that behavioural model comparison can only take us so far, then this needs to be discussed more fully.

Yes, the reviewer is correct that our intention is to argue that behavioural model comparisons can only take us so far. We certainly did not mean to suggest that Bayesian tests are not a good approach to model comparisons in general. We have amended the text in order to articulate this important point more clearly.

7. Related to the above point, there are other areas in which neural data may be essential for adjudicating between behavioural models. (A lot of neuroeconomics, for example, can be seen in this light.) The authors might want to consider discussing these parallels with other areas.

We thank the reviewer for this suggestion. Indeed, given the increasing trend toward integrating computational models with neural data across the cognitive neurosciences, our review touches on conceptual and methodological issues that transcend the literature on perceptual decision making. Although the space limitations preclude a thorough discussion of the parallels, we took the opportunity to at least highlight this general point and to orient the reader to a couple of excellent recent examples from the neuroeconomics and object categorisation literature (page 11).

8. The paper would be improved by the addition of a figure or two illustrating different approaches to relating cognitive and neuronal models/data.

We thank the reviewer for this suggestion. We have now included two figures in the manuscript. Figure 1 illustrates the dominant approaches to accounting for slow errors in behavioural models of perceptual decision making. Figure 2 illustrates neural observations

from rodents, monkeys and humans which highlight the parallelism and multi-tiered nature of the brain's decision making architecture.

Bridging Neural and Computational Viewpoints on **Perceptual** Decision Making

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Keywords (2-6): **Perceptual** decision making, computational modelling, sequential sampling, Lateral Intraparietal area (LIP)

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Abstract

Sequential sampling models have provided the dominant theoretical framework guiding computational and neurophysiological investigations of perceptual decision making. While these models share the basic principle that decisions are formed by accumulating sensory evidence to a bound, they come in many forms which can make highly similar predictions of choice behaviour despite invoking fundamentally different mechanisms. The identification of neural signals that reflect the core computations underpinning decision formation offers new avenues for empirically testing and refining major model assumptions. The goal of this review is to highlight recent efforts to explore these avenues and, in so doing, to consider the conceptual and methodological challenges that arise when seeking to infer decision computations from complex neural data.

Decision Making as a Core Component of Cognition

The term ‘decision making’ often calls to mind scenarios such as how to vote in an election or which course to take in college, yet even our perception of our sensory environment relies on a continuous stream of elementary judgments ([‘perceptual decisions’](#)) that can be equally life altering (e.g. is the traffic light red or green?). In the highly complex and dynamic environment that we inhabit, making accurate and timely decisions is a considerable challenge for the brain since the information it receives is almost always to some degree unreliable. Understanding how the brain overcomes this problem stands to illuminate principles of computation that extend to a wide range of cognitive operations [1].

The theoretical foundations for [modern research on perceptual decision making](#) were laid within mathematical psychology, with the development of ‘sequential sampling’ or **evidence accumulation** (see Glossary) models [2-6]. Not only do the models have a long history of successfully accounting for choice behaviour in a wide range of contexts, but the core computations that they specify appear to be mirrored in certain components of neural activity in the rodent [7], monkey [8, 9] and human brain [10]. [Consequently, recent years have witnessed a growth and confluence in research efforts to identify the computations through which perceptual decisions are formed as well as to map, measure and manipulate the neural structures and processes through which they are implemented, all anchored to the framework of sequential sampling. An expanding repertoire of approaches to combining neural and computational viewpoints has emerged on the back of this movement \[11\]. In this review we shine a spotlight on recent trends in using one such approach, where neural signals known to reflect key aspects of bounded evidence accumulation are used to inform abstract decision models. We demonstrate the potential of this approach in providing strong grounds for model adjudication where behavioral modeling alone falls short and thus for resolving important theoretical debates about decision computations, and also highlight the conceptual and methodological challenges involved.](#)

Abstract Decision Models and Challenges in Model Selection

Originally based on normative models for minimising the time taken to achieve a certain level of quality control accuracy [12], sequential sampling models provide quantitatively accurate accounts of behavior on a wide range of tasks including perceptual detections and discriminations, lexical memory, response inhibition and even social and value-based decisions [for comprehensive reviews see 13, 14]. This powerful class of psychological process models can explain both random and systematic variations in performance and decomposes choice reaction times and accuracy into meaningful latent parameters such as the strength of the evidence entering the decision process (‘drift rate’, i.e., the expectation of the evidence

distribution being sampled) and the cumulative quantity required to trigger commitment ('decision bound'). Ongoing research based on these behavioral models continues to fruitfully examine how our decisions are shaped by factors such as speed pressure, value, prior knowledge, distracting information and brain disorders [14].

Many model variants exist because there are many alternative implementations of a decision process based on sequential sampling (Box 1). In many cases, competing model variants based on fundamentally different mechanisms can produce the same behavioural signature. This problem of model mimicry significantly hampers adjudication between competing accounts and has given rise to several long standing debates. To take an instructive example, a current ongoing debate centers on whether the criterion amount of evidence that we require to reach commitment can dynamically change during the course of a decision.

In the most widely-subscribed models [13](see Box 1), although the bounds can be adjusted across different contexts to emphasise speed versus accuracy, in any given trial the bounds are assumed to be constant over time. Yet, collapsing bounds provide an optimal policy according to normative theory under the common situation where evidence strength varies unpredictably across trials and is sometimes very weak [15, 16], or where responses must be made within a strict deadline [15, 17]. One of the main reasons why collapsing bounds have not been incorporated in the dominant models is because key behavioral consequences of it, such as decreased accuracy for trials with longer reaction times, can be produced within a drift diffusion model with constant bounds via an alternative mechanism involving trial-to-trial variability in drift rate [13, Fig. 1].

Establishing the relative prominence of these alternative mechanisms in choice behavior has consequences far beyond matters of preference in model fitting approaches, because they reflect fundamentally different algorithmic elements that have important implications for our understanding of normal and abnormal decision making. For example, there has been an increasing application of sequential sampling models in studies seeking to better understand the decision making deficits observed in psychiatric populations [18, 19]. Establishing that relatively slow response times for errors in a given clinical population arise from a faster bound collapse (e.g. due to a more impulsive decision policy or aversion to missed deadlines) as opposed to greater drift rate variability (e.g. due to fluctuations in attentional engagement, see below for further discussion) would have very different implications both for explanatory accounts of the disorder and efforts to treat it. Similarly, an increasing trend in human neuroimaging research is to use decision model parameter estimates from behavioural data fits in statistical analyses to localize decision-relevant brain regions [11, 20]. Here, again, the particular choice of model could have major consequences both for the particular areas identified and the interpretation of the role they might actually play in decision formation [21].

Behavioral model comparison approaches provide a means to identify models that strike the best balance between parsimony and goodness of fit. Consequently, in adjudicating between two model mechanisms (e.g. collapsing bound versus drift rate variability) that produce the

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4 same qualitative behavioral pattern (e.g. slow errors) the choices that are made on the number
5 and nature of the parameters used to implement a particular mechanism can have a major
6 bearing on the outcome. For example, Hawkins et al [22] conducted formal model comparisons
7 using several human and monkey datasets. Most datasets were better explained, in the sense
8 of better Bayes Information Criterion (BIC), by a constant bound model with drift rate
9 variability. However, in this comparison collapsing bound models also included drift rate
10 variability in addition to several parameters describing the collapse (non-linear functions of
11 time), thus setting them at a disadvantage since BIC metrics penalise for complexity. In an
12 attempt to address this, a second main comparison was made with a collapsing bound model
13 contrived to have the same number of parameters as the constant bound model. Again, the
14 data favored constant bounds but the parameters that were omitted from the collapsing bound
15 model were ones that account for qualitatively distinct, and often significant aspects of
16 behavioral data (e.g. fast errors, distribution shape). The simplest way to implement a
17 collapsing bound, i.e. a linear function of time, was not considered. A more recent study that
18 did use such a linear implementation, in contrast, showed an improved BIC for a model that
19 included collapsing bounds alongside drift rate variability [23].
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29 **Neurally-Informed Decision Models**

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31 Discrepancies like the above highlight the difficulties that can arise when adjudicating between
32 alternative models based on behavioral data alone. A powerful way to break such impasses is to
33 additionally consider a model's ability to capture key observable aspects of the biological
34 implementation of the decision process [24-30]. Advances in both animal and human
35 neurophysiology have significantly broadened the possibilities for such an approach by
36 identifying signals that exhibit key dynamical characteristics of bounded evidence
37 accumulation. For example, in one line of work single neurons in the monkey lateral
38 intraparietal area (LIP) have been shown to exhibit highly choice-predictive activity that builds
39 at a rate proportional to physical evidence strength [31, 32], linearly grows in variance as more
40 evidence is sampled over time [33], and reaches a stereotyped firing level immediately prior to
41 the perceptual report [34]. More recently, human electrophysiology research has established
42 that signatures of bounded evidence accumulation can also be traced in global, non-invasively
43 recorded signals [23, 35-37](Box 2). In parallel, empirically-grounded, biophysically-based
44 models have been developed that describe plausible neural circuit configurations capable of
45 implementing computations such as temporal integration [e.g. 38, 39]. The ability to observe
46 neural signals reflecting decision formation is not only relevant to the construction of such
47 neural network models but can also provide critical guidance in constructing, constraining and
48 adjudicating between abstract, cognitive process models. Returning to our example above,
49 collapsing bounds and drift rate variability, in fact, each makes specific predictions for neural
50 signals relevant to decision formation, and much data already exist to examine such
51 predictions.
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Several recent neurophysiological studies in humans and monkeys have furnished evidence that decision bounds are, at least in certain contexts, adjusted dynamically during decision formation [23, 40-43]. For example, studying motion direction decisions, Hanks et al [41] demonstrated that the spiking activity of neurons in area LIP, in addition to its dependence on direction and evidence strength, also exhibited an evidence-independent component of buildup for both choice alternatives, and this **urgency signal** rose more steeply under speed pressure (Fig. 1d). By imposing a progressive reduction in the quantity of evidence needed to trigger commitment to any of the choice alternatives, urgency signals provide a neural mechanism for implementing the collapsing bounds proposed in mathematical models. In addition to this dynamic component, Hanks et al also observed that LIP **activity was elevated at the outset of the decision under speed pressure, consistent with an additional static component of the bound adjustment, and the findings of other human neuroimaging [44-46] and monkey [47] studies**. Despite these starting point and time-dependent variations, LIP activity converged to a common level prior to the perceptual report. Based on these observations, a model that allowed for both static and dynamic adjustments to the decision bound was constructed. Crucially, the additional parameters describing these bound adjustments were not fit to the behavioural data but measured directly from neural activity, and the only parameters that were free to vary were ones that did not differ between the two speed pressure conditions. The resultant model nevertheless provided a compelling fit to the behavioural data including the extent of the impact of speed pressure. Although it has been suggested that such urgency effects may be peculiar to monkeys [13], and species differences of this nature likely do exist, consistent effects have recently been reported in human electrophysiological indices of motor preparation [23]. **Alongside the growing number of empirical demonstrations of urgency and their increased incorporation into abstract models, new lines of research are seeking to identify plausible biophysical mechanisms for their generation. Neural network modelling studies have demonstrated the potential role of dynamic modulations of neural gain [48-50], in particular those mediated by neuromodulatory arousal systems [51], whose dynamic activity can be empirically examined via changes to pupil diameter [23].**

Drift rate variability is an undeniably convenient feature of abstract decision models for quantitative fitting of behavior [52] but it is seldom scrutinized in terms of possible neurophysiological underpinnings. The most obvious candidate underlying cause is the random trial-to-trial fluctuation in the mean firing rates of neurons encoding **sensory evidence**. In the context of two-alternative decisions, such fluctuations would have to take the form of random biases towards one alternative or the other rather than nonselective variations related to general arousal or task engagement, since drift rate is driven by differential evidence. Such fluctuations would also have to occur on the slow timescale of typical trial durations, and therefore should give rise to significant and broad autocorrelation in evidence-encoding neurons. This has been examined in several areas including monkey MT for motion decisions, where autocorrelation levels are, in fact, low and have short (on the order of <100 ms) timescales [53, 54], at least compared to higher brain areas [55]. This does not preclude variability in the weighting of such evidence signals as inputs to the accumulation process, and

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4 it is possible that broad fluctuations are more prominent in other sensory areas, other species
5 and/or other tasks. For example, during continuous monitoring for sensory targets occurring at
6 highly unpredictable times, one could speculate that the absence of time constraints may
7 minimize the influence of urgency signals, while the increased demands on sustained attention
8 may yield trial-to-trial fluctuations in sensory evidence that impact on the timing and
9 probability of target detections [56].
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13 In general, there are many different ways in which observations of decision-related neural
14 signal dynamics can inform psychological process modelling and thereby help to converge on a
15 computational account of the brain's decision mechanisms [11, 28]. The most effective use of
16 the neural data obviously depends on the nature of the data available, the paradigm employed,
17 and the particular mechanisms being examined. In the case of Hanks et al [41], the particular
18 set of stimulus conditions that was run enabled the time course of the urgency signal to be
19 derived directly from the neural data and applied as a constraint in the model [57]. More
20 generally the correspondence between discrete measures of neural signal dynamics (e.g. onset
21 time or rate of buildup of a decision signal) and model parameters (e.g. non-decision time or
22 drift rate) may not be sufficiently direct or "one-to-one" to warrant constraining the model
23 parameters themselves, in which case empirical neural dynamics can be compared to simulated
24 model dynamics [28].
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31 One powerful approach that is beginning to be employed is to quantitatively fit a given model
32 to both the neural signatures of decision formation and behavioral data combined, in a single
33 step [58]. This approach exploits a key benefit of neurally-informed modelling in relying on the
34 additional constraints brought by neural data to allow models to take on levels of complexity
35 closer to the neural reality. In cases where behavioral data alone provides sufficient constraints
36 for a reasonable fit, a "two-step" approach can be taken, where behavioral fits are used to
37 simulate dynamics for comparison with neural dynamics in a separate step. For example, in one
38 recent study of rapid, value-biased sensorimotor decisions in humans [59], several candidate
39 models invoking starting-point versus drift rate biases were first fit to behavior. As found in
40 most previous studies [e.g.60, 61], a starting-point bias produced the better fit under the
41 assumption of stationary (non-time-varying) drift rate. In contrast, when drift rate was instead
42 assumed to increase over time within a trial to take account of the gradual nature of early
43 sensory encoding processes when viewed on the timescale of very fast decisions, a drift rate
44 bias provided a better fit. When evidence accumulation dynamics were simulated for all
45 models, this value-biased, temporally increasing drift rate model made the unique prediction
46 that neural signatures of decision formation should exhibit a 'turnaround' pattern on low-value
47 sensory cues, where differential evidence is initially accumulated towards the wrong (but
48 higher-value) alternative and is then dynamically re-routed towards the correct alternative.
49 These very dynamics were observed in electrophysiological decision signals at both the level of
50 motor preparation and motor-independent evidence accumulation. This study illustrates how
51 qualitative model comparisons facilitated by electrophysiological signals tracing decision
52 formation can strongly bolster the outcomes of quantitative, behavioral model comparisons
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Neural signal analyses could similarly play a critical role in the application of models in research involving group comparisons. For example, consider the simple matter of choice of “scaling parameter” - a parameter whose value is fixed to anchor the model fit, and to set the arbitrary scale on which all other parameters are measured. A common choice in abstract decision models (e.g. DDM) is to set within-trial noise to a fixed value [62]; but what if, in reality, the major difference in the neural circuits of individuals with a clinical disorder is greater within-trial noise [63]? Differences such as this could in principle be observable relatively directly through neural recordings, thus helping to avoid misattribution of deficits among distinct mechanistic elements of the decision process.

An obvious caveat to any of the above approaches is that it must take account of how confident we are that the signals in question are tracing the core neural computations that give rise to decisions [64]. Since many brain signals (e.g. sensory and motor) are likely to be correlated in some way with the observer’s choices, examining signal dynamics during the period of deliberation and establishing a temporal relationship between those dynamics and choice commitment (e.g., reaction time), is an essential step to avoid an erroneous attribution of function. Thus, as much as with fitting of behavior alone, immediate-response paradigms that pinpoint the time of decision commitment provide critical constraints that enable more definitive model comparison [9, 34]. In addition, it is important to take account of the fact that the role that distinct brain areas and signals play in decision making is likely task-dependent (see below and Box 3).

Accounting for a multi-tiered neural architecture

Neurophysiological evidence from rodents, monkeys and humans is increasingly highlighting the multi-level nature of the brain’s neural architecture for implementing even the most elementary sensorimotor decisions [7, 10, 65, 66](Fig 2.). Explicitly representing each processing level in mathematical models may not usually be necessary to quantitatively account for the timing and accuracy of choice behaviour, but understanding how these distinct processing levels contribute to decision computations is essential if we are to develop a fuller systems-level understanding of the neural decision process as well as pinpointing the origins of decision making deficits. In some cases, behavioural effects emanating from different processing levels can be disentangled through experimental design. For example, a recent behavioural study demonstrated that choice biases arising from differences in the energetic cost associated with reporting each alternative, originate not at the motor level as one might expect, but at an upstream level of decision formation that is independent of motor effectors [67].

More generally, however, there are clear limits on the ability to localise effects among hierarchical processing levels using behavioural modeling alone. Several key parameters of

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4 sequential sampling models are likely subject to influences at multiple processing levels which
5 cannot be distinguished. For example, changes to the 'non-decision time' parameter (which
6 accounts for delays due to processes not directly associated with evidence accumulation) could
7 alternatively come from altered delays at the outset (e.g. sensory encoding) and/or at the end
8 (e.g. motor execution) of the decision process. There is also ambiguity in a parameter's
9 dependence on changes at a single processing level versus in the transmission of information
10 between levels; for example, drift rate is dependent not only on the strength and reliability of
11 sensory representations themselves but also on the weighting or reference values used in
12 casting those representations as an input to the accumulation process (e.g. "drift criterion"
13 setting [62]).
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21 Thus, there is much to be gained from examining decision-relevant neural dynamics at each of
22 the key processing levels underpinning decision formation. A key challenge for this goal is that,
23 even in the case of elementary sensorimotor decisions, we do not yet know how many levels of
24 processing there truly are in the computational sense. Multi-region recordings have revealed
25 that choice-selective signals are rapidly transmitted across many areas[68, 69], and as one
26 proceeds toward the motor end of the hierarchy, neural activity is progressively more closely
27 associated with the subject's action choice rather than the stimulus features[65, 70]. But
28 beyond this general principle, the distinct role played by each step of the pathway and its
29 individual contribution to implementing the algorithm employed by the brain to make a given
30 decision, is difficult to establish. In monkeys, for example, decision-related buildup activity with
31 comparable latencies has by now been observed in LIP [71], medial intraparietal area [72]
32 frontal eye field [73, 74], prefrontal cortex [75, 76], superior colliculus [77], basal ganglia [78,
33 79], dorsal [80] and ventral premotor cortex [81] and primary motor cortex [42], and not
34 surprisingly, many research efforts have turned to identifying the distinct contributions that
35 these areas make (Box 3, Fig 2.).
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44 Non-invasive human recording techniques naturally provide a global view over all processing
45 levels in tandem, though their lower resolution necessitates the use of paradigm designs and/or
46 analysis methods that aim to disentangle their measurement (Box 2). Human electrophysiology
47 studies have isolated two functionally distinct classes of decision signals reflecting accumulate-
48 to-threshold dynamics: effector-selective signals that, like signals in areas such as LIP, represent
49 the translation of sensory evidence into a specific motor plan [23, 37, 82], and a domain-
50 general signal that builds with cumulative evidence regardless of whether responses are
51 immediate, delayed or not required at all, or of the sensory feature or modality being decided
52 upon [35, 83](Fig 2c). The latter supramodal, motor-independent signal, termed the
53 centroparietal positivity (CPP), was also found to precede evidence-selective motor preparation
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4 signals in time [56] further suggesting that it operates at a level of processing intermediating
5 between sensory encoding and motor preparation.
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9 This discovery builds on longstanding assertions that the brain must house abstract-level
10 mechanisms to afford flexibility in mapping sensations to appropriate actions [84-88] by further
11 suggesting that such intermediate processes can operate the way more dedicated circuits do -
12 that is, by approximating an accumulation of sampled evidence towards a criterion or decision
13 bound. The intracranial origins of this signal are as yet unknown. Given the similarity in
14 bounded accumulation dynamics, it is tempting to link the CPP with activity in area LIP.
15 However, EEG picks up neural activity globally and, since build-up activity for the selected
16 alternative is mirrored by a roughly corresponding decrease in the activity of neurons coding for
17 the unselected alternative, it would be expected that much or all of LIP's choice-selective
18 buildup activity would be cancelled out at the level of the scalp. Interestingly, LIP neurons have
19 been found to encode goal-relevant stimulus categories (e.g. motion direction) in an effector-
20 independent fashion; however, it is not known whether these signals exhibit evidence
21 accumulation dynamics [88]. More generally, much work remains to be done to relate
22 intracranial and extracranial signals exhibiting decision-predictive dynamics in different species
23 [89](Box 4). These questions notwithstanding, the identification of an abstract accumulation
24 process in human brain recordings highlights the existence of an additional processing layer
25 whose precise role in decision formation remains to be determined.
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35 Although we may lack a complete picture of the essential computational layers for decision
36 making, studies that have recorded neural activity at multiple processing levels during the same
37 task have already furnished insights that are beyond the reach of behavioural modelling alone.
38 For example, recording from both MT and LIP during training on a motion direction
39 discrimination task revealed that improvements in behavioural sensitivity with learning were
40 attributable to changes in the motion-driven response of LIP neurons in the absence of any
41 change in the evidence-encoding MT neurons, suggesting that learning changes the read-out
42 but not the sensory representations themselves[90].
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49 In certain instances, multiple levels of processing can be examined within a single brain area.
50 For example, in the context of visual search decisions, salience encoding visual FEF neurons
51 provide the evidence that is accumulated by movement neurons, and these signals have also
52 been used to directly constrain mathematical models [27, 29, 47]. One such study examined the
53 impact of speed/accuracy emphasis in visual search on processing at these distinct levels [47].
54 Despite the fact that behavioural data fits of a popular bounded accumulation model (linear
55 ballistic accumulator, Box 1) indicated no difference in drift rate, speed pressure was found to
56 enhance evidence encoding in visual FEF. Meanwhile, evidence accumulating movement
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neurons exhibited a complex pattern of adjustments that were not predicted by any pre-existing decision model, including *increased* activity levels at the time of saccade execution under greater speed pressure. The authors went on to construct a multi-level model that could accommodate this seemingly paradoxical finding by positing an additional leaky integration step carried out by brainstem neurons known to exhibit a threshold-crossing relationship with saccade execution and to receive direct projections from movement neurons of the FEF. This model provided as good a fit to the behavioural data as the standard model while also capturing key qualitative features of the measured FEF activity including increased buildup rate in the visual neurons under speed emphasis. This study serves to highlight that, while abstract decision models can provide parsimonious accounts of choice behaviour, they may not necessarily capture all of the mechanistic steps that the brain performs and are therefore not always likely to correspond with neurophysiological dynamics observed at any one processing level. It also illustrates how models built from physiological knowledge of sensorimotor systems and their capabilities can play a pivotal role in facilitating the interpretation of decision-related neural activity patterns (Box 4).

Complementing computational modelling with neural recordings probing multiple processing levels (e.g., sensory evidence encoding, motor-independent accumulation, motor preparation and muscle activation) will be central to resolving a range of outstanding questions in the field. For example, thus far, neurophysiological research examining the impact on decision making of key factors such as speed pressure, prior probability and payoff information has mainly focussed on activity in neural circuits situated close to the motor output end of the sensorimotor hierarchy. Yet, research on attention [91], feature expectation [92] and reward expectation [93, 94] has demonstrated the capacity of the brain to exert top-down influences on basic sensory representations. *We do not know to what extent such modulations are employed when adapting decision processes to account for contextual factors, and modelling studies rarely consider their potential computational benefits.* The signals and techniques are now available for us to begin to answer these questions and, in any such endeavour, computational models can play an essential role in linking neural activity to the distinct algorithmic elements of decision formation.

Concluding Remarks

Sequential sampling models have provided a common, principled foundation to diverse investigations into decision making. Behavioral fits of the models have long been used to furnish meaningful, mechanistically-defined metrics to aid in understanding differences in how decisions are forged across stimulus conditions, task contexts and clinical groups. However, the

field has been grappling with a number of debates regarding key algorithmic elements of these models that are difficult or impossible to resolve based solely on quantitative fits to behavioural data. The newfound ability to observe neural signal dynamics underpinning the decision process provides a new means of guiding model development and recent studies demonstrate the unique insights that can be acquired by examining correspondences between abstract mathematical models and neurophysiological observations. Depending on the availability of neural signals that definitively reflect elements of decision formation, it is possible to construct models that are neurally-constrained (e.g. quantitatively setting a time-varying stopping criterion based directly on neural measurements), neurally-informed (e.g., including and fitting parameters for time-varying criterion settings based on qualitative patterns observed in the neural data), or at least neurally-cognizant (e.g., including and fitting a time-varying criterion based on pre-existing neurophysiological evidence for its general role). With the ongoing development of techniques and paradigms for measuring decision-relevant neural processes, we can expect to see increasing adoption of such approaches that integrate neural evidence into computational accounts of decision making (see Outstanding Questions). Adapting cognitive models to reflect the critical neural dynamics governing decision formation can also help substantially in establishing much needed linkages between the parameters and mechanisms of cognitive models and biophysically-based neural circuit models, which are rarely brought into direct contact [95](Box 4). [The conceptual and methodological challenges examined in this review have implications that extend beyond research on perceptual decision making as a trend toward integrating computational models and neural data is increasingly evident in many other research fields \[96, 97\].](#)

Box 1. Sequential sampling models: Different flavours for different research objectives

Over the years, several decision model variants have been developed based on the core principles of sequential sampling and bounded evidence accumulation. In standard, one-dimensional diffusion models, for example, a sequence of samples from a Gaussian distribution representing noisy sensory evidence with, say, mean $\mu\Delta t$ (“drift rate”) and variance Δt , is accumulated until the cumulant reaches an upper or lower bound. The drift rate scales with stimulus strength and the bounds are set to achieve a balance between speed and accuracy demands. A “non-decision” time is included to account for additional delays associated with encoding, routing [98] and/or motor execution processes, independent of the diffusion process itself. In a popular, versatile version of this model, it is extended to include random trial-to-trial

variability in starting point, drift rate and non-decision time, which provides significant flexibility to capture relatively fast or slow errors and specific RT distribution shapes [62].

More or less complex versions of this model are employed depending on research goals. In general, cognitive modeling is principally concerned with forging abstract mathematical accounts of behavior whose parameters serve as mechanistically interpretable metrics of task performance, and differs from neural modeling in not striving to represent details of neurophysiological implementation [99]. Several reduced models have been developed to achieve this with computational ease, for example by excluding trial-to-trial variability parameters, where the relative speed of error responses is not critical [100], or by excluding the within-trial noise parameter (“ballistic,” racing accumulators [101, 102]).

Toward the more complex end, the leaky competing accumulator model of Usher and McClelland [103] parameterizes both the degree of competition between alternative accumulators and the leak of information within them, which provides one way to explain limited improvements in accuracy with longer viewing durations. Cortical microcircuit models have been developed which reproduce complex dynamical aspects of neural buildup patterns as well as decision behavior [38, 104], and incorporate well-known motor control circuits such as the basal ganglia [105]. An ongoing challenge is to determine how the elements of these sometimes very complex circuit models relate in straightforward terms to the parameters of the abstract models. Although cognitive modeling and neural modeling have ostensibly distinct goals, there is valuable but under-exploited territory at the interface between them, where models could capture key elements of neural implementation at distinct levels of the sensorimotor hierarchy as well as detailed behavioral trends.

Box 2 Probing Decision-related neural activity in Non-Invasive Recordings

Significant advances in isolating decision signals from noninvasive human brain recordings open up possibilities for translating the detailed characterisations of decision mechanisms wrought from non-human neurophysiology to the human brain in both health and disease. Moreover, global brain recording techniques like electro-/magneto-encephalography (EEG/MEG) and fMRI can complement intracranial investigations by offering a unique systems-level view over processes underlying decisions of a wider range of complexity. A challenge, however, is that noninvasive assays suffer from poor resolution. In EEG/MEG, signals at the scalp reflect the sum of all concurrently active components of neural activity. Several approaches have been

employed to disentangle the components specifically playing a role in decision making. One approach is to design paradigms that by their nature produce signals related to the core ingredients for a decision (sensory evidence, its accumulation over time, and emergent motor preparation) while minimising decision-irrelevant neural activity components. For example, decisions based on gradual changes in the intensity of flickering visual or auditory stimuli readily furnish sensory evidence signals through steady-state flicker-response amplitudes and eliminate irrelevant early sensory-evoked potentials normally evoked by sudden intensity transients [35]. This allows observation of decision formation dynamics relatively directly without imposing any constraints on the form they should take. The downside is that the approach works best for very elementary decisions.

Other approaches have used signal-analytic methods to extract decision-relevant signals during more complex tasks involving higher-order categorizations. For example, using a task requiring accumulation of orientation information varying stochastically over discrete sequential samples, sample-by-sample regression analyses can furnish distinct signal components related to decision-irrelevant sensory changes and relevant decision-update processes [106, 107]. Another approach uses multivariate classification algorithms to derive functionally-defined EEG components that, like the observers themselves, discriminate between blurred images of high-level objects such as cars and faces [36]. Significant promise lies in combining the above paradigm-design and analytic approaches.

For the above noninvasive neurophysiology approaches, the ability to take measurements of dynamic decision signals at multiple hierarchical levels in the decision architecture has been demonstrated, yet the potential to use such measurements in **neurally-informed**, or even neurally-constrained, modeling is only beginning to be realised [23]. Joint neural-behavioral model fitting can also be done in a more data-driven manner, without necessarily singling-out signals independently verified to reflect decision formation dynamics. This is best exemplified in neuroimaging research. Although limitations in temporal resolution preclude measurement of dynamics, brain-wide BOLD activations can be used as constraints in model fits [108] and play a vital role in identifying candidate decision-related brain structures for potential follow-up in intracranial investigations.

Box 3 Causal Inference

Much research effort in decision neuroscience has been focussed on recordings from area LIP and this work has yielded insights into the computational mechanisms by which the brain accommodates speed-accuracy demands [41], prior biases [109], multiple alternatives [40], switching between alternate evidence dimensions [110], and other problems regularly faced by real decision makers. *As these insights have amassed, so also has the misconception that such findings imply that LIP's central function is to accumulate evidence for decisions. This is of course misguided.* LIP simply contains neurons whose properties, characterized over decades of careful

research into saccadic target selection [111, 112] make it possible to study transformations common to many decisions when experimental conditions are carefully contrived to render those neurons informative (e.g., when the decisions are based on simple feature discriminations and choices are reported via saccades towards or away from targets placed within the receptive field of the recorded neuron). Moreover, these studies typically record from a subset of LIP neurons that exhibit sustained firing during delay periods prior to saccade execution on the grounds that they are best equipped to trace a temporally extended decision process. Step outside of these conditions and the choice-relevant dynamics observed in LIP can change significantly. For example, in the context of visual search, neural signatures of evidence accumulation are observed in the frontal eye field [47, 73] while LIP activity has been linked more with the representation of salience as the core ‘evidence’ on which the search decision is based [113, 114]. Even in the case of motion discrimination, LIP is only one of many areas carrying functionally similar evidence accumulation signals [e.g. 72], and may not necessarily play any role in most decisions faced by the animal in its daily life. Indeed, across a range of tasks involving saccadic choices, inactivation of LIP and rodent PPC has varying, task-dependent impact but is never devastating to performance[e.g. 115, 116-119]. As was stated at the outset of this line of work [31], the build-to-threshold dynamics in LIP do not in themselves suggest that decisions are formed in LIP, but rather that LIP can provide a window onto decision processes and the computations they implement regardless of where the decision is initiated.

Box 4 Bridging across recording modalities in decision neuroscience

The neural bases of decision making have now been studied at a range of functional levels and scales running from single neurons, through neuronal microcircuits, to global activity measured

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4 in human electrophysiology/neuroimaging. With these expanding viewpoints comes the
5 imperative to integrate findings across these levels, and an obvious part must be played by
6 research on the biophysical translations between recording modalities. For example, in bridging
7 from the neuronal circuit level to noninvasive electrophysiology, local field potential (LFP) activity
8 and its relationship with multi-unit spiking forms an important bridge to scalp EEG, which mainly
9 reflects postsynaptic activity [120]. Such research has indeed been increasingly undertaken
10 recently at both the sensory level [e.g. 121] and the level of emerging action plans [e.g. 122], and
11 biophysical mechanisms by which extracellular LFPs translate to electric/magnetic signals at the
12 scalp surface [e.g. 123] and to BOLD activations [e.g. 124] remain active areas of investigation.
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19 Biophysically-based computational modeling represents a complementary, powerful approach
20 to integrating across levels of description while also specifying mechanisms of decision
21 formation. For instance, spiking neuronal network models have successfully captured aspects of
22 spiking dynamics and behavioral data during decision making (Wang, 2002). More recently, it has
23 been found that through training, such recurrent neural networks can capture various
24 idiosyncracies found in neuronal population recordings such as mixed, time-varying and
25 heterogeneous selectivity, across a variety of decision-making tasks [125-127]. Such models
26 reveal an additional layer of complexity of neural computation in decision-making, which may
27 not be accomplished using simplified cognitive models.
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34 Despite this progress, recurrent neural networks come with issues relating to stability and ease
35 of interpretation with respect to decision algorithms of lower complexity. One means to bridge
36 from spiking neuronal network models to simpler firing-rate, population-based models is through
37 theoretical mean-field approximations [104, 128], but the application of this approach to
38 heterogeneous networks is still in its infancy. Achieving a principled mapping of complex network
39 models to lower-dimensional descriptions is vital in order to make linkages to the reduced
40 cognitive models in widespread use in decision science [95], and has huge implications for model-
41 based analyses in neuroimaging given the already prevalent reliance on neural mass models (e.g.
42 dynamic causal modelling) to understand causal global brain dynamics [129], including in
43 perceptual decision making [130, 131].
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Glossary

Evidence Accumulation: According to sequential sampling models, accurate perceptual decisions can be achieved in the face of sensory noise by repeatedly sampling and integrating independent samples of evidence and withholding commitment until a predefined quantity has accrued in favour of one of the decision alternatives. There are multiple possible ways that this general process can be implemented both mathematically and neurophysiologically.

Model Parsimony: Mathematical decision models have traditionally been evaluated using statistical methods that balance a model's ability to account for observed behaviour against its complexity. Evaluation methods that consider fits to neural as well as behavioural data are needed to facilitate the development of more detailed models that can account for the neural implementation of the decision process.

Neural decision signal: A neural signal that traces the process of decision formation. Typically, the term is used to distinguish neural computations that are tied solely to the choice outcome from sensory responses that exhibit trial-to-trial correlations with choice behaviour (see 'Sensory Evidence Signal' below). Here, we use the term primarily to refer to neural representation of accumulated evidence supporting decision formation). Single-unit and non-invasive electrophysiological recording studies have isolated signals exhibiting evidence accumulation dynamics that account for the timing and accuracy of the observer's perceptual reports. The ability to directly observe and measure such signals opens new avenues for adjudicating between alternative decision models and developing new models that reflect the neural implementation of the decision process as well as its output.

Neurally-informed modeling: The practice of basing model construction or constraining model parameters using qualitative and/or quantitative observations from empirical neural data. This approach contrasts with model-informed neuroscience approaches in which an existing model is leveraged to furnish mechanistically-defined behavioral metrics for correlation with neural data. [For a comprehensive review of the distinct approaches to integrating mathematical and neurophysiological characterisations of decision making see \[11, 64\].](#)

Sensory Evidence Signal: A signal that reflects the sensory input to a perceptual decision. Any stimulus will elicit a range of sensory signals, many of which may be irrelevant to the task at hand. The key distinguishing characteristics of a sensory evidence signal are that its momentary

level should co-vary with a decision-relevant stimulus variable and its activity should predict choice behaviour in a stimulus-independent manner (also known as ‘choice probability’).

Urgency Signal: An evidence-independent component of neural decision signal activity that expedites choice commitment. Such signals can be accommodated in mathematical models as a dynamic adjustment to the quantity of evidence required to trigger commitment (i.e. a collapsing decision bound). The recent identification of urgency signals that grow as a function of deliberation time challenges the dominant view in the mathematical modelling literature that, once adjusted, decision bounds remain fixed for the duration of a decision.

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Figures

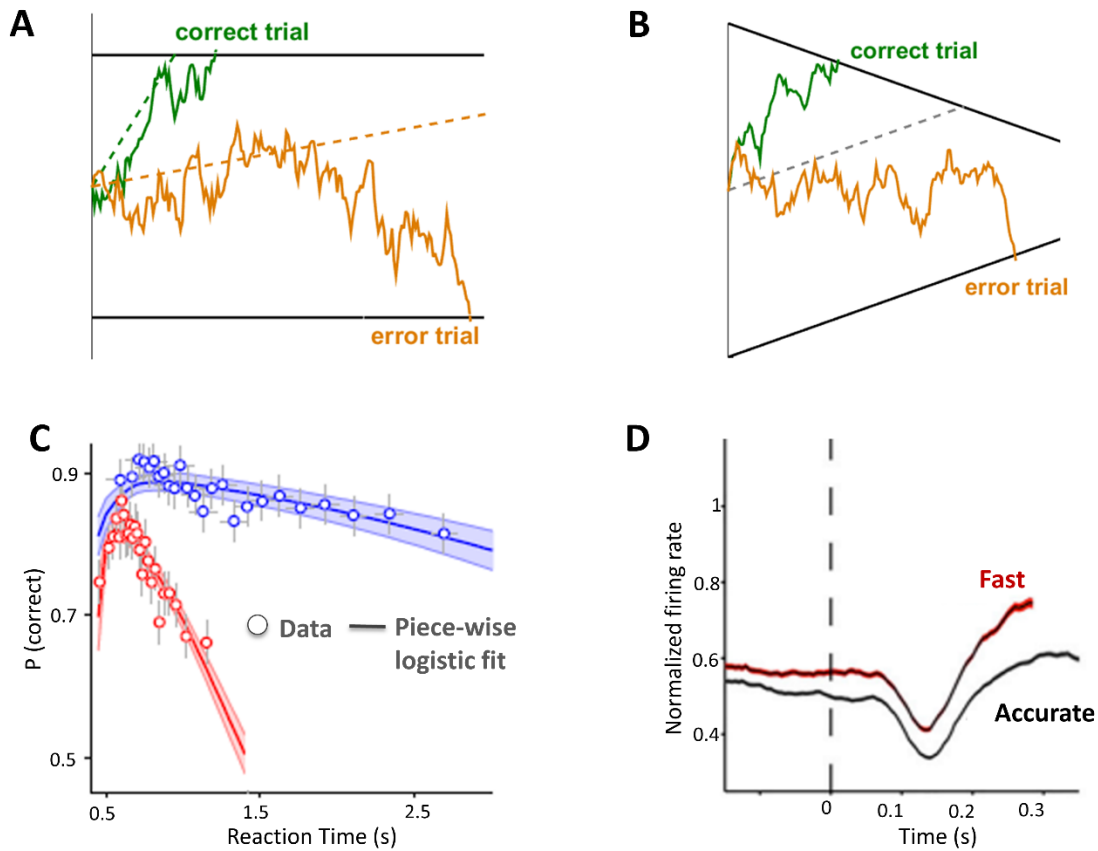


Figure 1. (A) Schematic illustrating how drift rate variability with static bounds can produce slow errors. Solid lines indicate the path taken by a diffusion decision variable on each of two example single trials, one resulting in a correct response (green) and one resulting in an erroneous (orange) choice. Dotted lines mark the drift rate for each of those two trials. **(B)** Schematic illustrating how collapsing bounds without drift rate variability can alternatively produce slow errors. Again two example single trials are shown, in this case arising from the same, fixed drift rate **(C)** Conditional accuracy functions illustrating the decrease in accuracy as a function of response time (RT). Blue and red lines represent data from two different task conditions emphasizing accuracy and speed respectively. Data from Murphy et al [23] **(D)** LIP firing rate data highlighting that speed emphasis leads to an increase in the starting level of activity at trial onset and also an evidence-independent acceleration of signal build-up over time, reflecting a dynamic urgency component whose impact is equivalent to a collapsing bound (B). Data from Hanks et al [41]

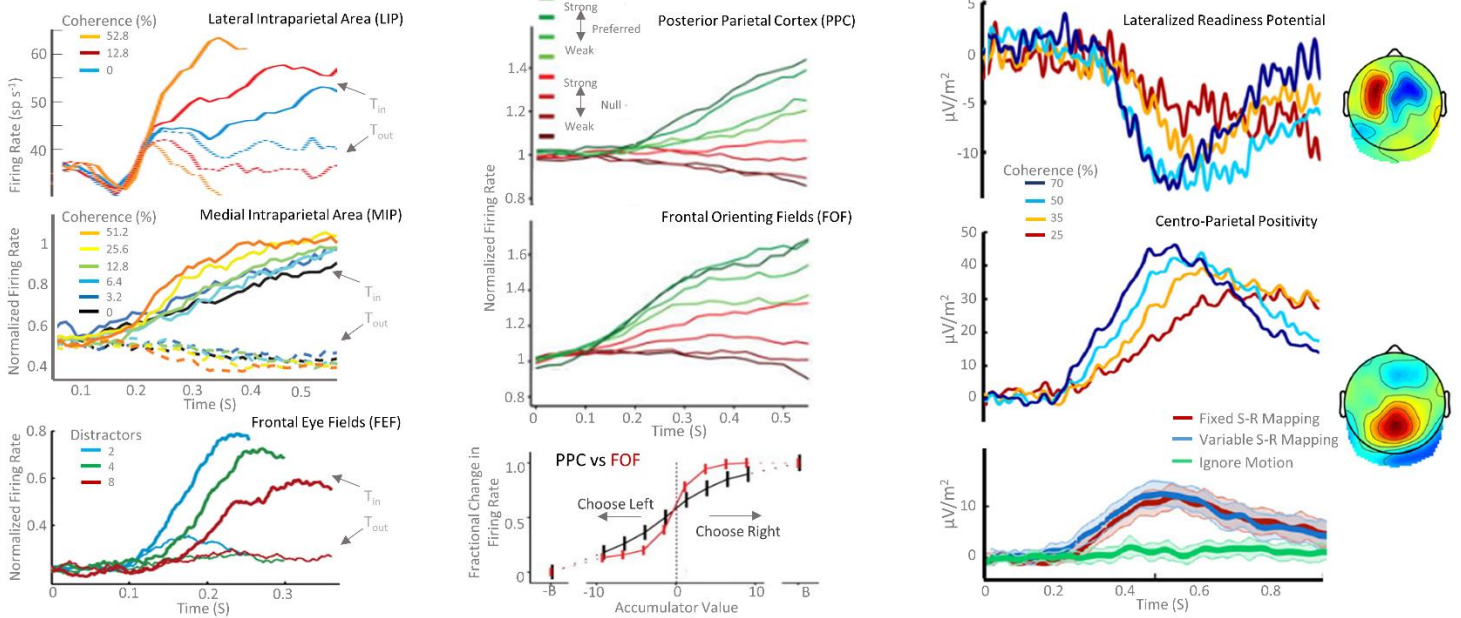


Figure 2. A multiplicity of decision signals. **(Left Column)** Top, when monkeys indicate motion direction discrimination decisions via saccade, neurons in area LIP exhibit accumulation-to-bound dynamics that are highly sensitive to variations in sensory evidence. Here, LIP neuron firing rates increase more rapidly when coherent motion more strongly favours a saccade to a target located within the neuron's response field (T_{in}). Although a great many intracranial recording studies of perceptual decision making have targeted area LIP, highly similar neural decision signals have been observed in a variety of other regions of the monkey brain. Middle, when monkeys make reach movements to indicate their decisions, instead of saccades, reach-related neurons in the medial intraparietal area (MIP) exhibit highly similar accumulate-to-bound dynamics (solid traces). Bottom, movement neurons in FEF exhibit evidence accumulation dynamics during visual search decisions reported via saccade. Thin lines represent trials on which a distractor appeared within the neuron's response field (T_{out}). Data from Roitman & Shadlen [34]; De Lafuente et al [72]; Purcell et al [29]. **(Middle Column)** When rodents performed an auditory decision task, evidence accumulation dynamics are observed in (top) posterior parietal cortex (PPC) and (middle) frontal orienting fields (FOF). However, tuning curve analysis (bottom) indicate that while PPC provides a graded representation of incoming evidence, momentary FOF activity reflects the currently favoured alternative in a more categorical fashion. This pattern accords with the general observation from multi-site recording studies that neural activity becomes progressively more closely linked to the observer's action

choices as one proceeds toward the motor end of the sensorimotor hierarchy. Data from Hanks et al [7] **(Right Column)** When humans make motion discrimination decisions, highly similar accumulate-to-threshold signals are observed in non-invasive electrophysiological recordings. This work has uncovered two functionally distinct classes of decision signal: Top, when observer's indicate their decisions via hand movement, contralateral motor preparation signals trace decision formation. These signals cease to trace decision formation if the stimulus-to-response mapping is withheld or when hand movements are not required. Middle, a centro-parietal positive (CPP) component in the event-related potential also traces evidence accumulation but does so irrespective of the sensory or motor requirements of the task. Bottom, when participants withheld motion direction decision reports until the appearance of a response cue (1600ms after stimulus onset). The CPP traced decision formation irrespective of whether the participant had foreknowledge of the stimulus-to-response mapping (Fixed Mapping) or not (Variable Mapping) and fell silent only when dot motion was rendered irrelevant to the task (ignore motion). Data from Kelly & O'Connell [132], Twomey et al [83]

Highlights

- Sequential sampling models have been widely embraced in contemporary decision neuroscience. The models come in many forms that, despite containing fundamentally different algorithmic elements, can make highly similar predictions for behaviour. Consequently, it can be difficult to definitively adjudicate between alternative models based solely on quantitative fits to behaviour.
- The discovery of brain signals that reflect the key neural computations underpinning decision making is opening new avenues for empirically testing and refining model predictions.
- Neurophysiological research is highlighting the multi-layered neural architecture for implementing even the most elementary sensorimotor decisions. We do not yet know how many processing layers are required nor what distinct computations are performed at each layer.

Outstanding Questions Box

- Can neural signal analyses be used to determine whether sequential sampling models provide accurate accounts of the essential neurocomputational adjustments through which factors such as prior information, conflicting information, redundant information, energetic costs, spatial attention, perceptual learning, value and brain disorders influence decision making behaviour? In addition to dominant criterion adjustments are there modulations exerted at the sensory level that model fitting alone cannot detect?
- The versatility of popular sequential sampling model variants is partly owed to the inclusion of certain parameters (e.g. variability in drift rate and starting point) that greatly aid the flexibility with which the models can account for different behavioural patterns. What predictions do these parameters make regarding neural activity and how can these predictions be tested? Can neural signatures of such processes be identified?
- Build-to-threshold decision signals have been observed in a variety of brain areas. What distinct computations do these signals and areas perform during decision formation?
- What precise role do abstract evidence accumulation signals play in decision formation? How do non-invasively recorded human brain decision signals relate to the signals observed in single-unit activity in monkeys and rodents?