Annual Review of Neuroscience

Neurophysiology of Human Perceptual Decision-Making

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Annu. Rev. Neurosci. 2021. 44:495–516

The *Annual Review of Neuroscience* is online at neuro.annualreviews.org

https://doi.org/10.1146/annurev-neuro-092019-100200

Keywords

perceptual decision-making, evidence accumulation, cognitive modeling, EEG, MEG, fMRI

Abstract

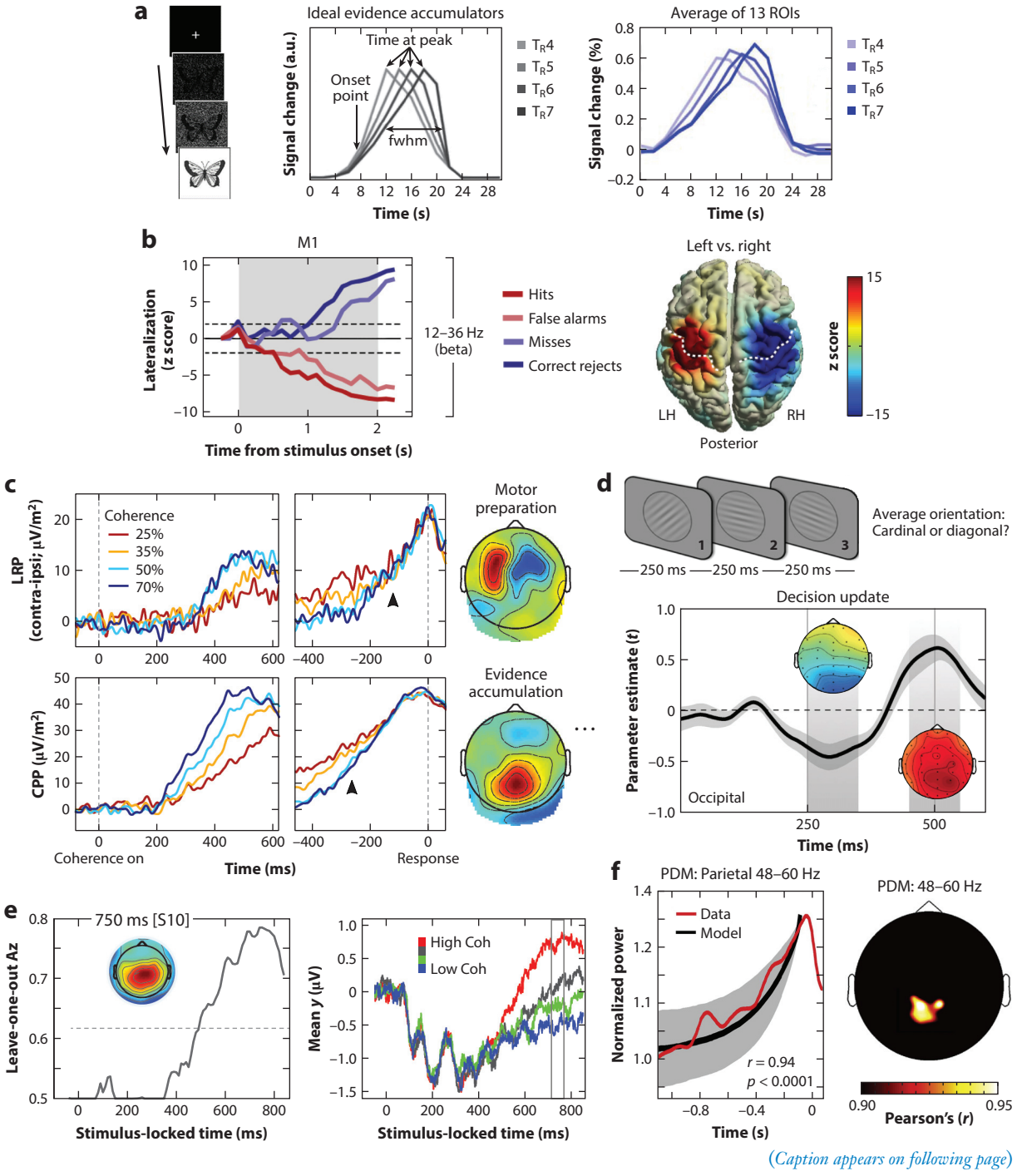
The discovery of neural signals that reflect the dynamics of perceptual decision formation has had a considerable impact. Not only do such signals enable detailed investigations of the neural implementation of the decision-making process but they also can expose key elements of the brain's decision algorithms. For a long time, such signals were only accessible through direct animal brain recordings, and progress in human neuroscience was hampered by the limitations of noninvasive recording techniques. However, recent methodological advances are increasingly enabling the study of human brain signals that finely trace the dynamics of the unfolding decision process. In this review, we highlight how human neurophysiological data are now being leveraged to furnish new insights into the multiple processing levels involved in forming decisions, to inform the construction and evaluation of mathematical models that can explain intra- and interindividual differences, and to examine how key ancillary processes interact with core decision circuits.

Contents

NEURAL SIGNATURES OF DECISION FORMATION IN THE HUMAN BRAIN

Perceptual decisions entail translating sensory information into judgments, beliefs, or actions. They have been intensively studied across diverse disciplines, because they provide a tractable test bed for examining brain mechanisms and behavioral phenomena that are core to cognitive function more generally (Shadlen & Kiani 2013). Progress in the neuroscientific study of decision-making accelerated with the discovery that neurons in certain areas of the monkey brain exhibit activity consistent with the accumulation of sensory evidence toward a decision bound in a manner similar to that predicted by long-standing mathematical accumulation-to-bound models (Gold & Shadlen 2007, Ratcliff et al. 2016, Schall 2003). For example, areas that plan decision-reporting actions, such as the lateral intraparietal area (LIP) (Shadlen & Newsome 1996) and frontal eye fields (Hanes & Schall 1996) for saccades and dorsal premotor cortex (PMd) (Cisek & Kalaska 2005) for reaching, exhibit spike-rate increases throughout the period of deliberation that scale with the strength of the evidence and coalesce to a stereotyped level of activity at the time of commitment to one alternative. Since these discoveries, such dynamics have been observed in several more areas of the monkey brain (de Lafuente et al. 2015, Ding & Gold 2010, Kim & Shadlen 1999, Ratcliff et al. 2003, Romo et al. 2004) and also in rodents (Erlich et al. 2015, Hanks et al. 2015, Licata et al. 2017, Yartsev et al. 2018). This ability to directly observe and measure the neural decision process as it evolves has been leveraged to gain rich insights into the neural circuits, systems, and algorithms serving decision formation and key phenomena such as the speed–accuracy trade-off (e.g., Hanks et al. 2014, Heitz & Schall 2012, Thura & Cisek 2016), the prioritization of more probable (e.g., Hanks et al. 2011) or more valuable (e.g., Rorie et al. 2010) alternatives, and confidence (e.g., Fetsch et al. 2014, Kiani & Shadlen 2009).

Compared to monkey and rodent neurophysiology, tracing the dynamics of neural decision processes in humans has been classically more challenging due to the limitations inherent to low-resolution, noninvasive recording methods (Kelly & O'Connell 2015). However, several methodological advances in recent years, ranging from novel signal processing techniques (Philiastides & Sajda 2006, Ratcliff et al. 2009, Wyart et al. 2012a) and model-based approaches (Forstmann et al. 2016, Turner et al. 2015) to the use of task designs that facilitate the isolation of decision-relevant neural activity (Heekeren et al. 2004, O'Connell et al. 2012, Ploran et al. 2007), have succeeded in overcoming these limitations to a significant degree (**Figure 1**). These methodological advances have enabled human neurophysiological investigations to produce a growing set of advances in our understanding of the neural underpinnings of decision-making that both complement and expand the knowledge gained through invasive recordings in animals. In this review, we highlight recent work contributing to such advances in three specific domains: in illuminating the key processing



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Identification of neural signals consistent with evidence accumulation in noninvasive human recordings. (*a*) In order to cater for the low temporal resolution of functional imaging, Ploran et al. (2007) devised an object recognition task in which the period of decision formation was elongated by presenting stimuli that emerged over the course of several seconds. Blood oxygen level–dependent (BOLD) signals from a network of 13 brain regions were found to adhere to predictions of an ideal evidence accumulator, exhibiting peak latencies that covaried with the time of reported object recognition. Panel *a* adapted from Ploran et al. (2007, copyright 2007 Society for Neuroscience). (*b*) When the choice alternatives in a visual motion detection task (yes vs. no) were mapped to movements of the left and right hand, evidence accumulation dynamics were reflected in the buildup of differential motor preparation over time (*left*), indexed by the difference in spectral magnetoencephalographic power in the beta range over motor cortex (M1) contralateral vs. ipsilateral to the eventually executed movement (*right*). Panel *b* adapted with permission from Donner et al. (2009). (*c*) Similarly, when participants performed motion direction discriminations that were mapped to the left and right hands, differential motor preparation (*top*) was also reflected in the lateralized readiness potential (LRP; difference between contralateral and ipsilateral signals over premotor brain areas) in human electroencephalography (EEG), which builds at a rate proportional to motion coherence. By designing this task so that coherent motion is preceded by a lead-in of incoherent motion, evoked potentials, which in typical paradigms are generated by sudden luminance transients, are eliminated. This provides an unobscured view on another event-related component exhibiting evidence-dependent buildup dynamics, the centroparietal positivity (CPP; *bottom*). Panel *c* adapted from Kelly & O'Connell (2013). (*d*) Tasks requiring the averaging of sequentially presented, discrete tokens (e.g., orientation) enable detailed examination of the temporal dynamics of decision processing by regressing the EEG signal against increments in decision evidence. Through this approach, the neural encoding of evidence samples and their weighting into the final choice (expressed as a parameter estimate in *t* units) were found to fluctuate rhythmically at a delta (~2 Hz) timescale. This rhythmicity contrasts with the assumption in standard decision models that successive samples of evidence are integrated at a constant rate. Panel *d* adapted with permission from Wyart et al. (2012a). (*e*) Evidence-dependent buildup signals have also been isolated in human EEG using classification techniques from machine learning. In one such application, dimensions in multielectrode space were identified that maximally discriminate high- and low-coherence trials in a motion discrimination task. The dynamics of both classification accuracy (*left*, Az) and the activity component projected onto that dimension (*right*, *y*) can thus be traced with high temporal resolution. Panel *e* adapted from Philiastides et al. (2014). (*f*) Bounded accumulation dynamics are manifest in gamma-band EEG activity over posterior electrodes for value-based and perceptual decisions. In this case, the signals were identified by spectral amplitude time courses with the predicted response-aligned dynamics simulated from a bounded evidence-accumulation model fit to behavior. Panel *f* adapted with permission from Polania et al. (2014). Note that there are many more excellent examples that due to space limitations we cannot include here.

levels intermediating between sensation and action, in guiding the construction and constraining the estimation of mathematical process models of decision-making, and in characterizing the important role of ancillary processes in mediating adaptive decision formation.

MULTIPLE PROCESSING LEVELS FOR PERCEPTUAL DECISION-MAKING

In contrast with most mathematical decision models, which capture behavioral patterns through a single evidence-accumulation process, the neurophysiological processes underlying decision-making appear to involve many neural signals and circuits. Decision-related activity, identified most commonly by its selective prediction of the chosen decision alternative, has been observed in a wide variety of areas of the monkey (e.g., de Lafuente & Romo 2006, Siegel et al. 2015) and rodent (Steinmetz et al. 2019, ter Wal et al. 2020) brains and, more recently, in intracranial human brain recordings (ter Wal et al. 2020). With this multiplicity of choice-predictive brain areas comes the challenge of parsing their distinct functional contributions. One fundamental distinction is between signals that encode the moment-to-moment sensory information on which the decision is based—the evidence—and the decision variables that evolve based on present and past evidence throughout the period of deliberation and culminate in a choice. Even such an apparently straightforward classification can be hard to establish in practice because these signal types will often closely coincide in time and exhibit similar correlations with choice. Moreover, in noninvasive global brain recordings, typical task stimuli elicit multiple sensory response components, many of which may be irrelevant to the decision at hand.

In recent years, a number of approaches have been developed that enable the isolation of signals that selectively encode the choice-relevant sensory information in a variety of noninvasive recording modalities. For example, a time-resolved readout of cortical selectivity for visual contrast and orientation can be obtained by convolving trial-to-trial variations in these features with a canonical tuning function and regressing them against electroencephalography (EEG) data (Tang et al. 2018, Wyart et al. 2012b) or by flickering stimuli to evoke steady-state responses (O'Connell et al. 2012). Research using such methods is increasingly highlighting that factors such as prior knowledge (Kok et al. 2017, Tang et al. 2018, Wyart et al. 2012b), choice history (St. John-Saaltink et al. 2016), and time pressure (Steinemann et al. 2018) engender significant sensory modulations in addition to the strategic, decision-level adjustments that have been more commonly examined in the computational and neurophysiological literature. Meanwhile, other human magnetoencephalography (MEG) and EEG research has succeeded in isolating two functionally distinct classes of decision variable signals that exhibit similar dynamic characteristics as the signals observed in single-unit recordings from animals: They build gradually during the period of deliberation at a rate proportional to evidence strength, peak around the time of the decision-reporting movement, and predict choice accuracy and reaction time (RT). The first class of signal is analogous to the effector-selective signals characterized in monkeys; specifically, classic signatures of motor preparation such as decreases in spectral EEG/MEG activity in the mu/beta bands (de Lange et al. 2013, Donner et al. 2009, Pfurtscheller & Lopes da Silva 1999, Steinemann et al. 2018) (**Figure 1*b***) build gradually throughout decision formation up to a threshold level for a particular action (e.g., over the motor cortex contralateral to a left/right hand movement). The second is a centroparietal positivity (CPP), for which recent studies have demonstrated several interesting characteristics that distinguish it from other intra- or extracranially recorded decision signals (see also the sidebar titled The P300 as an Evidence-Accumulation Process). This signal is remarkably versatile, exhibiting the same accumulator-like buildup dynamics for any sensory feature in any sensory modality so long as that feature is the one being decided upon; for example, we initially showed that the CPP reflects evidence accumulation for contrast-decrease and contrast-increase detection targets, auditory detection targets defined by volume or frequency changes (O'Connell et al. 2012), and coherent motion discrimination (Kelly & O'Connell 2013). Since then, the signal has been

THE P300 AS AN EVIDENCE-ACCUMULATION PROCESS

Long before the centroparietal positivity (CPP) was characterized, it was well established that another centroparietal event-related potential component—the P300 or P3b—was evoked by goal-relevant targets in any modality, scaled inversely with stimulus probability, and covaried with the timing (McCarthy & Donchin 1981) and accuracy (Hillyard et al. 1971) of responses. The P3b has been among the most intensively studied human brain signals for its omnipresence in cognitive tasks and its sensitivity to numerous brain disorders (Polich & Criado 2006). Early research pointed to a potential role in decision formation, but in the absence of a concrete proposed mechanistic link, the idea was superseded by alternative accounts (Donchin & Coles 1988, Kok 2001, Nieuwenhuis et al. 2005, Polich 2007, Verleger 1988). We have proposed that the P3b reflects the same evidence-accumulation process as the CPP based on several observations: They are both supramodal and contingent on relevance, their amplitude and topographic loci are tightly correlated across subjects, and the P3b exhibits bounded evidence-accumulation dynamics even in the standard oddball tasks classically used to elicit it (Twomey et al. 2015). This link situates the classic P3b within a principled theoretical and computational framework for explaining its variation across experimental conditions and groups.

characterized by a number of laboratories within the same decision theoretical framework for tasks involving face/car discrimination (Philiastides et al. 2014), detection of statistical changes in auditory textures (Boubenec et al. 2017), visual orientation comparison (Steinemann et al. 2018), color discriminations (Afacan-Seref et al. 2018), color-orientation conjunctions (Rungratsameetaweemana et al. 2018), sequential vibrotactile difference discrimination (Herding et al. 2019, von Lautz et al. 2019), sequential motion coherence difference discrimination (von Lautz et al. 2019), sequential comparisons of numerical and reward magnitude (Luyckx et al. 2019, Spitzer et al. 2017), and face similarity to a simultaneous or remembered reference (van Vugt et al. 2019).

There are additional key characteristics of the CPP that distinguish it from effector-selective decision signals. Crucially, the CPP traces evidence accumulation even in conditions where no overt action is required and motor preparation signals are silent (O'Connell et al. 2012), or when the stimulus-response mapping is not yet known while evidence is viewed (Twomey et al. 2016). Furthermore, incoming evidence modulates the buildup of the CPP a significant amount of time (>100 ms) before it is reflected in scalp-recorded motor preparation signals (Kelly & O'Connell 2013) (**Figure 1*c***). Finally, the two signals exhibit qualitatively different strategic adjustments: Contralateral mu/beta activity reaches a threshold level at response execution irrespective of RT, difficulty, or prior knowledge but undergoes systematic shifts in starting levels over both hemispheres in accordance with time constraints (O'Connell et al. 2012, Steinemann et al. 2018) and prior probability (Kelly et al. 2020). Recent work has also highlighted that mu/beta motor preparation signals exhibit an evidence-independent, temporally increasing component to their buildup, which would have the effect of progressively reducing the amount of cumulative evidence required to reach the motor threshold (see below for further discussion) (Kelly et al. 2020, Murphy et al. 2016, Steinemann et al. 2018). In contrast, the CPP exhibits no changes in its starting level and no evidence-independent component under the same experimental conditions, but its prechoice amplitude decreases systematically as a function of increasing RT, speed emphasis, and stimulus probability (Kelly et al. 2020, Steinemann et al. 2018). Thus, the CPP appears to encode a pure, motor-independent representation of cumulative evidence whose amplitude at the time of commitment is determined by strategic influences operating at the motor level. This interpretation accords with the recent demonstration that subjective ratings of stimulus intensity are exquisitely sensitive to variations in the CPP's amplitude (Tagliabue et al. 2019).

Together, these studies establish that the CPP provides a neural readout of cumulative evidence. However, we do not yet know for certain how such a representation is generated in the brain or what specific role it plays in decision-making. One possibility is that no single neuron equivalent of the CPP exists and that it emerges from the summed evidence-dependent activity of a diversity of effector-selective neural populations. Alternatively, the CPP could arise from neuronal populations that encode goal-relevant stimulus categories, independent of the actions they entail, or from neurons that prepare abstract, nonmotor acts such as the implementation of a rule or the initiation of a further decision (Shadlen et al. 2008), or from neurons that furnish abstract cumulative evidence representations to inform choice confidence. If the CPP does reflect a distinct process, then a further question is whether that process is necessarily interposed between sensory encoding and action selection or computed in parallel alongside a more direct sensorymotor pathway. Addressing these questions will ultimately require invasive recordings in the brain areas that generate this signal, along with inactivation and microstimulation protocols to establish causal contributions (e.g., Derosiere et al. 2019, Fleming et al. 2015, Hanks et al. 2006, Katz et al. 2016, Yartsev et al. 2018, Zhou & Freedman 2019). So far, however, an intracranially recorded signal with the same supramodal, fully motor-independent properties as the CPP has not been

identified in either humans or nonhumans (O'Connell et al. 2018), and understanding its neural origins remains an important goal for ongoing research.

In fact, an extensive line of human functional MRI (fMRI) research has sought to draw a comprehensive map of the brain's decision-making circuitry, and a key focus of much of this work has been to establish where the brain may house decision representations that are independent of any particular stimulus or response modality. These studies have compared decisions involving different sensory modalities and/or effectors and identified a number of brain areas that are activated in common, including the dorsolateral prefrontal cortex, intraparietal sulcus, inferior frontal cortex, and right insula (Ho et al. 2012a,b; Liu & Pleskac 2011; Tosoni et al. 2008). However, despite better spatial resolution and coverage in comparison to methods like EEG and MEG, the low temporal resolution of fMRI precludes direct observation of evidence-accumulation dynamics, and thus, there is a lack of firm, empirically grounded criteria for identifying putative decision-making areas based solely on BOLD response effects (Kelly & O'Connell 2015).

A varied range of criteria have been used in the literature, and in certain cases, directly contradictory yet equally plausible criteria have been applied. For example, a criterion applied in some studies using delayed-response tasks has been that the peak BOLD signal of a putative decision region should increase with evidence strength (e.g., Heekeren et al. 2004), which relies on the assumption that a decision signal's activity would remain elevated through the decision period, as observed for LIP activity (Roitman & Shadlen 2002). Meanwhile, other studies have made the opposite prediction, based on the assumption that motor-independent decision signals would fall silent following choice commitment (e.g., Liu & Pleskac 2011). Heterogenous criteria and methodologies have led to inconsistencies in the regions identified, and individual areas have even been associated with different roles in different studies. For example, inferior parietal activation has been associated with abstract accumulation in one study (Levine & Schwarzbach 2017) but with effector-selective accumulation in another (Tosoni et al. 2008). These issues notwithstanding, fMRI studies have played a valuable role in highlighting candidate decision-making structures whose precise roles can be further probed via complementary techniques. Ultimately, uncovering the essential decision-computing brain networks will entail using such imaging methods hand-in-hand with the newfound approaches that trace the neural dynamics underpinning human decision formation in MEG/EEG. For example, human electrophysiology analyses could be used to generate empirically grounded BOLD signal predictions in future fMRI studies (Twomey et al. 2016).

NEURALLY INFORMED MODELING

Mathematical decision models are being used more and more extensively in both basic and clinical research on decision-making (Forstmann et al. 2016). In human neuroscience, a common approach has been to use model parameter estimates from fits to behavioral data as regressors for neurophysiological data (Forstmann et al. 2016, Mansfield et al. 2011, van Maanen et al. 2011; for evolving versions of this approach, see Turner et al. 2019). A powerful aspect of this approach is that it allows the functional role of particular brain areas and signals to be probed and interpreted within a formal mathematical framework and thereby linked to choice behavior. For example, Boehm et al. (2014) used an accumulation-to-bound model to estimate response caution (i.e., distance between starting point and bound) and established a correlation with the amplitude of a slow, anticipatory event–related potential component known as the contingent negative variation (CNV). This observation accorded with the authors' initial hypothesis that the CNV reflects a process that drives a lowering of response thresholds. Similarly,

Gherman & Philiastides (2018) used a decision model to estimate levels of choice confidence in order to verify an EEG signal component's relationship to confidence reports. The authors then identified a correlation between this signature and BOLD activation in the ventromedial prefrontal cortex—a region not previously associated with choice confidence.

A limitation associated with directly applying parameters from behavioral model fits to neural analyses is that the functional characteristics of the identified brain areas or signals may be misconstrued if the chosen model does not accurately reflect the algorithm that the brain is really using. This concern is underlined by the fact that there are now many alternative decision model variants that sometimes can be made to fit behavior equally well yet can lead to very different conclusions. The identification of well-characterized, time-resolved neural signatures of decision formation offers a remedy in that they provide model-free measurements that can be used alongside behavior to directly inform model selection in a number of ways. First, neural decision signals can inform model construction by providing an alternate means of detecting the operation of certain algorithmic elements that may be difficult to discern through purely behavioral analyses. Second, where a straightforward correspondence has been established between certain neural signal measurements and a model parameter, those neural data can potentially be used to directly estimate that parameter value. In principle, imposing such constraints would facilitate the development of models that can capture a broader range of parameters and effects without increasing the number of free parameters and thereby the risk of overfitting (O'Connell et al. 2018, Purcell & Palmeri 2017, Turner et al. 2015). Third, neural data can also play an important role in model validation, providing a means of empirically testing the predictions that competing models make regarding the dynamics of the decision process. We illustrate each of these aspects through the example of a recent study in which we consulted neural decision signal dynamics to model human motion discrimination performance under varying task demands (Kelly et al. 2020).

A key consideration when initially constructing our decision model was whether or not to include a process known as urgency. Urgency is an additional evidence-independent buildup component, which effectively lowers the quantity of evidence required for choice commitment as time elapses. Urgency is a central feature in some sequential sampling models (Churchland et al. 2008, Cisek et al. 2009), and has significant implications for our understanding of the psychological processes that regulate speed-accuracy trade-offs. Although studies of decision signals in the monkey brain have identified such urgency components (Churchland et al. 2008, Hanks et al. 2014, Thura & Cisek 2016), there are enduring disagreements regarding how important a role they play in human decision-making (e.g., Boehm et al. 2020, Evans et al. 2020, Ratcliff et al. 2016) because their inclusion is usually not critical to achieving good quantitative fits to behavior (Hawkins et al. 2015, Voskuilen et al. 2016). Kelly et al. (2020) found that motor preparation signals commenced building toward their threshold level even before the evidence was presented (**Figure 2*a***). We took this to reflect an urgency component that continued to increase during the presentation of evidence, consistent with other effects reported in previous human and monkey studies (Hanks et al. 2014, Murphy et al. 2016, Steinemann et al. 2018). By constraining certain parameters to match corresponding decision signal measurements, we were able to add this urgency component (**Figure 2*b***) without increasing the degrees of freedom of the model. For example, the starting levels of motor preparation relative to the decision bound in the model could be reasonably equated to the baseline levels of EEG signatures of effector-selective motor preparation, based on the fact that these signals exhibit race-to-threshold characteristics and variations in their starting levels that are predictive of RT and choice (e.g., de Lange et al. 2013, Donner et al. 2009, Steinemann et al. 2018, O'Connell et al. 2012).

The resultant neurally informed model provided better fits to behavior than did the DDM and indicated certain effects that directly contradicted the conclusions of the DDM (**Figure 2*c***).

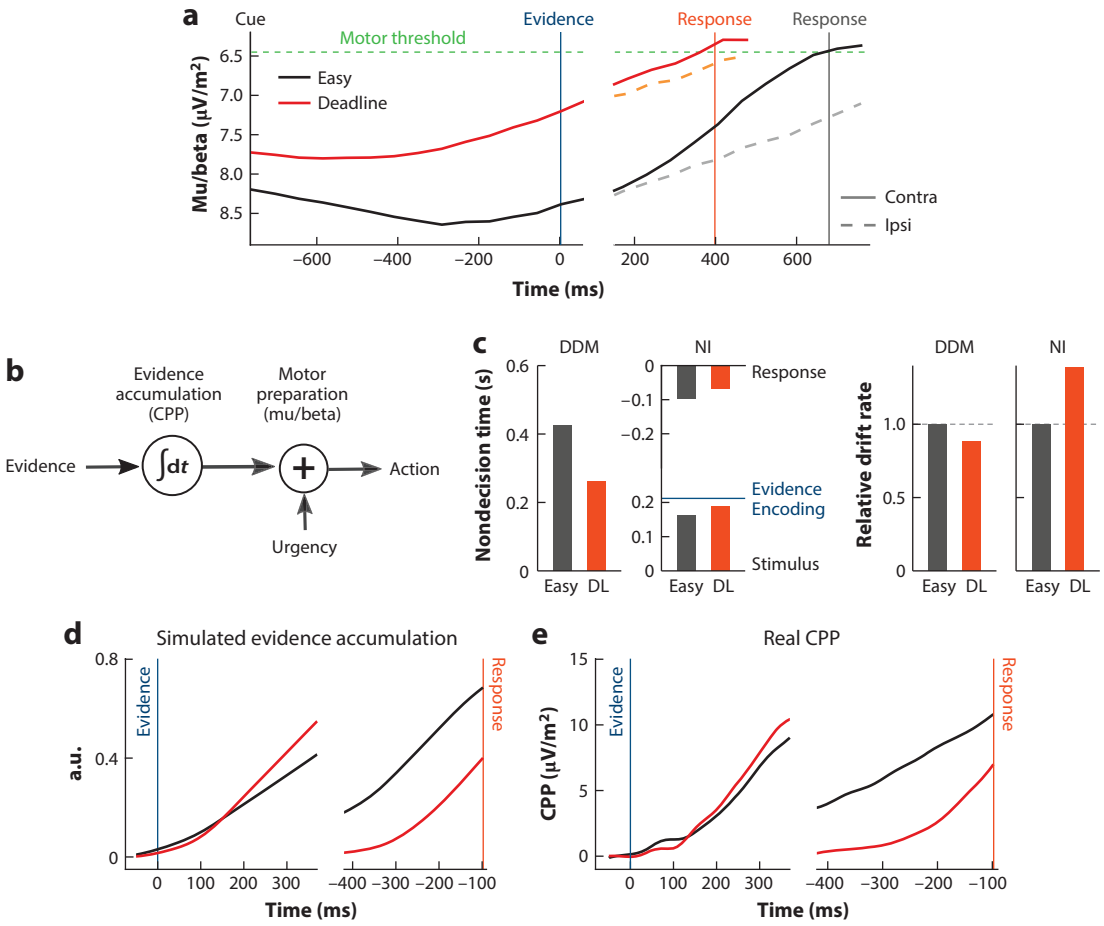


Figure 2

The use of neural decision signals to construct, constrain, and validate a neurally informed (NI) model of motion direction decisions under regimes with little (Easy) versus intense [Deadline (DL)] speed pressure. (*a*) Motor preparation, reflected in spectral amplitude in the mu/beta bands (8–30 Hz), begins to build up approximately 300 ms before the presentation of evidence. This anticipatory, evidence-independent buildup results in a greatly elevated starting level under speed pressure. Response-aligned motor preparation [shown aligned to the mean reaction time in each respective regime; *right*] reaches a fixed threshold level just before response for the mu/beta signal contralateral to the responding hand. (*b*) In the neurally informed model, we assume that the anticipatory buildup in motor preparation reflects an evidence-independent urgency component that continues to grow linearly through the period of evidence presentation. Cumulative evidence and urgency are additively combined to create motor preparation signals that race toward an action-triggering threshold. The starting levels of motor preparation relative to threshold are quantitatively constrained to match the corresponding levels measured in the mu/beta signals. (*c*) A standard drift diffusion model (DDM) indicated a greatly shortened nondecision time (*left*) and reduced drift rate (*right*) under speed pressure, whereas the neurally informed model indicated much smaller nondecision time adjustment (*left*; separated into pre- and postaccumulation components) and a steeper drift rate (*right*). (*d*) Simulated mean evidence accumulation traces (excluding the urgency component) from the neurally informed model. (*e*) Empirical signature of evidence accumulation captured in the centroparietal positivity (CPP), which was not used in the construction of the model yet recapitulates the dynamics simulated from the neurally informed model and validates the similarity of accumulation onset and drift rate enhancement under speed pressure. Figure adapted from Kelly et al. (2020).

Most saliently, the neurally informed model indicated that in a task regime with increased speed pressure, subjects boosted their drift rate (a parameter that scales with the quality of encoded evidence being accumulated), whereas the DDM, like some previous modelling studies (Arnold et al. 2015, Dutilh et al. 2019, Rae et al. 2014), suggested the opposite. Which should be believed? In addition to conventional model comparison and recovery procedures, we were able to provide a strong, independent validation of the neurally informed model through examination of the dynamics of evidence accumulation reflected in the CPP, which was not used in the construction or constraint of the model. The CPP exhibited effects consistent with those predicted by the neurally informed model, including a steeper buildup rate under speed pressure. In fact, the empirical CPP waveforms (**Figure 2*e***) closely resembled the average dynamics of evidence accumulation simulated from the neurally informed model (**Figure 2*d***) and showed no signs of the timing and buildup rate effects predicted by the DDM.

The above study adds to a growing body of work using neural decision signals to verify or directly inform process models of perceptual decision-making. For example, Cheadle et al. (2014) evaluated a sequential sampling model in which adaptive gain processes rapidly (i.e., within the time frame of a single decision) adapt the weighting applied to samples of evidence to the statistics of the local sensory environment. In addition to providing an excellent fit to behavior, the model furnished the key prediction that the influence each evidence sample exerts on the decision variable should increase or decrease according to its consistency with the preceding sample. This very relationship was found to be manifest in both fMRI and EEG signatures of decision formation. In another example, Fischer et al. (2018) proposed a multistage variant of the DDM that accounted for posterror behavioral adaptations through a combination of elevated decision bounds, greater suppression of distracting information, and weaker evidence accumulation. The authors provided compelling support for the model by demonstrating a remarkably close correspondence between its simulated decision variable time courses and those observed in premotor beta-band activity. Elsewhere, indices of muscle activation in electromyographic activity have been used to infer latent partial activation thresholds, and these measurements have been directly incorporated into diffusion models aimed at explaining the effects of response conflict on choice behavior (Servant et al. 2015, 2016).

The neurally informed modelling approach also holds significant promise in examinations of intergroup and interindividual differences. In clinical and aging research, it is often not feasible to collect the large behavioral data sets that have been the norm in modelling research. This is of concern, because a model with many free parameters like the full DDM can provide unreliable estimates of intergroup parameter effects when trial numbers are low, even when the data are simulated from the DDM itself (van Ravenzwaaij et al. 2017). Here too, neurophysiological data can play a pivotal role by indicating which aspects of the model can be constrained without necessitating strong a priori assumptions regarding the origins of the relevant group effects.

Illustrating this potential, a recent study applied a neurally informed modelling approach when examining the effects of aging (McGovern et al. 2018). Older and younger participants performed two tasks in which they monitored continuously presented stimuli for intermittent targets defined by a gradual reduction in contrast or a transition from incoherent to coherent motion, respectively (McGovern et al. 2018). To focus on the contrast task as an example, elderly participants surprisingly outperformed the younger participants, detecting more targets with no difference in RT (**Figure 3*a***). Application of the DDM to the behavioral data indicated that the older group had elevated decision bounds, consistent with the preceding literature (e.g., Forstmann et al. 2011, Starns & Ratcliff 2012; for a review, see Dully et al. 2018), and increased drift rates (**Figure 3*b***). However, there were marked discrepancies between these model-based observations and the age-related effects observed in the neural data: There were no significant group differences in the

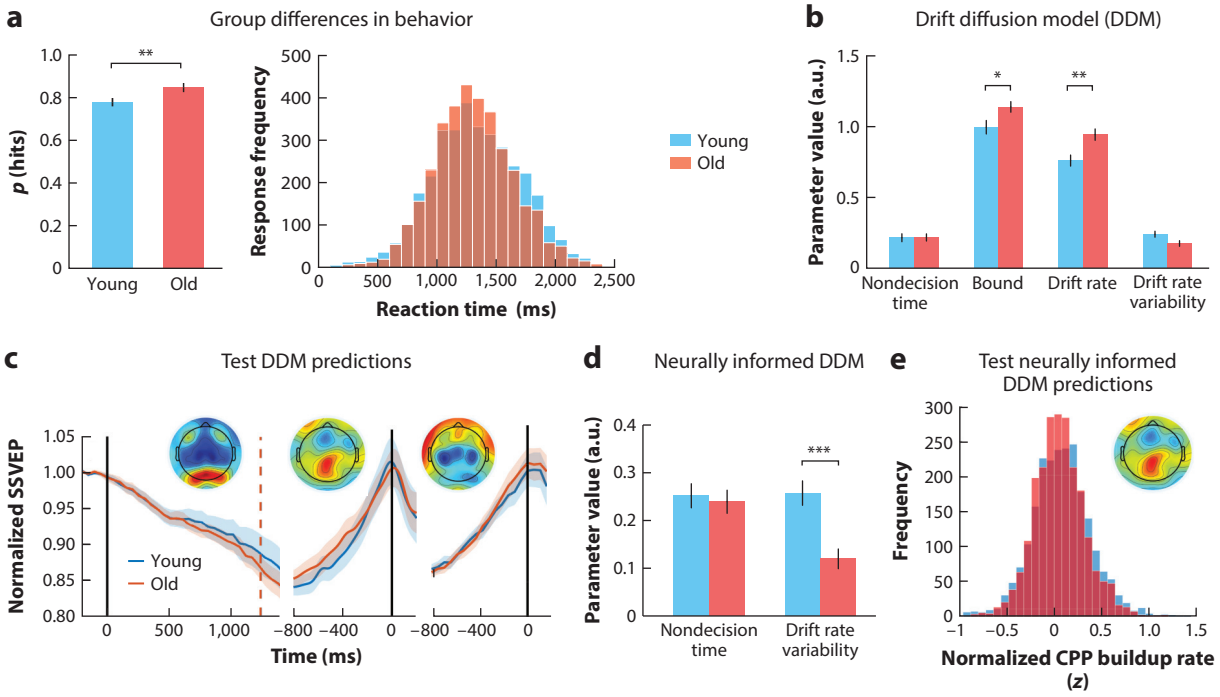


Figure 3

Conventional and neurally informed variants of the drift diffusion model (DDM) yield markedly different accounts of how aging affects perceptual decision-making. (*a*) Older subjects had higher hit rates (*left*) and similar mean reaction times (*right*) compared to younger subjects during performance of a task requiring the detection of unpredictable stimulus contrast changes. (*b*) The conventional DDM attributed these group differences to increased drift rates and decision bounds among older subjects. (*c*) Model-independent neural signal analyses did not support these predictions. Inconsistent with a drift rate effect, we observed no group differences in the sensory evidence represented in changes of contrast-dependent steady-state, visual-evoked potentials (SSVEP; *left*) with target contrast or in the buildup rate of either the centroparietal positivity (CPP; *middle*) or motor-selective mu/beta activity (*right*). In addition, whereas the DDM predicted higher decision bounds in older subjects, there were no reliable differences in the preresponse amplitudes of the CPP and mu/neural decision signals. (*d*) Accordingly, constraining both of those parameters to be equal across all subjects regardless of age group gives rise to a novel difference, whereby drift rate variability is reduced in the older group. (*e*) This predicted difference received independent support from the observation of reduced trial-to-trial variability in the buildup rate of the CPP in the older group. Figure adapted from McGovern et al. (2018).

preresponse amplitudes or buildup rates of either the CPP or mu/beta motor preparation signals and no differences in the encoding of the sensory evidence in early visual responses (**Figure 3*c***).

As a first step toward reconciling model and neural findings, these neurophysiological observations were used as a basis to constrain the bound- and drift-rate parameters of the DDM to be invariant across subjects and groups to the benefit of parsimony. In addition to striking a better balance between parsimony and goodness of fit, the constrained model furnished novel predictions regarding other features of the neural data, which were subsequently empirically validated. For example, the new model highlighted a beneficial reduction in between-trial variability in accumulation rates among older adults (**Figure 3*d***), which was mirrored in reduced variability in CPP buildup rates (**Figure 3*e***) and alpha-band activity, indicative of more stable attentional engagement. In the case of the motion discrimination task, the groups exhibited a different pattern of model parameter and decision signal differences, yet the neurally informed modeling approach led to similar inferential gains. Specifically, poorer detection performance in the older group was

explained by a higher bound in the unconstrained DDM. However, constraining the bound to be equal based on neural decision signal observations instead revealed a reduction in drift rate that, in turn, was validated by a reduced buildup rate of the CPP. This observation prompted further interrogation of the neural data, which revealed corresponding differences in the variability of posterior alpha-band activity. Posterior alpha is a well-established marker of attentional engagement (e.g., Hanslmayr et al. 2007, O'Connell et al. 2009), suggesting that younger adults may have experienced greater attentional fluctuations during task performance. An important distinction of McGovern et al.'s (2018) paradigm relative to the tasks classically employed in ageing studies is that, rather than using stimuli with sudden, easily detectable onsets, McGovern et al.'s task involved continuous monitoring for subtle feature changes, and in this context, a higher-bound policy would carry a greater risk of missed targets. Consequently, McGovern et al.'s findings do not necessarily undermine previous reports of age-related boundary elevation but do indicate that they are not evident in all contexts.

The application of neurally informed modelling to human data is at a very early stage, and many more aspects of decision formation appear ripe for such investigations in light of the additional constraints neural data afford. For example, another key decision process component is leakage, where past evidence samples are dynamically discounted in the running cumulative sum. Leakage is omitted for the sake of parsimony in the most widely applied models (Brown & Heathcote 2008, Ratcliff et al. 2016), but it is a core feature of others (Ossmy et al. 2013, Usher & McClelland 2001) and can explain certain well-known, time-dependent accuracy effects (e.g., recency bias) that standard models cannot (Usher & McClelland 2001). In some models, leakage is so strong that temporal integration is regarded as playing barely any role at all (Thura et al. 2012), and recent behavioral modelling and simulation work has indicated that many of the criteria that have typically been used to infer an integration strategy are also consistent with a strategy of extremum detection involving no integration (Stine et al. 2020). Thus, the general role of leakage, its task dependence, and its potential strategic adaptability are issues that are likely to be central to ongoing perceptual decision research and will benefit from the additional constraints offered by neural decision signal measurements.

Another element of complexity that is seeing increasing attention in decision modelling work relates to time dependence of the drift rate of the decision process. Although standard models assume drift rate to be stationary throughout a given decision, dynamically changing drift rates have been implicated under several circumstances, including during sensory interference tasks (Servant et al. 2015, White et al. 2011); due to adaptive gain control (Cheadle et al. 2014); during value-biased, rapid perceptual decisions (Afacan-Seref et al. 2018); and even in standard motion tasks where the evidence has been proposed to dynamically grow over time (Smith & Lilburn 2020). Here, again, the greater constraints of combined neural and behavioral data are likely to offer a key advantage in ongoing work.

Of course, neurally informed modeling using noninvasively recorded human brain data has inherent challenges that bear ongoing examination. As with animal neurophysiology, linking propositions, which specify the nature of the assumed correspondence between signals and model parameters, should be subject to continual validation and revision when necessary (Schall 2004, 2019). Furthermore, while some parameters have a sufficiently straightforward correspondence with neural signal properties to justify fixing the parameter values to match those neural measurements [e.g., the starting points/bounds in Kelly et al. (2020), as described above], others do not. For example, Purcell & Palmeri (2017) showed by simulation that variations in drift rate could result in spurious apparent differences in accumulation onset time. In the case of MEG/EEG recordings, signal overlap issues create further problems for the precise measurement of decision signals even where they correspond well to model parameters, necessitating careful paradigm

designs and analyses to improve signal isolation. Useful measures include avoiding luminance transients to eliminate irrelevant transient-evoked potentials and examining variations as a function of RT to help to disentangle overlapping signal components (Kelly & O'Connell 2013, Ouyang et al. 2011), which can also present more detailed signal patterns for guiding, constraining, or further validating decision models (e.g., de Lange et al. 2013, Kelly et al. 2020, Murphy et al. 2016). As with many kinds of modeling, the more data points set out to be captured, the better the traction on the problem, but also the more model development iterations that may be called for to achieve an accurate joint fit to behavior and neural signals. With this comes a greater imperative to replicate, reproduce, and generalize. Further, while these noninvasive signals have been functionally characterized to a sufficient degree to provide insights into decision algorithms, the future establishment of these signals' biophysical origins will enable them to inform circuit-level models that describe the neural implementation in greater detail (e.g., Wong & Wang 2006).

In addition to these cautionary notes, the application of neurally informed modelling to clinical or intergroup investigations carries some unique challenges. Most prominent among these is the need to account for the fact that intersubject variations in EEG signal amplitudes will partly reflect differences in cortical geometry and skull thickness or vasculature, which may have no bearing at all on decision-making behavior. Another challenge is that large quantities of data must typically be collected in order to achieve reliable and detailed neural measurements, which may not always be feasible in the context of clinical investigations. These issues can be addressed through the application of more advanced techniques for signal quality enhancement, which are continually emerging (Debettencourt et al. 2011, Luo & Sajda 2006, Tuckute et al. 2019, Zheng et al. 2018).

ANCILLARY PROCESSES

Another prominent contribution of recent human neurophysiology investigations has been to expose important functional interactions between the core sensorimotor circuits governing perceptual decisions and a range of key supporting processes. In particular, extensive research has highlighted that several interlinked systems associated with conflict and arousal are involved in the setting of decision bounds. Convergent data spanning multiple species and neural measurement modalities have established that representations of choice conflict or uncertainty generated in the posterior medial frontal cortex (pMFC) are predictive of future behavioral adjustments (Ebitz & Platt 2015, Cavanagh & Frank 2014, Sheth et al. 2012). In human EEG investigations, uncertainty signals reflected in peri-choice midfrontal theta-band activity are associated with a slowing of response times on forthcoming trials (Cavanagh & Frank 2014, Cavanagh et al. 2011, Cohen & Donner 2013), a relationship that mathematical modelling attributes to a transient raising of the decision bounds (Cavanagh et al. 2011). Thus, prefrontal uncertainty signals may play an important role in promoting more conservative decision policies.

In parallel, a significant effort has also been made to identify the neural pathways through which decision bounds are regulated. Functional imaging and connectivity analyses have indicated that the subthalamic nucleus (STN) is involved in raising response thresholds when conflict is detected (Frank 2006, Jahfari et al. 2011, London et al. 2019, Mansfield et al. 2011). Application of deep brain stimulation to STN induces faster, more impulsive response styles and disrupts the positive correlation between pMFC theta and future decision bound adjustments (Cavanagh et al. 2011). Whereas the STN is thought to act as a break on motor execution (Frank 2006), greater striatal activation has been linked with cortical disinhibition and lower response thresholds (Forstmann et al. 2008, Mansfield et al. 2011, van Maanen et al. 2016; but see Winkel et al. 2016). For example, variations in white matter integrity in tracts connecting the striatum to the presupplementary

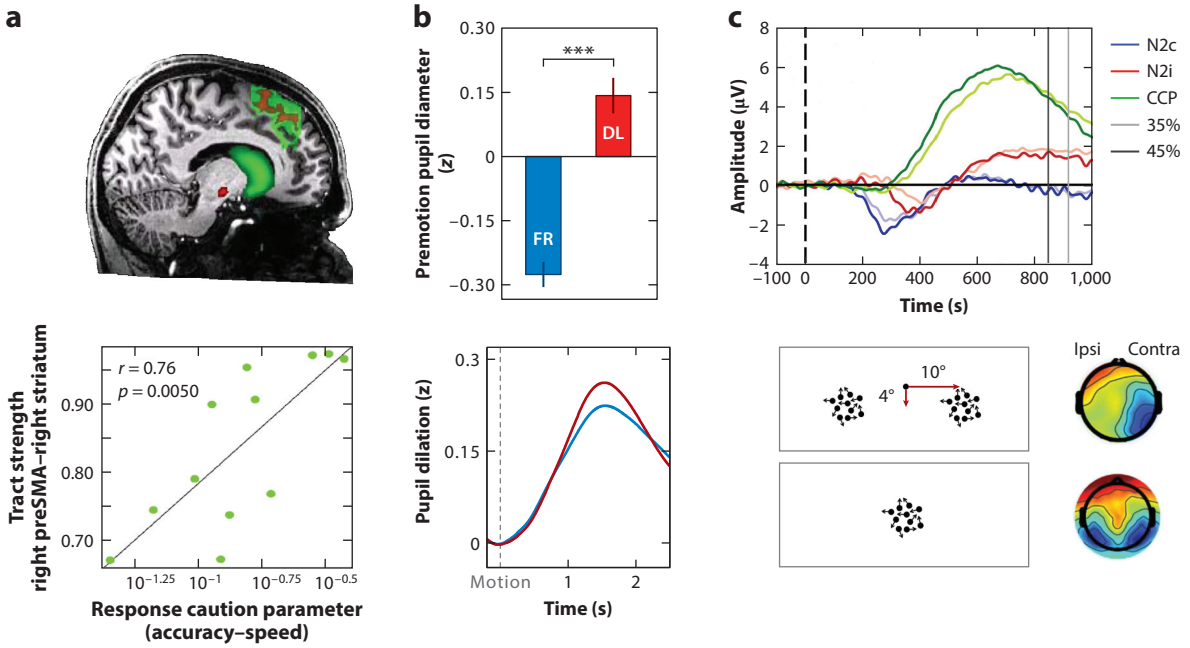


Figure 4

Three studies exemplify how investigations of human neurophysiology are revealing critical functional interactions between core decision circuits and other brain systems. (*a*) The strength (connection probability) of tracts connecting the striatum to the presupplementary motor area (preSMA) measured using probabilistic tractography is positively correlated with interindividual differences in the capacity for flexibly adjusting response caution (distance between starting point and bound as estimated by a sequential sampling model) when instructed to emphasize accuracy versus speed. Panel *a* adapted from Forstmann et al. (2010). (*b*) Normalized prestimulus pupil diameter measurements (*top*) exhibit a significant increase when participants are required to make their responses within a strict deadline (DL) compared to a condition in which no deadline is applied and points are awarded solely as a function of choice accuracy [free response (FR)]. Baseline-corrected, stimulus-evoked pupil dilations (*bottom*) were also larger under speed emphasis, and linear systems analysis indicated that, similar to the motor preparation signatures described above, these responses exhibited time-dependent buildup components, consistent with dynamic urgency. This observation accords with the hypothesis that dynamic urgency is reflected in the activity of neuromodulatory arousal systems. Panel *b* adapted from Murphy et al. (2016) (CC-BY 4.0). (*c*) Target selection signals appear to influence the timing of evidence accumulation when the onset and location of sensory evidence cannot be precisely predicted. When participants monitor two random-dot motion patches for unpredictable periods of coherent motion in either patch, coherent motion elicits an early posterior N2 component over contralateral scalp sites that scales with coherence and immediately precedes the onset of a neural signature of evidence accumulation [centroparietal positivity (CPP); *top*]. This contralateral enhancement produces the classic N2pc component in subtraction waveforms, a signal that has been implicated in spatial orienting and distractor suppression. However, we observed the same N2 signals, this time with equal amplitudes over both hemispheres, when participants monitored a single-dot motion stimulus at fixation, suggesting they play a more general role in detecting goal-relevant sensory changes (*bottom*). Panel *c* adapted with permission from Loughnane et al. (2016).

motor area are predictive of the extent to which individuals lower their decision bounds when placed under increased time pressure (Forstmann et al. 2010, 2011) (**Figure 4*a***).

In parallel, there is mounting evidence to suggest that diffusely projected neuromodulatory arousal systems support the instantiation of decision bound adjustments via brain-wide modulation of neural gain. Global gain modulation has been identified as a plausible mechanism for the generation of urgency signals in neural network modelling (Niyogi & Wong-Lin 2013, Shea-Brown et al. 2008, Thura et al. 2012) and accords with recent demonstrations that experimental manipulations of speed emphasis affect processing across the sensorimotor hierarchy (Heitz & Schall 2012, Spieser et al. 2017, Steinemann et al. 2018, Thura & Cisek 2016).

Correspondingly, linear systems analyses have indicated that arousal-linked pupil responses are driven by a sustained input throughout the course of decision formation and exhibit static and time-dependent urgency effects mirroring those observed in behavioral and EEG data (de Gee et al. 2014, Murphy et al. 2016) (**Figure 4*b***). Several lines of evidence suggest that prefrontal uncertainty signals are an important driver of these decision-related arousal responses. Pupil responses are highly sensitive to model-derived indices of choice uncertainty (Colizoli et al. 2018, Urai et al. 2017) and correlate with conflict signals reflected in human midfrontal theta activity (Lin et al. 2018) and single-unit spiking in the dorsal anterior cingulate region of the monkey brain (Ebitz & Platt 2015).

While most work to date has examined how uncertainty signals shape future behavioral adjustment, both midfrontal theta activity and decision-related pupil responses manifest as choices are still being formed and are therefore well positioned to influence decision processes online (de Gee et al. 2014, 2017; Murphy et al. 2015). Indeed, peri-choice theta responses have been shown to predict the likelihood that participants will report the current choice to be erroneous (Murphy et al. 2015), while peri-choice pupil responses have been linked to a suppression of the influence of prior biases on the emerging decision (de Gee et al. 2014, 2017). Taken together, this work examining the neural bases of boundary adjustments illustrates how even a single parameter of the decision process can bear functional relationships to a complex set of interacting systems processes and pathways. Such findings offer a guide to invasive research, which can go further to establish the finer details of these neural circuits and to probe causal influences.

Elsewhere, research has identified additional supporting processes that impact on other parameters of the decision-making process. An extensive human and monkey neurophysiology literature has examined so-called target-selection signals that are elicited at an early latency following abruptly occurring, goal-relevant sensory events (Theeuwes 2010, Cohen et al. 2009). Although such signals have been mainly associated with spatial orienting, Loughnane et al. (2016) recently demonstrated that a human manifestation of target-selection processes plays a much broader role. Specifically, the authors identified bilateral occipitotemporal responses—which together form the classic N2pc component (Eimer 2014, Luck 2012)—that encode the onset of goal-relevant sensory events and that predict RT via a relationship with the onset and buildup rate of the neural evidence-accumulation process indexed by the CPP (**Figure 4*c***). Elsewhere, work by Nunez et al. (2019) has since demonstrated a strong correlation between N2 latency and model-derived nondecision time estimates, consistent with the view that it marks the completion of predecisional processing and the onset of evidence accumulation. Surprisingly, Loughnane et al. (2016) found that these signals were evident and predictive of RT even when participants monitored a single, fixated stimulus stream, suggesting that target selection responses play a role that extends beyond spatial orienting or distractor suppression. These observations raise the possibility that the brain relies on target-selection responses to trigger evidence accumulation. Indeed, the idea that the flow of sensory information to evidence-accumulation processes is gated has already been incorporated into mathematical models of visual search (Purcell et al. 2012). Such a gating or triggering process could, in principle, obviate the need for continuous, presumably leaky, integration in continuous monitoring tasks so long as stimulus transitions are sufficiently detectable. A fruitful area of future investigation may thus be to probe the interplay and strategic adaptability of transition-detection and continuous accumulation processes.

The work covered in this section represents only an illustrative subset of human neurophysiology research exploring interactions between sensorimotor decision processes and other systems. Distinct lines of research have also examined the influence of a range of other ancillary processes, including representations of trial difficulty (Philiastides et al. 2006) and subjective value (Polanía et al. 2014), rhythmic sampling mechanisms (Wyart et al. 2012a), mechanisms of focused and

divided attention (Wyart et al. 2015), microsaccades (Loughnane et al. 2018), and prestimulus variations in attentional engagement (Kelly & O'Connell 2013) and arousal (van Kempen et al. 2019). Aside from exposing these important influences, these investigations are also yielding a novel set of neural metrics that can greatly expand the range of decision-making scenarios that are amenable to neurophysiological investigation.

CONCLUDING COMMENTS

The examples we have discussed show that advances in human neuroscience methods and modelling approaches have led to findings in humans that can complement those in animals. In particular we have highlighted how human brain studies have (*a*) identified effector-independent as well as effector-selective decision signals, (*b*) begun to incorporate these signals into neurally informed modelling approaches, and (*c*) exploited the global view on brain function offered by noninvasive techniques in order to examine functional interactions between sensorimotor decision circuits and a range of ancillary processes. Thus, the field of decision neuroscience is at an exciting juncture. It is now possible for researchers to trace comparable neural signatures of decision-making in invertebrates, rodents, monkeys, and humans within a shared experimental, computational, and theoretical framework. This ability in turn will facilitate the integration of methods and findings across human and animal studies. Establishing the biophysical and functional linkages between intra- and extracranially recorded decision signals will be essential to the further progression of the field and stands to tell us much about how single-neuron action potentials are translated into systems-level computations. Building on the progress already being made in computational work (Huys et al. 2016), the next few years are sure to see significant progress in applying these new insights, methods, and neural signals to furthering our understanding of decision-making deficits arising from brain disorders.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors wish to thank Peter Murphy for helpful feedback on an early draft of this paper. R.G.O. was supported by Horizon 2020 European Research Council Starting Grant Human Decisions 63829 and European Research Council Consolidator Grant IndDecision 865474. S.P.K. was supported by research grants from Science Foundation Ireland under grant number 15/CDA/3591 and The Wellcome Trust (219572/Z/19/Z).

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