CHAPTER

11

Spatiotemporal Characteristics and Modulators of Perceptual Decision-Making in the Human Brain

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Abstract

Perceptual decision-making is the process of choosing between two or more alternatives based on an evaluation and integration of sensory information. Converging evidence from electrophysiology, neuroimaging, and theoretical modeling work suggests that the decision process relies on a cascade of neural events. Sensory input is first encoded by the neural modules selective to the choice alternatives before it is passed on to a decision center, which compares the sensory outputs in a noisy process of gradual accumulation of evidence that ultimately leads to a decision. In this chapter we start out with an introduction to the general principles guiding perceptual decision-making. We then take a critical turn to look beyond sensory information as the decisive variable for the decision, and discuss additional factors that interact with, and contribute to, the decision process. Specifically, we review the influence of the following factors: prestimulus state, reward and punishment, speed−accuracy trade-off, learning and training, confidence, and neuromodulation. We show how these decision modulators can exert their influence at various stages of processing, in line with predictions derived from sequential-sampling models of decision-making.

INTRODUCTION

Perceptual decision-making is the act of selecting one option or course of action from a larger set of alternatives on the basis of available sensory information [1]. This process has frequently been modeled using sequential sampling models, such as the well-known drift-diffusion model [2], which assumes that the decision formation hinges on a noisy (stochastic) accumulation of incoming sensory information [3−6] (also see Chapter 12). More specifically, these computational accounts suggest that perceptual decisions involve an integrative mechanism whereby the difference in sensory evidence supporting the alternatives accumulates over time to a preset internal decision boundary, which ultimately determines the choice (Fig. 11.1).

Correspondingly, several nonhuman primate (NHP) electrophysiology studies have revealed patterns of single-unit activity that are in line with this integrative mechanism [7]. Using a visual motion direction-discrimination task [random-dot kinematogram (RDK) task], these studies revealed that, whereas sensory areas responsive to motion direction [such as the middle temporal area (MT)] encoded the amount of evidence for each alternative, higher-level regions known to orchestrate choice [such as the lateral intraparietal area (LIP), the frontal eye fields, and the superior colliculus] accumulated the evidence for the decision. Specifically, firing rates of individual neurons in these areas built up gradually over time at a rate proportional to the amount of evidence for the decision (i.e., difficulty of the task), eventually converging on a common firing level (decision boundary) as animals committed to a choice [7−9].

More recently, human studies using time-resolved electroencephalography (EEG) signals were able to measure the process of evidence accumulation on the scalp [10−12]. Philiastides et al. [11], using a visual binary categorization task (e.g., is the stimulus a face or a car/house), showed that population responses on the scalp (with a broad centroparietal topography) can capture activity that builds up gradually over time with a rate proportional to the amount of sensory evidence in the stimulus (Fig. 11.2A). The buildup rate of this accumulating activity was consistent with the properties of a drift-diffusion-like process as characterized by computational modeling (i.e., EEG buildup rate correlated with

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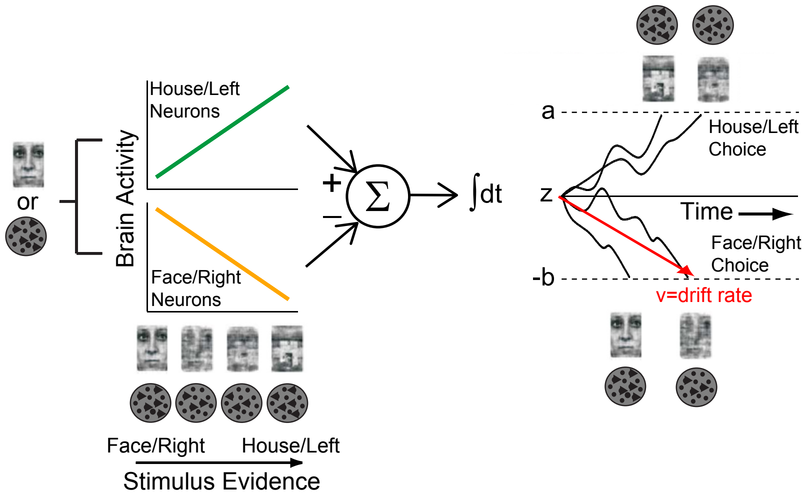

FIGURE 11.1 Representation (left) and integration (right) of sensory evidence in perceptual decision-making. Sensory areas/neurons encoding each of two decision alternatives (e.g., face/house or right/left motion) respond parametrically to the amount of evidence in the stimulus. For example, face-responsive regions respond stronger to clear than to noisy images of faces and even less to images of houses. Conversely, house-responsive regions respond stronger to clear than to noisy images of houses and even less to images of faces. The difference signal between the two competing areas or groups of neurons is subsequently integrated over time in the decision process from a starting point (z) toward one of two internally set decision boundaries (a or $-b$) representing the possible choices. The rate at which the evidence is accumulated [drift rate (v) in the diffusion model of simple decision-making] is proportional to the amount of stimulus evidence. *Adapted from Philiastides MG, Heekeren HR. Spatiotemporal characteristics of perceptual decision making in the human brain. In: Dreher J-C, Tremblay L, editors. Handbook of reward and decision making. Academic Press; 2009. p. 185–212.*

drift rate in the model; Fig. 11.2B) and it was additionally shown to predict participants' choice accuracy as in the NHP work described earlier (Fig. 11.2C).

Intriguingly, regions of the parietal and prefrontal cortices were linked to this accumulating activity in humans, via functional magnetic resonance imaging (fMRI). A study by Ploran et al. [13] recorded the time of recognition of noisy pictures that were revealed gradually over the course of several seconds. During this period the authors identified a gradual buildup in the fMRI signal, peaking in correspondence with the time of recognition in a set of regions, the inferior temporal, frontal, and parietal regions. Similar patterns of activity were also reported using a face/house categorization task [14].

Heekeren et al. [15] directly tested whether a comparison operation is also at work (as shown in Fig. 11.1) using a similar face/house categorization task. A brain region in the posterior portion of the left dorsolateral prefrontal cortex (DLPFC) uniquely correlated with the

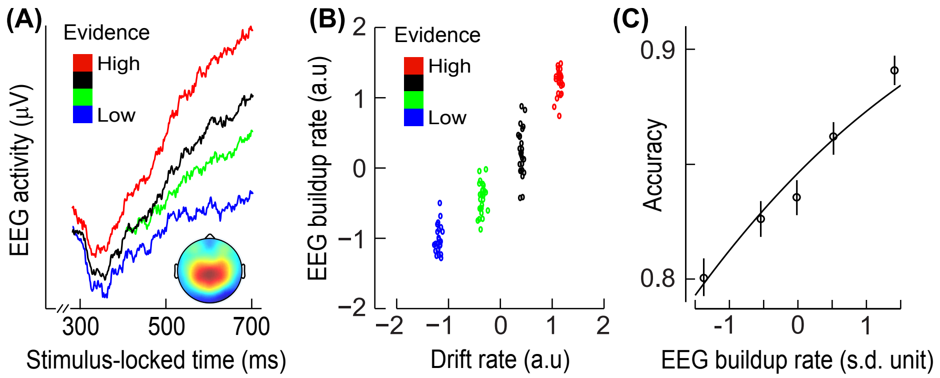

FIGURE 11.2 Evidence accumulation in human EEG recordings during a face/car categorization task. (A) Ramp-like activity consistent with a process of evidence accumulation recorded on the surface of the scalp. As sensory evidence increases so does the buildup rate (slope) of the evidence accumulation. Scalp topography depicts the spatial distribution of the accumulating activity. (B) The buildup rate of the EEG activity correlates with drift rate estimates from a diffusion model analysis of individual subject behavioral responses. (C) The buildup rate of the accumulating activity is predictive of participant's choice accuracy, even after accounting for task difficulty. *Adapted from Philiastides MG, Heekeren HR, Sajda P. Human scalp potentials reflect a mixture of decision-related signals during perceptual choices. J Neurosci 2014;34:16877–89.*

difference between the output signals of face- and house-responsive regions and it additionally predicted behavioral performance in the categorization task. This finding was replicated using a direction discrimination task and two different response modalities (i.e., eyes and hands) [16] and was shown to persist even when the perceptual decision was fully decoupled from the impending motor response [17].

Finally, Philiastides et al. [18] showed that hindering activity in the left DLPFC with transcranial magnetic stimulation resulted in behavioral impairments (relative to sham stimulation) that were attributed to changes in the efficiency of integration (drift rate) in a diffusion model fit to the behavioral data. Taken together these findings suggest that the left DLPFC plays a causal role in the integration of the outputs of lower-level sensory regions and uses a subtraction operation to compute perceptual decisions.

It is noteworthy that similar findings have been reported during decision-making in other domains (e.g., auditory [19,20] and somatosensory [21–23]), suggesting that the process of sensory evidence accumulation supporting perceptual decisions generalizes across sensory modalities. Nonetheless, in addition to the sensory input, decisions can also be affected by other factors (i.e., decision modulators), which have the capacity to influence different processing stages along the decision stream as highlighted in Fig. 11.1 (e.g., from early sensory encoding to the decision formation itself). In this chapter we will review the role of the following factors on perceptual decision-making: prestimulus state, reward and punishment, speed–accuracy trade-off, learning and training, confidence, and neuromodulation.

FACTORS AFFECTING PERCEPTUAL DECISION-MAKING

Prestimulus State

An important factor that can influence the course of the decision process is the state of the neural activity prior to any task-relevant sensory stimulation. For example, a strong link has been observed between the trial-to-trial fluctuations in prestimulus oscillatory activity and the behavioral outcome of the perceptual decision [24–27]. In one such study, Van Dijk et al. [27] asked participants to perform a simple visual discrimination task, which involved detecting whether a contrast difference was present in a target stimulus. Magnetoencephalography (MEG) recordings showed that spontaneous prestimulus oscillations in the alpha-frequency band, within occipitoparietal areas, were negatively correlated with subjects' performance, such that as alpha power increased, discrimination ability decreased. Similar effects of prestimulus alpha activity have been shown in other studies [24–26,28] and are theorized to reflect variability in attentional processes exerting top-down modulatory influence on information processing [29].

The temporal locus of this influence on the decision-processing stream, however, remains an active topic of debate. Some studies suggest that prestimulus alpha power exerts its influence on early sensory processing. Mazaheri et al. [28] asked subjects to perform perceptual discriminations in which, on some trials, auditory and visual stimuli were presented simultaneously, with only one of the stimuli, cued in advance, requiring a perceptual judgment. On these trials, prestimulus alpha power was suppressed in the early sensory regions relevant to the target stimulus (i.e., early visual areas for visual stimuli and the supramarginal gyrus for auditory stimuli) and enhanced in the region relevant to the distractor sensory modality. The authors proposed that alpha activity might serve the role of gating or modulating information flow to sensory areas.

A different study by Lou et al. [30] directly sought to identify the temporal stage(s) of the decision process likely to be affected by prestimulus alpha activity during a face/car categorization task. Prestimulus alpha-band power was negatively correlated with the magnitude of an early EEG stimulus-discriminating component hypothesized to reflect early sensory evidence encoding [31–34], such that lower prestimulus alpha power was associated with higher absolute value of the discriminant component (Fig. 11.3A). Conversely, no correlation was found between prestimulus alpha power and a later decision-related discriminating component.

There has also been evidence to suggest a later influence directly affecting the evidence accumulation stage of the decision. Kelly and O'Connell [12] used an RDK task and found that prestimulus alpha power correlated positively with subjects' response time and negatively with the efficiency of decision formation, as indexed by the buildup rate of a centroparietal positivity potential in the stimulus-aligned EEG signal [35]. Their results are consistent with a top-down influence of prestimulus attentional fluctuations on the decision, whereby lower prestimulus alpha power (i.e., enhanced attention) leads to a more efficient evidence accumulation in the post-stimulus period.

Modulatory effects of prestimulus state on the perceptual decision have also been linked to spontaneous prestimulus oscillatory activity in the gamma-frequency band. Wyart and Tallon-Baudry [26] used a visual detection (present/absent) task in which the locations of the stimuli were precued with partial validity on each trial (i.e., the cues were correct on only 65% of the trials). They found that gamma-band activity in the lateral occipital cortex was predictive of subjects'

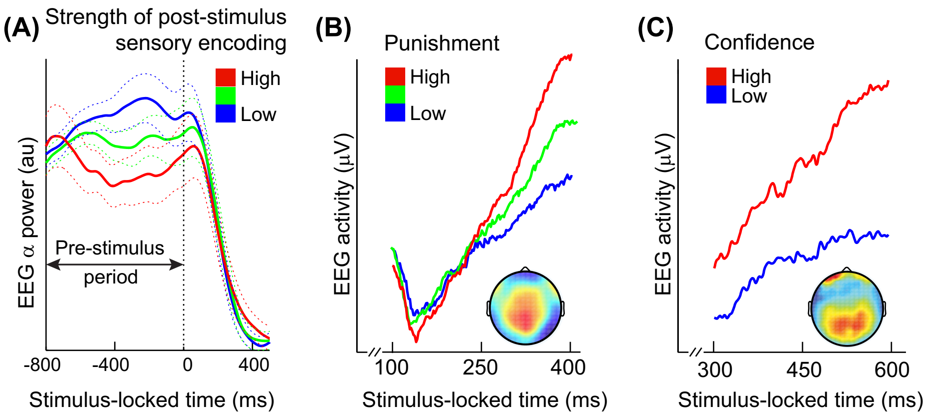

FIGURE 11.3 **Influence of different modulators on perceptual decision-making during a face/car categorization task.** (A) Prestimulus alpha power influences the encoding of early sensory evidence, whereby lower prestimulus alpha leads to a more reliable poststimulus sensory encoding. *(Adapted from Lou B, et al. Prestimulus alpha power predicts fidelity of sensory encoding in perceptual decision making. NeuroImage 2014;87:242–51.)* (B) Modulating the level of punishment associated with incorrect perceptual decisions affects the efficiency of evidence accumulation in the decision, whereby higher punishment levels lead to a steeper rate of evidence integration. *(Adapted from Blank H, et al. Temporal characteristics of the influence of punishment on perceptual decision making in the human brain. J Neurosci 2013;33:3939–52.)* (C) Choice confidence during perceptual choices reflected in the process of decision formation, with more confident trials leading to a higher rate of evidence accumulation. *(Adapted from Gherman S, Philiastides MG. Neural representations of confidence emerge from the process of decision formation during perceptual choices. NeuroImage 2015;106:134–43.)*

choices, increasing for detected versus undetected reports. The authors demonstrated that its perceptual impact resembled a decision bias at stimulus onset, thus making one response more likely than the other. Moreover, this did not appear to be due to changes in attentional focus, but rather to spontaneous predictions about the upcoming stimulus, potentially biasing the starting point of evidence accumulation.

Overall, it appears that variability in prestimulus activity can play an important role in altering the course of the decision, likely through top-down modulatory effects on information processing. It is possible that, at least in some circumstances, these internal fluctuations possess a volitional/adaptive component aimed at maximizing reward/performance; however, when and how these differ from spontaneous fluctuations remains to be explored.

Reward and Punishment

In a natural environment, the ultimate aim of any behavioral response is to try to maximize an organism's utility function (i.e., maximize rewards or minimize punishments) (also see Chapter 4). Value-based decision-making in humans, especially in the context of reinforcement learning and reward-related activity in dopaminergic systems [36] (also see Chapter 2), has already been studied extensively. Surprisingly, however, less has been done to explore the potential effects of reward and punishment on perceptual decision-making, whether on early encoding of sensory information or on later decision-related processing and action selection.

Weil et al. [37] collected fMRI data while subjects performed an orientation discrimination task and were given monetary rewards for correct decisions. Greater rewards improved behavioral performance and increased fMRI activity in areas of the reward network (e.g., ventral striatum and orbitofrontal cortex). More importantly, however, the authors found that positive outcomes also led to increased activity in early visual areas (e.g., V2 and V3) at the time of reward delivery (presented auditorily) when no visual stimuli were being presented. Finally, rewarded trials led to improved performance on the subsequent trial and enhanced visual activity contralateral to the judged stimulus. In a related fMRI work, Schiffer et al. [38] used a face/house categorization task in which subjects received monetary rewards and punishments for correct and incorrect choices, respectively. At the time of outcome delivery, the authors found reward-predictive activity in visual areas associated with faces (i.e., fusiform face area) and houses (i.e., parahippocampal place area) when subjects made face and house choices, respectively. Not only these activations were dependent on the perceptual decision, they also covaried with activity in reward structures (e.g., ventral striatum), indicating an interaction between the human reward network and the early sensory cortex.

Similar results were obtained by Pleger et al. [39] in the somatosensory domain. The authors used fMRI and a tactile discrimination task in which subjects had to compare the frequency of two successive tactile stimuli applied to the same finger. The task was performed under different reward rates for each correct trial. Higher rewards enhanced behavioral performance and increased fMRI activity in both the primary somatosensory cortex (S1) and the ventral striatum. More importantly, however, these authors demonstrated that during reward delivery and in the absence of somatosensory stimulation, the S1 contralateral to the judged finger was reactivated and this reactivation was proportional to the amount of reward. Finally, they showed that reward magnitude on a particular trial influenced responses on the subsequent trial, with better behavioral performance and greater somatosensory responses for higher rewards. Taken together the results presented above clearly demonstrate that the systems involved in valuation interact with early sensory systems. More specifically, in situations in which the value of outcomes depends on decisions associated with different perceptual representations, reward and punishment signals are propagated back to sensory systems, in the form of a "teaching signal" whereby they can shape early sensory representations to optimize future choices and maximize reward.

In addition to the effects on the early sensory system, more recent studies focused on the influence of reward and punishment on the dynamics of the process of evidence accumulation during the decision itself. In an EEG study by Blank et al. [40] subjects performed a face/car categorization task, during which the level of punishment associated with incorrect choices changed in a block-wise fashion (three levels: low, medium, high). EEG activity discriminating between the three levels of punishment appeared mostly late in the trial. This activity exhibited a ramp-like response profile (Fig. 11.3B) and had a spatial topography consistent with the process of evidence accumulation defined earlier (compare Fig. 11.2A with Fig. 11.3B). Crucially, the buildup rate of this activity increased parametrically with the amount of punishment (Fig. 11.3B) and it was further predictive of the size of the behavioral improvements induced by punishment across participants. Finally, the trial-by-trial changes in prestimulus power in the alpha and gamma bands were good predictors of this accumulating activity, suggesting that different decision modulators (here prestimulus state and punishment) can interact to shape perceptual decisions. Similar results are obtained using manipulations of reward magnitude. These findings indicate that reward and punishment can exert a top-down influence (e.g., via attention and motivation) on the decision process itself, leading to more efficient integration of sensory evidence.

In another study, Green et al. [41] had participants perform an RDK task in blocks with identical duration but different reward/punishment schedules. Behavioral and diffusion modeling results indicated that subjects adjusted their decision boundaries (i.e., controlled the amount of accumulated evidence) to maximize the reward rate, consistent with earlier computational modeling work [42,43]. fMRI results from Green et al. [41] indicated that these changes in the decision boundaries were achieved by adjusting the connectivity within corticostriatal systems, responsible for accumulating sensory evidence, and cerebellar—striatal systems, responsible for temporal processing. These connectivity patterns were strongest for those individuals who obtained greater rewards by making greater adjustments in their decision boundaries. Similarly, Domenech and Dreher [44] showed decision boundary adjustments as a function of prior knowledge and the predictability of upcoming stimuli. These findings provide another source of evidence that in perceptual decision-making, reward and punishment can directly modulate the dynamics of the decision process itself.

Speed Versus Accuracy Trade-Off

The previous section offered evidence on how reward maximization in perceptual decision-making can be achieved by optimally adjusting the decision boundaries in the process of evidence accumulation to meet the payoff contingencies of the environment. Within the framework of sequential sampling models of decision-making, these boundary adjustments are thought to implement a speed—accuracy trade-off (SAT) [45] (also see Chapter 12 for additional discussion on SAT). More generally, SAT is considered a mechanism by which a reasonable balance between the competing demands of speed and accuracy can be achieved. While the likelihood of making a correct decision increases as information continues to accumulate over time, delaying decisions to ensure they are certainly correct may render them ineffective. Within this framework, studies have started to look at how SAT is implemented in the brain and how it influences the process of decision formation.

In an fMRI study by Forstmann et al. using the RDK task [46], subjects were instructed to increase either speed or accuracy on individual trials. As expected, subjects were fast but less accurate during the speed compared to the accuracy instruction and computational modeling analysis confirmed that this effect was driven by a reduction in the distance between the decision boundaries. fMRI analysis showed that the speed instruction was associated with increased activity (relative to the accuracy instruction) in the striatum and the presupplementary motor area, regions known to be involved in voluntary motor planning (see also van Maanen et al. [47]). Moreover, individual differences in the level of activation in these regions were correlated with individual variations in the decision boundaries estimated via a bounded-accumulation model. In a follow-up structural connectivity study, Forstmann et al. [48] provided additional evidence that decreases in decision boundaries are likely to be mediated via increased activation from cortex to striatum, releasing the motor system from inhibition (striatal hypothesis), rather than from decreased activation from cortex to the subthalamic nucleus (STN hypothesis). This evidence is consistent with a flexible mechanism of response caution adjustment in accordance to environmental (task) demands.

In a related study, using fMRI and the RDK task, Ivanoff et al. [49] showed that, in addition to the results described above, SAT also affected the activity of the lateral prefrontal cortex in a region known to be involved in evidence accumulation during the decision process. More specifically, the authors showed that emphasizing the speed rather than the accuracy of the perceptual decision lowered the amount of evidence-related activity in the lateral prefrontal cortex, consistent with a reduction in the decision boundary. Interestingly, this effect was not observed in sensory areas providing the evidence for the decision (e.g., MT), suggesting that SAT affects the dynamics of the decision process itself, rather than exerting an influence on early sensory processing.

More recently, Wenzlaff et al. [50] provided additional evidence on how the influence of SAT develops over time using MEG. The authors used a face/house categorization task and reported ramp-like activity consistent with the process of evidence accumulation that was modulated by SAT. Specifically, source analysis of this activity showed that supplementary motor areas and the medial precuneus increased their level of activation in the speed compared to the accuracy instruction. Increases in activity in these regions correlated with a reduction in the decision boundary (i.e., a negative correlation) as estimated by a diffusion model applied to the behavioral data, consistent with the results of the fMRI studies described earlier [46,49]. In addition, the authors reported that the level of activation in the DLPFC correlated positively with the model's boundary parameters as in the aforementioned Ivanoff et al. fMRI study [49].

Collectively, these neuroimaging studies offered strong support that SAT is implemented by changes in decision boundaries in (pre)motor and decision-related brain structures. However, evidence from NHPs challenged this view and provided evidence for an alternative account [51,52]. For example, Hanks et al. [52] found that during SAT, LIP neurons known to accumulate evidence for the decision did not exhibit a change in their decision boundaries. Instead, during the speed instruction these neurons showed an increased initial firing rate (i.e., evidence-independent activation), ultimately enabling the animal to make a decision on the basis of less information. In contrast to the human neuroimaging results, these findings suggest that SAT could be mediated by changes in the amount of decision-related activity itself rather than through decision boundary adjustments.

Learning and Training

Another way to augment and optimize performance during perceptual choices is through learning. More specifically, training and experience are required to induce long-lasting improvements in our ability to make perceptual decisions based on ambiguous sensory information. This phenomenon is commonly referred to as perceptual learning [53] and though it has been studied extensively, especially in early vision [54,55], its effect on the decision-making process itself remains less well explored. The traditional view on the neural plasticity underlying learning has been that the influence of training is on the early parts of the perceptual system, such as in early visual cortex. An alternative view, however, is that learning in the context of perceptual decision-making can additionally affect higher-level areas responsible for driving the decision itself via enhanced cortical coupling with early sensory cortex.

The traditional view has been corroborated by human neuroimaging studies by Furmanski et al. [56], who used fMRI to measure neural signals in primary visual cortex before and after a month-long perceptual training period in which subjects learned to detect oriented patterns. They observed an increase in response in V1 that correlated with improvements in behavioral performance. Similarly, Jehee et al. [57] used an orientation discrimination task that was performed daily over the course of several weeks. They reported significant improvements in discrimination ability and corresponding enhancement in neural activity along the early visual areas (V1 to V4), albeit for only the trained orientations and locations. Correspondingly, single-cell recordings in NHPs by Yan et al. [58] showed that learning to discriminate visual contours led to strengthening and accelerating of neural responses in primary visual cortex, and that these changes correlated highly with behavioral performance.

Despite these results, evidence supporting the alternative view (i.e., late influences of learning on decision-making) has also been provided. For example, computational work [59] suggests that perceptual improvements are mediated by higher-level decision-related centers of the brain that learn to read out and reweight V1 inputs through training. In related work, Li et al. [60] asked subjects to decide whether a visually presented stimulus was radial or concentric by comparing the external sensory input to different internal decision criteria that they learned through training with feedback on separate sessions. After each training session, subjects performed the categorization task during fMRI. The authors used multivoxel pattern analysis of the fMRI signals to predict subjects' behavioral choices, and showed that category learning affects decision-related regions in frontal and higher occipitotemporal brain regions implicated in flexible adjustment of the decision criterion required for the task. These effects were not observed in regions responsible for early encoding of the stimulus or those controlling motor preparation and execution. Collectively, these studies provide evidence that perceptual learning effects extend beyond the perceptual system and can influence higher-level brain areas implicated in the decision process itself.

This interpretation is further supported by experiments in NHPs. Law and Gold [61] trained animals over several sessions to discriminate the direction of visual motion in an RDK task while activity in areas MT and LIP (thought to reflect the sites of sensory evidence encoding and evidence accumulation, respectively) was measured. The neurons in area LIP, but not MT, showed increased responsiveness to the decision evidence as a function of learning, reflected in steeper evidence-accumulation slopes. Correspondingly, there was a correlation between the neural responsiveness of these neurons and the performance on the task. This study provides evidence that perceptual learning does not change how sensory information is represented in the brain, but rather how sensory representations are interpreted, particularly by higher areas in the brain involved in decision-making.

In a follow up study, the same authors [62] showed that their results could be explained in terms of a reinforcement learning (RL) mechanism [63], whereby the connections between sensory neurons and the decision process are strengthened via a reward prediction error, gradually enhancing the readout of relevant information and improving perceptual sensitivity. This explanation was corroborated by work in humans by Kahnt et al. [64], who trained subjects on an orientation discrimination task over the course of 4 days. The authors explained behavioral improvements using an RL model that updated the decision evidence on every trial in accordance with a prediction error signal. Using fMRI, the authors showed that stimulus orientation was encoded in both early visual and higher cortical areas in lateral parietal and medial prefrontal cortices. However, only activity in the medial prefrontal cortex tracked the trial-by-trial changes in the decision variables estimated from the RL model. These findings suggest that a reinforcement-guided learning mechanism might be at work during both reward-related and perceptual learning.

Confidence

The previous section highlighted that the process of perceptual decision-making can undergo long-term optimization, which ultimately serves to fine-tune behavior and maximize reward. It was suggested that a potential mechanism by which perceptual learning is facilitated is the ability of a system to estimate the reliability of a perceptual decision [65]. In addition to providing an evaluation of the decision process itself, this sense of confidence in our judgments can also help predict choice outcome and ultimately motivate learning and inform future choices. Correspondingly, there has been growing interest in understanding the neural basis of decision confidence, in both the NHP and the human literature [66–68].

In particular, the relationship between confidence and the decision process has been the subject of some debate. Generally, decision confidence has been studied as a metacognitive (i.e., postdecisional) process. For instance, Fleming et al. [69] examined the spatial correlates of metacognition by asking subjects to perform a face/house categorization task and rate their confidence in their decisions after each choice. fMRI activity in the rostrolateral prefrontal cortex (RLPFC) was found to correlate with confidence at the time of rating, and was enhanced during confidence rating compared to a control task. Importantly, the strength of the relationship between RLPFC activity and confidence reports was predictive of subjects' ability to evaluate their own performance (i.e., metacognitive ability). Relatedly, Fleming et al. [70] demonstrated that metacognitive ability is correlated with the gray matter volume of the anterior portion of the prefrontal cortex, as well as the white matter projections to this region. While these studies have addressed important questions regarding the spatial characteristics of choice confidence in the postdecision period, it is not clear whether confidence might be arising earlier in time, during the decision process itself.

Evidence from animals suggests that information about confidence becomes available earlier in the decision stream [71,72]. Specifically, in the primate and rat brains, choice confidence appears to develop simultaneously with the decision process and is encoded by the same neural populations that form the decision. Only a handful of studies have tried to characterize choice confidence in the human brain as it develops in time during the decision process. In Zizlsperger et al. [73], subjects performed an RDK task and rated their confidence in the decision while EEG data were recorded. Event-related potentials locked to stimulus onset began to show a separation between high- and low-confidence trials soon after stimulus presentation, and almost concomitant with modulation by task difficulty, a finding consistent with a decisional account of confidence.

In line with this account, Gherman and Philiastides [10] used EEG to study the temporal characteristics of choice confidence during a delayed-response face/car categorization task that rewarded correct trials. On half of the trials, before indicating their choice, subjects were allowed to opt out of the task for a smaller but certain reward. This manipulation encouraged subjects to opt out of the decision when they were uncertain of their choice or ignore this option and commit to a choice when they were certain. A comparison between the neural signals for certain versus uncertain choices showed that discrimination between the two conditions increased gradually after the stimulus was presented, peaking before subjects initiated a response. These confidence-related signals exhibited a ramp-like response profile (Fig. 11.3C) and had a spatial topography consistent with the process of evidence accumulation defined earlier (compare Fig. 11.2A with Fig. 11.3C) [11]. Importantly, the accumulation rate of this activity was predictive of confidence on a trial-by-trial basis, even when difficulty effects were controlled for, offering strong evidence that confidence develops continuously as the decision process unfolds. Taken together, these studies suggest that confidence arises early after stimulus presentation and thus may help shape the course of the decision process itself.

One hypothesis as to how this can be achieved is that confidence may act as a learning signal, shaping subsequent decisions and optimizing performance. For instance, Hebart et al. [65] found that during an RDK task, fMRI activation increased with confidence in the ventral striatum. Using a connectivity analysis, they demonstrated a flow of information from areas of the brain correlating with the decision (i.e., parietal and prefrontal sites) to the ventral striatum, suggesting confidence computed within this region is derived from, and computed in parallel with, the ongoing decision signal. The authors proposed a potential role of the ventral striatum in confidence-driven learning, suggesting that introspective signals (e.g., the feeling of reward associated with a choice) serve to reinforce optimal behavior on subsequent choices. Thus, in this sense, confidence may be thought of as an implicit reward signal, which is being propagated back to the decision systems to optimize the dynamics of the decision process, possibly by means of an RL-like mechanism.

Neuromodulation

Although much effort is being invested in assessing the various influences on perceptual decision-making at the systems level, less attention has been devoted to understanding how neurotransmission affects the decision process. There has been some evidence pointing to a potential role of the neurotransmitter dopamine in the efficiency of information processing. MacDonald et al. [74] examined the influence of aging-related decline in dopaminergic activity on cognitive processing, using a speeded reaction-time task that relied on executive control. The authors demonstrated a tight link between the decrease in D1 receptor binding potential and intraindividual trial-to-trial variability in reaction time, a measure commonly used to indicate the precision of information processing [75]. Interestingly, another study by Ratcliff et al. [76] demonstrated that age-related decreases in processing efficiency during a brightness discrimination task were linked to the rate of decision-related evidence accumulation. Together, the two studies suggest that disruptions in dopaminergic activity can have an influence on the efficiency of decision formation; however, a direct link between the two is yet to be demonstrated empirically.

Additional evidence for the involvement of dopamine in the perceptual decision process comes from research on molecular genetics. The catechol-*O*-methyltransferase (COMT) protein, which metabolizes catecholamine neurotransmitters, has been shown to play a role in regulating prefrontal dopamine [77], and may affect processing in various decision-making centers. Saville et al. [78] demonstrated that Met/Met carriers of the COMT Val^{158}Met polymorphism showed greater intrasubject variability during an *n*-back reaction-time task, both in behavior (response time) and in the latency of the P3b event-related potential, compared against Val/Val carriers. The P3b component, which has often been associated with decision-related processes [79], has been argued to reflect the formation of the perceptual decision itself [11,35,80]. Together, these findings suggest a potential link between COMT-related individual differences in dopaminergic activity and decision formation.

Dopaminergic activity may also have an indirect influence on the perceptual decision, via its involvement in reward-related activity. Nagano-Saito et al. [81] tested the effect of reward-related dopaminergic activity on visual perceptual discrimination by temporarily hindering dopamine transmission in healthy subjects. Specifically, participants performed an RDK task in which cues presented prior to each trial informed them on the availability of a reward for a correct response. Behaviorally, availability of reward led to increased decision thresholds (as inferred using an accumulation-to-bound model), suggesting subjects prioritized accuracy over speed on these trials. During the anticipatory period leading to stimulus presentation, fMRI activation was greater for rewarded trials in the ventral striatum and prefrontal cortex, and interestingly, the magnitude of the activation was positively correlated with the threshold of the impending decision. Crucially, decreasing dopaminergic transmission eliminated both the blood oxygen level-dependent activation and its correlation with the decision threshold, pointing to a causal role in decision formation.

New insights on the neuromodulation of perceptual decision may also be gained from the study of pupil size changes across the time course of the decision process. Pupil size fluctuations in conditions of constant illumination are thought to reflect arousal state and have been shown to correlate with activity in the locus coeruleus, the center of the neuroadrenergic system [82] (for a review, see Aston-Jones and Cohen [83]). In one such study, Murphy et al. [84] demonstrated that spontaneous, stimulus-independent fluctuations in pupil diameter during an RDK task could be explained by the variability in the accumulation of decision evidence, a parameter derived by fitting a diffusion model to the behavioral data. Specifically, slow increases in pupil size, reflective of heightened arousal state, were associated with greater variability in the rate of evidence accumulation.

Similarly, De Gee et al. [85] measured pupil size fluctuations while subjects performed a visual detection task wherein they determined the presence (or absence) of low-contrast grating stimuli. Authors demonstrated that pupil dilation predicted subjects' behavior (i.e., whether they made a "present" vs "absent" response), and more importantly, it was best explained by a sustained component that persisted throughout the decision phase (i.e., starting at stimulus onset and ending when the subject made a response), suggesting pupil dilation contains information about the formation of the perceptual decision. As has been previously postulated by theoretical modeling work [86,87], it is plausible that the perceptual decision process may rely on noradrenergic modulation mediated by the locus coeruleus; however, this is still open to further investigation. The increase in availability of effective, transient, and noninvasive techniques for studying neuromodulatory systems in humans (e.g., amino acid challenge and depletion techniques, see Ref. [88]) may offer new opportunities for further understanding of their roles in perceptual decision-making.

CONCLUSION

In this chapter, we provided an overview of the general neurobiological principles guiding perceptual decision-making and reviewed the influence of various modulators on the process of decision formation. We also discussed how these influences could be understood in terms of changes in parameters of sequential sampling models of decision-making. Finally, we offered a general discussion on how the influence of these decision modulators can be thought of in the framework of reward maximization, whereby the perceptual decision-making system adjusts to adaptively optimize behavior. This perspective highlights possible future research directions into the role of reinforcement-guided learning, not only in reward- and value-based decision-making, but also in our understanding of perceptual decision-making.

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