The neural systems that mediate human perceptual decision making

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Abstract | Perceptual decision making is the act of choosing one option or course of action from a set of alternatives on the basis of available sensory evidence. Thus, when we make such decisions, sensory information must be interpreted and translated into behaviour. Neurophysiological work in monkeys performing sensory discriminations, combined with computational modelling, has paved the way for neuroimaging studies that are aimed at understanding decision-related processes in the human brain. Here we review findings from human neuroimaging studies in conjunction with data analysis methods that can directly link decisions and signals in the human brain on a trial-by-trial basis. This leads to a new view about the neural basis of human perceptual decision-making processes.

Decision variable
A quantity that is monotonically related to the relative likelihood of one alternative occurring versus another occurring. In perceptual decision-making tasks, the link between the sensory representation and the commitment to a choice is thought to involve the computation of a decision variable.

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Consider driving home from work in clear weather. Stopping at a traffic light, you see pedestrians waiting to cross the street. Effortlessly, you discern whether one of them is your spouse, your boss or a stranger, and connect the percept with the appropriate action, so you will either be waving frantically, greeting respectfully or taking another sip of coffee. During a rainstorm, however, the sensory input is noisier and you thus must look longer to gather more sensory data in order to make a decision about the person at the light and the appropriate behavioural response. This sort of decision-making process is crucial not only for such mundane situations as the one described above, but also for more biologically and socially important situations[1].

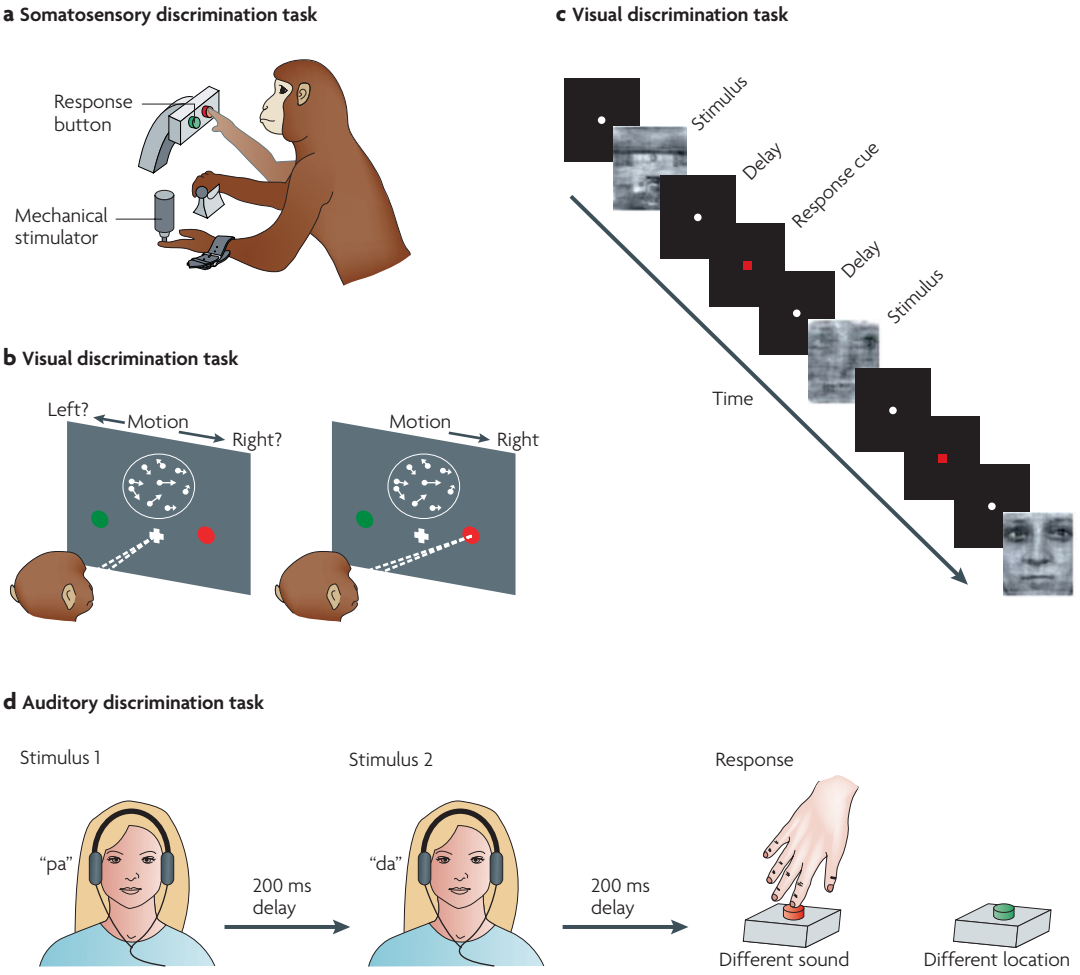
The process by which information that is gathered from sensory systems is combined and used to influence how we behave in the world is referred to as perceptual decision making. Typical experimental approaches that have been used to investigate the mechanisms of perceptual decision making are described in BOX 1. Recent advances in both neurophysiological studies in monkeys (for reviews, see REFS 1–5) and functional brain imaging methods have inspired studies of perceptual decision making in humans.

Perceptual decision making is influenced not only by the sensory information at hand, but also by factors such as attention, task difficulty, the prior probability of the occurrence of an event and the outcome of the decision[6,7]. Although traditional psychological theories conjecture that the decision-making process consists of components that act in a hierarchical manner, with serial progression from perception to action (for example, see REF. 8; however, see also REF. 9), more recent neuroscientific findings indicate that some of the components of this process happen in parallel. The neural architecture for perceptual decision making can be viewed as a system that consists of four distinct but interacting processing modules. The first accumulates and compares sensory evidence; the second detects perceptual uncertainty or difficulty and signals when more attentional resources are required to process a task accurately; the third represents decision variables and includes motor and premotor structures; and the fourth is involved in performance monitoring, which detects when errors occur and when decision strategies need to be adjusted to maximize performance.

A unique contribution of neuroimaging to the study of perceptual decision making is its ability to probe the interactions between these different brain systems, including sensory areas, and identify the role of higher-level decision-making structures. This is now possible because current neuroimaging techniques and data analysis methods have evolved to the point where we can directly link behavioural measures (that is, decisions) to signals in the human brain on a trial-by-trial basis.

To motivate the four-module conceptualization of perceptual decision making and the studies that underpin it, we begin this Review by providing a description of perceptual decision making, as gleaned from findings in monkey experiments that made use of single-unit recordings. Then we provide an overview of what is known about the neural systems that are involved

Box 1 | **Experimental approaches to perceptual decision making**



The general experimental approach to study perceptual decision making is to have study subjects (monkeys or humans) perform sensory discriminations, with the sensory input being more or less degraded. To study perceptual decision making in the somatosensory domain, several studies have used a vibrotactile frequency-discrimination task (for example, see REFS 4,15,43). In this task, subjects have to decide which of two sequentially presented flutter stimuli has a higher frequency of oscillation (see figure, part **a**). To study perceptual decision making in the visual domain, many studies have used a direction-of-motion discrimination task (for example, see REFS 5,17,61) in which subjects have to decide whether the net motion of a noisy field of dots is in one direction or the opposite direction (for example, leftward or rightward) and indicate their choice either with a quick eye movement to the target on the appropriate side[17] (see figure, part **b**) or with a button press[61]. Also in the visual domain, Heekeren *et al.* have used a face–house categorization task[46] in which participants had to decide whether an image presented on a screen was a face or a house and indicate their decision with a button press (see figure, part **c**). To investigate perceptual decision making in the auditory domain, Kaiser *et al.* used a two-alternative forced-choice task in which participants had to decide whether two syllables presented sequentially were the same or different with respect to their identity (for example, "pa" and "ba") or the same or different with respect to their perceived location (that is, left or right)[54] (see figure, part **d**). Part **a** of the figure modified, with permission, from REF. 4 © (2003) Macmillan Publishers Ltd. Part **b** of the figure modified, with permission, from REF. 75 © (2005) Macmillan Publishers Ltd. Part **c** of the figure modified, with permission, from REF. 46 © (2004) Macmillan Publishers Ltd.

Functional MRI
(fMRI). An imaging technique that measures the brain's haemodynamic response to changes in neural activity.

Electroencephalography
(EEG). A technique used to measure neural activity by monitoring electrical signals from the brain that reach the scalp. EEG has good temporal resolution but relatively poor spatial resolution.

Magnetoencephalography
(MEG). A method of measuring physiological activity across the cortex by detecting perturbations in the magnetic field that is generated by the electrical activity of neuronal populations.

in perceptual decision making in humans, including findings from functional MRI (fMRI) studies; studies that made simultaneous electroencephalogram (EEG) and fMRI recordings; single-trial analyses of EEG, magnetoencephalogram (MEG) and fMRI data; and spatiotemporal neuroimaging studies that used EEG and/or MEG. We end by describing possible future research directions.

Perceptual decision making in monkeys

A series of elegant single-unit recording studies has investigated decision making in the somatosensory and visual domains in monkeys. From these experiments, some important concepts of perceptual decision making have emerged that concern the representation and integration of sensory evidence in different brain structures, the importance of motor structures in decision making,

and the role of the posterior medial frontal cortex in performance and error monitoring and in signalling the need for behavioural adjustment.

Representation of sensory evidence. Single-unit recording studies in monkeys have provided evidence of a close link between behaviour and the activity of neuronal populations in sensory regions (such as the primary somatosensory cortex[10] and visual area MT[11,12]). Further, electrical microstimulation studies have indicated that this link is causal, in both the somatosensory[10] and the visual domains[13,14]. Beyond demonstrating that representations of evidence in sensory regions are used to make perceptual decisions, these studies have produced detailed knowledge about the nature of these representations and how evidence can be separated from the decision variable.

For instance, Romo and colleagues recorded from single neurons in the primary somatosensory cortex (SI) while monkeys performed a vibrotactile task in which they had to decide which of two sequentially presented flutter stimuli had a higher frequency of oscillation (BOX 1). The results showed that the monkeys' choices could be predicted from trial-to-trial fluctuations in the firing rates of SI neurons[10]. Also, the average firing rate of the SI neurons increased monotonically with increases in the stimulus oscillation frequency. Furthermore, when the vibrotactile stimuli were replaced with direct electrical microstimulation of SI, the monkeys' behavioural patterns were very similar to their patterns under normal conditions[15,16].

In a similar vein, Newsome, Shadlen and colleagues recorded from neurons involved in visual-motion processing in area MT while monkeys performed a direction-of-motion discrimination task[17] (BOX 1). Here the monkeys had to decide whether a noisy field of dots was moving in one direction or the opposite direction (for example, upward or downward) and indicate their choice with a quick eye movement to a target on the respective side. The activity of relatively small numbers of directionally selective neurons closely correlated with the monkeys' behaviour[11,12]. Subsequent studies showed that electrical microstimulation of directionally selective neurons in area MT caused a monkey to choose the neurons' preferred direction more often: for example, when neurons tuned to rightward motion were stimulated the monkey was more likely to make an eye movement to the target on the right[14]. Also, microstimulation of these neurons quickened the decision in favour of the preferred direction and slowed the decision in favour of the opposite direction[14]. Thus, in both the visual and the somatosensory domains, microstimulation studies have provided proof of a tight, causal link between the representation of sensory evidence in sensory regions and perceptual decisions.

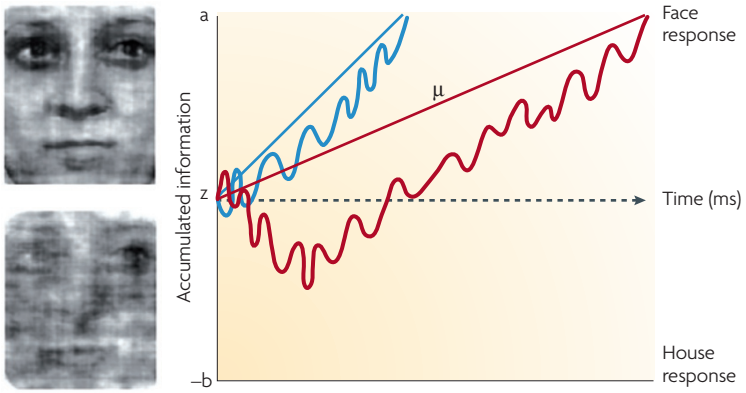
Do these findings extend to higher-level categorical decisions? In monkeys performing a 'face'/'non-face' categorization task, stimulation of face-selective neurons in the temporal cortex biased the monkeys' decisions in favour of the face category[18]. These data not only support a causal relationship between the activity of face-selective neurons and face perception, but also indicate that, even for higher-level categories, decisions are based on the sensory evidence that is represented in lower-level sensory regions.

Integration of sensory evidence and formation of the decision variable. Another important concept that has emerged from neurophysiological studies in monkeys is that perceptual decisions are made, at least in part, by integrating the sensory evidence that is represented by sensory neurons[4,19]. These studies have shown that neuronal activity in areas involved in decision making gradually increases and then remains elevated until a response is made. Importantly, the rate of increase in neural activity is slower during difficult trials than during easier trials. During the vibrotactile frequency-discrimination task described above, cells in regions of the monkey brain that are downstream from the primary and secondary sensory areas, such as the prefrontal, medial premotor and ventral premotor cortices, form a decision by computing the difference between the activities of populations of sensory neurons in the secondary somatosensory cortex (SII) that prefer high or low frequencies[20–23]. Similarly, during the direction-of-motion visual discrimination task, cells in regions downstream from area MT, such as the lateral intraparietal area (LIP), the frontal eye field (FEF) and the dorsolateral prefrontal cortex (DLPFC), form a decision by computing the difference between the activities of populations of neurons in area MT that code for opposite directions of motion[24]. Thus, in both sensory systems a simple subtraction operation seems to explain the behavioural effect; this integration of noisy sensory information over time can be modelled as a diffusion-to-boundary process[25–27] (BOX 2).

Another fundamental process in the making of a perceptual decision is the contribution of memory. Our past sensory experiences — which are stored in memory and brought online in working memory — are combined with current sensory inputs to inform our perceptual decisions. In monkeys, this process has been extensively described by Romo and colleagues for decisions made in the vibrotactile discrimination task (see above), which allowed the authors to distinguish between the comparison process (the combination of the memory trace and the current sensory stimulus) and the motor response[22,28–31].

The role of the motor system. It is noteworthy that regions in the monkey brain that have been implicated in both representing decision variables and performing the comparator operation are the same areas that select, plan and execute motor responses. In other words, the boundaries between sensory processing, decision-related activity and motor-related processing are not as distinct as is often thought. For example, when monkeys must decide in which direction a random-dot-motion stimulus is moving and indicate their decision with an eye movement, decision-related as well as saccade-related activity can be found in the FEF[32]. Similarly, when monkeys perform the vibrotactile discrimination task, activity in the medial and ventral premotor cortices reflects the temporal evolution of the decision-making process

Box 2 | **Stochastic diffusion processes as a model for the neurobiology of decision making?**



Decision-making research has led to the development of mathematical models of the assumed underlying cognitive processes. Diffusion models are particularly successful in explaining response-time and accuracy data in two-choice reaction-time tasks. These models assume that decisions are formed by continuously accumulating sensory information until one of the two response criteria (a or –b) is reached[25,27] (see figure). Once a boundary has been reached, the decision process is concluded and a response is elicited. Moment-by-moment fluctuations in the sample path reflect noise in the decision process. The drift rate (μ) is related to the efficacy of information processing and depends on the strength of the sensory signal and on the accumulation rate (that is, the increase in the decision variable that quantifies how much evidence is accumulated per time interval). Clear images of faces contain more sensory evidence than degraded images, and therefore the drift rate is greater for clear images (blue trace in the figure) than for degraded images (red trace).

Recent studies have also modelled neurophysiological data as a diffusion process[19,89,90]: a dual-diffusion model provides a quantitative account of both the behaviour in simple perceptual decision making and the patterns of activity in competing neuron populations[89,90]. In these studies, monkeys performed a brightness-discrimination task and made saccades to one of two peripheral targets. Task difficulty was manipulated by varying the ratio of black to white pixels. A diffusion model was fitted to the behavioural data. Based on the hypothesis that the neuronal firing rate is linearly related to the accumulated evidence, simulated paths from the model were compared with neural activity. Similar to the behavioural data, the firing-rate data showed delayed availability of discriminative information for fast, intermediate and slow decisions when activity was aligned on the stimulus. By contrast, the firing rate showed very small differences in discriminative information when activity was aligned on the saccade.

The first study to link human brain signals with parameters of the diffusion model was that of Philiastides *et al.*[62]. These authors estimated diffusion rates for different noise levels on the basis of behavioural data from a face–car categorization task. Notably, these diffusion rates were highly correlated with the strength of the difficulty-related component in their single-trial electroencephalogram (EEG) analysis. These findings indicate that the late EEG component represents the post-sensory evidence that is fed into the diffusion process that ultimately determines the decision. Face–house images in part **b** of the figure reproduced, with permission, from REF. 46 © (2004) Macmillan Publishers Ltd.

that leads to action selection[22,23]. Other neurophysiological studies have revealed that decision variables are represented in the superior colliculus, a midbrain region that is involved in the generation of saccadic eye movements[33,34]. These studies thus support theoretical and modelling studies[35,36], which suggest that the motor system should be considered an integral component of decision-making processes (see also REFS 9,32,37).

It should be noted, however, that in most of the monkey studies discussed in this Review, the monkeys were trained to indicate their perceptual decision with a particular action. In other words, the monkeys could treat the perceptual decision as a problem of movement selection. Seen in this light, it is not surprising that motor structures seem to have a role in decision formation. It is not yet clear how these structures contribute to decisions that are not linked to particular actions[32].

Performance and error monitoring. Decisions have consequences, and for decision making to be efficient and flexible we have to monitor the outcomes of our decisions. When deviations from action goals or errors are detected, behaviour needs to be adjusted. Neurophysiological studies in monkeys have implicated the posterior medial frontal cortex, especially the supplementary eye field and the rostral cingulate motor area, in performance monitoring and signalling the need for adjustments of behaviour[6,38–40]. This evidence stems mainly from experiments on visual saccadic decision making (for reviews, see REFS 3,41). How performance-related and error-related signals generated in the monkey posterior medial frontal cortex influence sensory representations during perceptual decision making is not yet clear.

Perceptual decision making in humans

Is there evidence that the principles that have emerged from the neurophysiological work in monkeys also apply to the human brain? If so, then these basic neural mechanisms have been conserved during brain evolution. Here we review findings from recent studies using neuroimaging methods that allow direct trial-by-trial links to be made between decisions and signals in the human brain. These methods have recently been used to investigate perceptual decision making in the domains of somatosensation, vision and audition (for a review on other forms of

Transcranial magnetic stimulation
(TMS). A technique that delivers brief, strong electrical pulses through a coil placed on the scalp. These create a local magnetic field that in turn induces a current in the surface of the cortex, temporarily disrupting local neural activity.

Discrimination thresholds
In discrimination tasks, this is a measure of the smallest detectable change in a stimulus or the smallest difference between two stimuli that can reliably be detected. It is often defined as the difference for which the correct discrimination is made 75% (or sometimes 82%) of the time.

perceptual decision making, such as olfaction, see REF. 42). Similar to the studies in monkeys, the representations of sensory evidence can now also be measured and manipulated in the human brain and can be distinguished from representations of decision variables.

Representation of somatosensory evidence. Inspired by the work of Romo and colleagues, recent fMRI studies have used vibrotactile frequency-discrimination tasks (BOX 1) to study somatosensory decision making in the human brain. Consistent with neurophysiological data in monkeys, the primary somatosensory cortex exhibited increased activity during the encoding phase (processing of the first stimulus) of tactile decision making[43]. Similarly, using a somatosensory discrimination task in which participants had to compare the frequencies of two successive electrical tactile stimuli, Pleger *et al.* found that tactile stimuli *per se* evoked activity in, among other regions, the somatosensory cortex[44].

The most direct support for the concept of representation of sensory evidence in the somatosensory domain comes from a transcranial magnetic stimulation (TMS) study which showed that stimulation of the primary somatosensory cortex lowered two-point discrimination thresholds of the right index finger and enlarged the finger's neural representation, as assessed with fMRI[45]. Notably, this enlargement correlated with the individual TMS-induced perceptual improvement. Taken together, the results of the studies described above support the idea that, similar to the findings in monkeys, the human primary somatosensory cortex represents sensory evidence during tactile decision making.

Representation of visual evidence. Heekeren *et al.* used fMRI and a face–house categorization task (BOX 1; FIG. 1) to investigate perceptual decision making[46]. Previous neuroimaging studies had identified regions in the human ventral temporal cortex that are activated more by faces than by houses and vice versa: the fusiform face area (FFA) and the parahippocampal place area, respectively[47–51]. The face–house task can thus be used to identify these two brain regions and test whether they represent the sensory evidence that is relevant to the task. There was a greater response in face-selective regions to clear images of faces ('easy' trials) than to degraded images of faces ('difficult' trials), whereas degraded images of houses evoked a greater response than clear pictures of houses in these face-selective areas. The opposite pattern was found in house-selective regions (FIG. 1). These results support the concept that face- and house-selective regions in the brain represent the sensory evidence for the two respective categories.

Recent studies have also taken advantage of new approaches to the analysis of EEG data and have identified sub-components of the perceptual decision-making process that would be indistinguishable in fMRI studies, which use the relatively sluggish blood-oxygenation-level-dependent (BOLD) signal. One recent EEG study

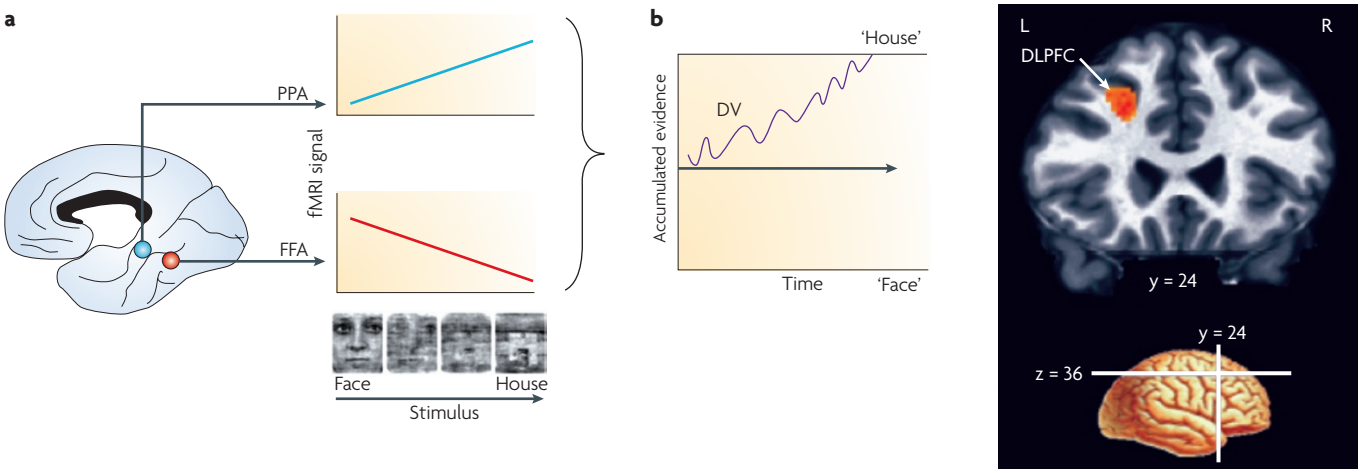


Figure 1 | **Representation of sensory evidence in lower-level sensory regions and perceptual decision making in the posterior DLPFC. a** | The representation of sensory evidence in category-selective brain regions. When participants had to decide whether an image was a face or a house, there was a greater response in face-selective regions (the fusiform face area (FFA)) (red line) to clear images of faces than to degraded images of faces. In addition, house-selective brain regions (the parahippocampal place area (PPA)) showed a greater response to clear images of houses than to degraded images of houses (blue line). **b** | The comparison of sensory evidence in higher-level brain regions. Neurophysiological data[5] as well as modelling studies (BOX 2) suggest that a decision variable is computed by comparing the output of pools of selectively tuned lower-level sensory neurons. In this example the output of category-specific brain regions (the FFA and the PPA) is integrated over time. The decision variable (DV) drifts between the two boundaries and once one of them is crossed the corresponding decision is made (here, 'house'). Findings from neurophysiological and neuroimaging studies indicate that the decision variable is computed in downstream cortical regions (that is, regions further along the processing chain), such as the lateral intraparietal area and the dorsolateral prefrontal cortex (DLPFC). Brain image in part **a** reproduced, with permission, from REF. 104 © (2006) Macmillan Publishers Ltd. Face–house images in part **a** reproduced, with permission, from REF. 46 © (2004) Macmillan Publishers Ltd. fMRI image in part **b** reproduced, with permission, from REF. 46 © (2004) Macmillan Publishers Ltd.

Box 3 | **Linking decision-making behaviour and neural processes**

A fundamental goal for cognitive neuroscience is to understand how mental (cognitive) and neuronal processes map onto each other[91]. Progress in this regard was pioneered in monkeys by Newsome and colleagues (for example, see REF. 17). Some of the neuroimaging studies reviewed in this paper used similar approaches in humans, whereas others drew on machine-learning algorithms to show that neuroimaging signatures can be used to predict choice behaviour on a trial-by-trial basis. One study used single-trial analysis of electroencephalogram (EEG) data that were acquired during a face–car discrimination task. A component occurring approximately 300 ms after stimulus onset was a notably good match to the psychometric function that described the individual's performance in this task[62]. Similarly, single-trial analysis of functional MRI (fMRI) data based on signal-detection-theory methods allow one to quantify the link between fMRI signals and behavioural choice by determining choice probabilities. Notably, in one study fMRI signals could reliably predict behavioural choice in a quantitative fashion at levels that were comparable with neuronal data[87]. Magnetoencephalography (MEG) allows one to link oscillatory brain activity and behaviour in single trials. One study showed that MEG responses in the beta frequency band predicted correct choices[92]. Specifically, single-trial beta-band activity in prefrontal and parietal cortices tended to be higher before 'correct rejects' than before 'false alarms' in the physical absence of the target. Thus, this mass activity does not predict the decision (yes or no) *per se* — rather, it reflects the accuracy of the decision process[92]. The simultaneous acquisition of EEG and fMRI data allows one to characterize the temporal dynamics of information processing on a single-trial level in spatially well-defined neural networks. This was shown in a study in which single-trial error-related negativity of the EEG was systematically related to behaviour[68]. Moreover, this trial-by-trial EEG measure of performance monitoring predicted the fMRI activity in the rostral cingulate zone[68,93].

used single-trial analysis (BOX 3) to identify the cortical correlates of decision making during a face–car discrimination task that is similar to the face–house task described above. Two EEG components maximally discriminated between face and car trials. The earlier of these components is consistent with the well-known N170, which is commonly associated with face perception, and therefore seems to represent the sensory evidence[52]. Taken together, these results from the visual domain also provide strong support for the concept that populations of lower-level sensory neurons (here, object-category-sensitive neurons) represent the sensory evidence that is used in the decision-making process.

Representation of auditory evidence. In the auditory domain, no study has investigated perceptual decision making in monkeys and relatively few studies have investigated perceptual decision-making processes in humans. In one recent fMRI experiment, human participants identified speech sounds that were masked by varying levels of noise[53]. The fMRI signal in a cortical region that lies close to the primary auditory cortex positively correlated with the speech-to-noise ratio. Thus, in this case as well, the lower-level sensory region seems to represent the sensory evidence that is relevant for the decision.

A recent MEG study by Kaiser *et al.* investigated the temporal dynamics of auditory decision making[54]. This study used a two-alternative forced-choice task (BOX 1) in which individuals had to decide whether two syllables presented sequentially were the same or different with respect to their identity or the same or different with respect to their perceived location. Activity in the gamma frequency band increased over the left inferior frontal cortex in response to changes in acoustic pattern (that is, identity) and over the right parietal cortex in response to spatial (that is, location) changes. Importantly, relative increases in gamma-band activity over these areas were more pronounced for easy than for difficult decisions — that is, when the two syllables differed clearly from each other in their acoustic patterns or in their perceived positions. This response pattern supports the selectivity of these regions for the perceptual alternatives that were relevant for a given task (pattern changes versus location changes) and were thus related to sensory evidence. Because the fMRI signal and the gamma-band activity correlate closely[55], this finding is analogous to what was found in the fMRI study that used degraded images of faces and houses[46]: just as there was a greater increase in gamma-band activity during the easy relative to the difficult decisions regarding acoustic stimuli, the fMRI study found a greater increase in the BOLD signal in the easy relative to the difficult decisions regarding visual categories.

Next we review recent human neuroimaging studies that provide support for the notion that the comparison of accumulated sensory evidence is a mechanism for perceptual decision making.

Integration of sensory evidence and formation of the decision variable. The single-unit recording studies in monkeys have shown that neuronal activity in areas that are involved in decision making gradually increases and then remains elevated until a response is made. Importantly, the rate of increase in neural activity is slower during more difficult trials than during easier trials. Furthermore, these studies have shown that downstream cortical regions (that is, regions further along the processing chain), such as the LIP and the DLPFC, can form a decision by comparing the output of pools of selectively tuned sensory neurons.

A recent fMRI study in humans showed how the BOLD signal can be used to examine the process of sensory-evidence accumulation. Pictures were revealed gradually over the course of 12–20 seconds and participants signalled the time of their recognition of a picture with a button press. In several occipital regions, the fMRI signal increased primarily as stimulus information increased, suggesting that these regions have a role in lower-level sensory processing. In addition, there was a gradual build-up of the fMRI signal, peaking at a time that corresponded with the time of recognition, in inferior temporal, frontal and parietal regions, which suggests that these regions accumulate sensory evidence.

Heekeren *et al.* directly tested whether a comparison operation is also at work in the human brain, using the face–house discrimination task described above[46]. Specifically, based on the neurophysiological data in monkeys, Heekeren *et al.* proposed that higher-level decision areas should fulfil two criteria. First, they should show the greatest BOLD activity on trials in which the weight of evidence for a given perceptual category is greatest — that is, there should be a higher fMRI signal during decisions about clear images of faces and houses

Beta frequency band
Neural activity in the frequency range of 12–25Hz.

Gamma frequency band
Neural activity in the frequency range of 30–80Hz.

Box 4 | **Prefrontal contributions to perceptual decision making**

What is the contribution of the prefrontal cortex to perceptual decision making, besides the integration of sensory evidence (described in the main text)? In one positron-emission tomography (PET) study, the left posterior dorsolateral prefrontal cortex (DLPFC) was activated when participants performed a conditional visual task, such as 'If you see a red cue, point to the pattern with stripes, but if you see a blue cue, point to the pattern with red circles' (REF. 94). In addition, Petrides *et al.* carried out a series of experiments involving monkeys and humans with lesions in the posterior DLPFC and reported impairments in conditional discrimination tasks in both species[95].

Previous functional MRI (fMRI) and PET studies have suggested a role for the posterior DLPFC in selecting a response on the basis of task contingencies and sensorimotor context[96], as opposed to a role that is directly related to the preparation of a specific motor response. In an fMRI study that used a somatosensory discrimination task in which participants had to compare the frequencies of two successive electrical tactile stimuli[44], BOLD activity changes in a part of the left DLPFC were proportional to the relative stimulation difference, but only when the participants made the correct judgement. This suggests that activity in the left DLPFC encodes stimulus representations of tactile decisions in humans.

An additional role for the prefrontal cortex in perceptual decision making has been proposed on the basis of a recent fMRI study. Summerfield *et al.* suggested that the brain resolves perceptual ambiguity by using 'predictive coding'; that is, it anticipates the sensory environment by generating a template against which incoming sensory evidence is matched. Specifically, they found a neural representation of predicted perception in the medial frontal cortex during a face-detection task[97]. Moreover, perceptual decisions about faces were associated with an increase in top-down connectivity from the frontal cortex to face-sensitive visual areas, consistent with the matching of predicted and observed evidence for the presence of faces.

(easy trials) than during decisions about degraded images of these stimuli (hard trials). Second, these areas' BOLD signals should correlate with the difference between the signals in brain areas that are selectively tuned to the different categories involved — in this case, in face- and house-responsive regions.

Only one brain region fulfilled both criteria[46]: the posterior portion of the left DLPFC uniquely responded more to clear relative to degraded stimuli, and the activity of this region correlated with the difference between the output signals of face- and house-responsive regions (FIG. 1). Thus, when people make categorical decisions about face and house stimuli, this brain region seems to integrate the outputs from lower-level sensory regions and use a subtraction operation to compute perceptual decisions. Notably, activity in the left DLPFC also predicted behavioural performance in the categorization task[46]. Hence, even for complex object categories, the comparison of the outputs of different pools of selectively tuned neurons seems to be a general mechanism by which the human brain computes perceptual decisions.

Support for this interpretation comes from recent EEG and MEG studies. A single-trial analysis of EEG data acquired during a face–car categorization task revealed a discriminating component that occurred approximately 300 ms after stimulus onset. This component was a good match to the psychometric curve that described participants' performance in this task. As the evidence for faces versus cars in the stimuli decreased, the onset of this component systematically shifted later in time. Additionally, a choice-probability analysis indicated a strong correlation between this component and the participants' behavioural judgements[52].

Psychometric curve
A plot of the percentage of correct behavioural responses as a function of changes in the properties of the test stimulus.

The MEG study by Kaiser *et al.* described above revealed a similar component during auditory decision making[54]. In this study, gamma-band activity over the DLPFC was more pronounced at approximately 280–430 ms for easy relative to difficult decisions, regardless of the type of acoustic change (identity or location). Furthermore, changes in gamma-band activity over the DLPFC correlated with the activity difference between posterior parietal and left inferior frontal sensors. These results support the idea that the DLPFC is part of a decision-related network that integrates information from sensory areas that represent the sensory evidence. Other studies have also identified contributions of the prefrontal cortex to perceptual decision making; these are discussed in BOX 4.

Uncertainty, attention and task difficulty. The human neuroimaging studies we have reviewed so far used single-unit-recording findings as a constraint to predict decision-related changes in fMRI signals[56]. Specifically, neuronal activity in areas that are involved in decision making gradually increases with increasing sensory evidence and then remains elevated until a response is made, with a greater rate of increase during easier trials than during more difficult trials. This leads to the prediction of an enhanced fMRI response during easy relative to hard trials in decision-making areas.

A different approach to the identification of regions that are involved in perceptual decision making has been taken by investigators who characterized decision-making regions on the basis of correlations between the BOLD signal and accuracy or response time[53]. This approach is grounded on Donders' findings that the time that an individual needs to deliberate before responding to a stimulus increases with task difficulty, and this time can thus be used to differentiate sensory and decision processes[57]. Therefore, in contrast to the neurophysiological work and neuroimaging studies reviewed above, these investigators have reasoned that BOLD activity in decision-related regions should be correlated with response time; specifically, it should show a greater response during difficult trials than during easy trials.

Binder *et al.* manipulated difficulty so as to affect both accuracy and response time (RT) in a phonetic discrimination task[53]. As task difficulty decreased, accuracy increased sigmoidally from chance performance in difficult trials to nearly perfect performance in easy trials. By contrast, RT was biphasic, with shorter RTs for easy items and hard items and longer RTs for items of intermediate difficulty. These authors found that BOLD activity in regions that lie adjacent to the primary auditory cortex correlated with accuracy, whereas BOLD activity in the anterior insula and the inferior frontal gyrus positively correlated with RT. These data were interpreted as supporting a sensory processing role (namely auditory identification) for the areas in which the BOLD signal correlated with accuracy and a decision-related role for areas in which the BOLD signal correlated with RT.

A related goal of some investigators has been to eliminate differences between trials in terms of stimulus evidence and thereby reduce the overall influence of either attention or task difficulty on the fluctuations in BOLD signal that are thought to characterize decision-making regions. For instance, Thielscher and Pessoa[58] asked study participants to decide whether a given face expressed fear or disgust. They focused their analysis on trials in which no facial expression was visible in the stimuli (that is, neutral faces) and therefore there was no trial-to-trial difference in the amount of sensory evidence[58]. Similar to Binder *et al.*[53], they postulated that decision-related regions should show a positive correlation between RT and fMRI signal amplitude. They too found that BOLD activity was positively correlated with RT in the inferior frontal gyrus/anterior insula, as well as in the anterior cingulate cortex.

A similar strategy was adopted by Grinband *et al.*[59], who manipulated perceptual uncertainty without altering the actual stimulus evidence. They asked individuals to classify a line segment as being either long or short on the basis of a learned, abstract categorical boundary. They identified regions in a frontostriatal–thalamic network — including a large region of the medial frontal gyrus — in which activity increased with perceptual uncertainty that was independent of stimulus evidence, and suggested that these regions might be involved in comparing a stimulus with a categorical boundary.

All of the studies cited above[53,58,59] (as well as REF. 60) have associated the medial frontal gyrus and the inferior frontal gyrus/anterior insula with perceptual decision making, on the basis of the finding that in these regions the BOLD response was greater during difficult than during easy trials. We have found a similar response pattern in these regions[46,61]. However, we have suggested that their role in perceptual decision making is to bring to bear additional attentional resources in order to maintain accuracy in decision making when the task becomes more difficult. Thus, we agree that these regions might participate in decision making, but assign to these regions a different role.

How might these different conceptualizations be resolved? Recent studies by Philiastides and colleagues might provide a resolution. As described above, using a face–car discrimination task these investigators identified two EEG components that had larger amplitudes on easy trials than on difficult trials — that is, these components reflected the accuracy of a perceptual decision[62]. A third component in between the two accuracy components correlated with task difficulty. This third component might thus be involved in signalling task difficulty and might have a crucial role in the recruitment and allocation of attentional resources to compute a difficult decision. A recent fMRI study that was based on these EEG results showed that the source for this difficulty-related component might include the anterior cingulate and anterior insular cortices as well as the bilateral DLPFC[63]. Therefore, taken together these results suggest how the system for the accumulation and integration of evidence and the system that is related to task difficulty and uncertainty might contribute jointly to the perceptual decision-making process.

The role of the motor system. Neurophysiological studies in monkeys, as well as modelling studies, suggest that the brain regions that are involved in selecting and planning a certain action have an important role in forming decisions that lead to that action.

To test whether this result also holds for the human brain, Heekeren *et al.*[64] asked human observers to make direction-of-motion judgements about dynamic random-dot-motion stimuli and indicate their judgements with an eye movement-to one of two visual targets. In each individual, the authors localized regions that are part of the oculomotor network, namely the FEF and an eye-movement-related region in the intraparietal sulcus (IPS) that presumably corresponds to the LIP of monkeys[65]. Importantly, during the period of decision formation (between the onset of visual motion and the cue to respond), the percent change in the BOLD signal in both the FEF and the IPS was highly correlated with the strength of the motion signal in the stimuli[64]. These data are thus consistent with the single-unit studies in monkeys that reported that the FEF and the LIP participate in the process of forming a perceptual decision.

The results are also similar to those from a study of oculomotor decision making by Heinen *et al.*[66], who had participants play 'ocular baseball' while undergoing fMRI. In this game, the subjects had to decide whether or not the trajectory of a dot moving across a computer screen was likely to cross into a visible 'strike' zone. If the participants decided that the dot was likely to enter the strike zone, they had to make an eye movement; in the other case, their eyes had to remain fixed on a point in the centre of the screen. When the results of a task with identical motor behaviour were compared to the 'baseball' trials, decision-related signals were found in the superior parietal lobule, the FEF and the ventrolateral prefrontal cortex. In line with the monkey data, these results suggest that when a decision is associated with a specific movement, the formation of the decision and the preparation of the behavioural response have a common neural substrate. Put more generally, the findings support the view that the human motor system also has an important role in perceptual decision making.

More recently, Heekeren *et al.* investigated whether decisions might be transformed into motor actions in the human brain independently of motor planning and execution — that is, at an abstract level[61]. Individuals performed the direction-of-motion discrimination task (BOX 1) and responded with either button presses or saccadic eye movements. Areas that represent decision variables at a more abstract level should show a greater response to high coherence (easy) relative to low coherence (difficult) trials, independently of the motor system that is used to express the decision. Heekeren *et al.* found four such areas: the left posterior DLPFC, the left posterior cingulate cortex, the left IPS and the left fusiform/parahippocampal gyrus. Most importantly, the increase in BOLD activity in these regions was

independent of the motor system that the participants used to express their decision. The results from this fMRI study are in line with the finding by Kim and Shadlen that, in monkeys, neural activity increases proportionally with the strength of the motion signal in the stimulus[24]. However, the findings in humans suggest that the posterior DLPFC is an important component of a network that not only accumulates sensory evidence to compute a decision but also translates this evidence into an action independently of response modality.

Notably, to date neurophysiological studies in monkeys have not found neurons with an activity that reflects decisions independently of response modality. In fact, one could conclude from the neurophysiological studies in monkeys that "to see and decide is, in effect, to plan a motor-response" (REF. 67). By contrast, in humans, Heekeren *et al.* found regions of the cortex that responded independently of the motor effectors used[61]. Based on these findings, one could speculate that humans might have evolved a more abstract decision-making network that allows a more flexible link between decision and action.

Performance and error monitoring. Neuroimaging studies have corroborated neurophysiological findings in monkeys by showing that the posterior medial prefrontal cortex (also referred to as the anterior cingulate cortex) has an important role in performance monitoring, error monitoring and signalling the need for adjustments of behaviour[6,68] (however, see REF. 69). An intriguing possibility is that these monitoring systems might selectively adjust the sensitivity in sensory brain regions rather than change the decision criteria. Evidence for this comes from a recent fMRI study which showed that monitoring mechanisms enhance performance by transiently amplifying cortical responses to task-relevant information. In this study, Egner and Hirsch monitored fMRI activity in the FFA while participants performed a task in which face information was sometimes relevant and sometimes irrelevant[70]. Brain activity during trials that followed incongruent trials (in which the face information was a possible confound with the non-face information) was compared with activity during trials that followed congruent trials. Egner and Hirsch found that the BOLD response in the FFA was significantly increased by task relevance. The study also showed that amplification of FFA activity was mediated by the DLPFC, as the level of interaction between the DLPFC and the FFA was greater during the high-FFA-activity trials that immediately followed incongruent trials. Thus, this study showed how the performance-monitoring system and the system that represents sensory evidence interact during perceptual decision making.

Relation between neurophysiological monkey data and human neuroimaging data. Despite the differences in the techniques that are used to assess brain activity, the extent to which the hypotheses that were based on measurements of monkey physiology have been consistent with neuroimaging observations in humans is quite remarkable. For example, single-unit studies in monkeys measure the rate of spiking activity in individual neurons with exquisite spatial and temporal resolution but over a very small field of view. By contrast, fMRI provides a dynamic map of haemodynamic signals over the entire brain. The fMRI BOLD signal is primarily driven by local cortical inputs and local processing (for example, inhibitory and excitatory postsynaptic potentials and Ca^{2+} currents) and thus might reflect sub-threshold modulation of neural activity in a restricted region rather than the local spiking output (for example, action potentials)[71]. Given these underlying differences between the measurements, it was not a given that the same principles would emerge from the monkey and the human work.

Turning to non-invasive measures of brain electrophysiology in humans, the scalp EEG reflects the extracellular currents in a local population of neurons (comprising a few square millimetres or centimetres of neural tissue) that are originally caused by transmembrane ion flows following synaptic activation. MEG measures tiny changes in the scalp magnetic field and is most sensitive to intracellular current flow in the apical dendrites of pyramidal neurons. Whereas intracellular and extracellular currents are tightly coupled and MEG and EEG are therefore closely related measures of brain activity (MEG is traditionally considered to be spatially the more accurate), there is one important difference: EEG is sensitive to both radially and tangentially oriented dipolar sources (relative to the scalp surface) whereas MEG is mostly sensitive to only the tangentially oriented component of neural currents[72]. Although both MEG and EEG provide high temporal resolution, reconstruction of the neural currents (source localization) that produce a given signal cannot be done analytically and requires the assumption of additional constraints to obtain a unique solution; thus, it continues to be a challenge for researchers who use EEG or MEG.

To summarize, all of these different methods are complementary to each other. A promising strategy for research will be to combine them and use identical perceptual decision-making tasks (for example, visual-motion discrimination or flutter discrimination) in both primates and humans. In primates, single-unit physiology and microstimulation could be recorded simultaneously or in parallel with fMRI[73,74]; in humans, non-invasive fMRI and EEG could be combined with MEG (for example, see REF. 63).

Functional architecture

The results of human neuroimaging studies allow one to sketch a neurobiological model of human perceptual decision making (FIG. 2). First, the same principles that were identified in single-unit recording studies in monkeys seem to hold for the human brain, namely representation of sensory evidence in lower-level sensory regions, accumulation of sensory evidence, and comparison of sensory evidence in higher-level regions. Yet, the human neuroimaging data can add a systems-level viewpoint regarding interactions among the systems that underlie these processes.

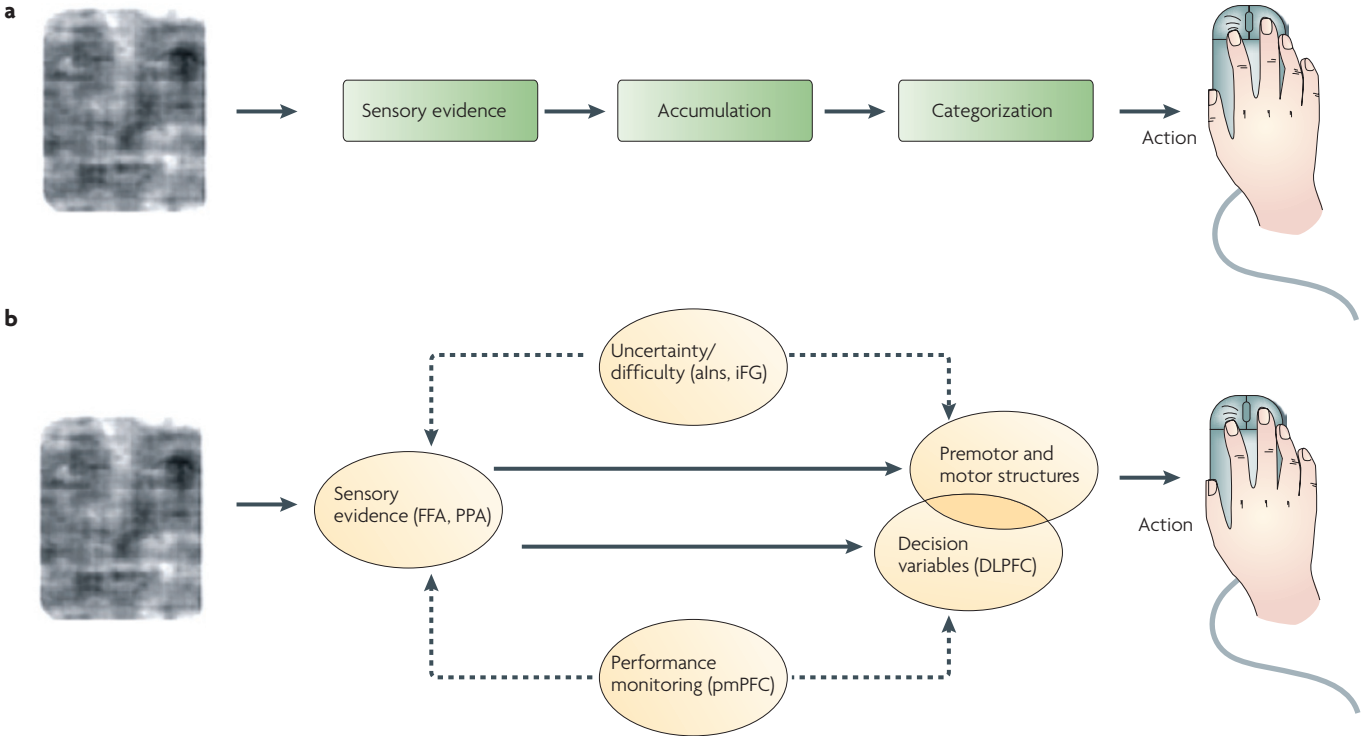


Figure 2 | **A neural system for human perceptual decision making. a** | Some models conjecture that perceptual decision making consists of components that act in a hierarchical manner, with serial progression from perception to action[8,105]. **b** | Based on the human neuroimaging studies reviewed here, we propose a different model for perceptual decision making that consists of at least four complementary, and in parts overlapping, systems. As with the hierarchical model depicted in part **a**, our model contains a system that represents sensory evidence (for example, one comprised of the fusiform face area (FFA) and the parahippocampal place area (PPA) for a face–house discrimination task) and a system that accumulates and compares sensory evidence to compute a decision variable (for example, the dorsolateral prefrontal cortex (DLPFC) is part of this system). In addition, our model conjectures that the system that represents decision variables extends to motor and premotor structures. Furthermore, there is a system that detects perceptual uncertainty or difficulty (for example, the anterior insula (aIns) and the inferior frontal gyrus (iFG)) and that signals when more attentional resources (that is, brain areas that are part of the attentional network, such as the frontal eye field) are required to process a task accurately. Finally, the system that is involved in performance monitoring (the posterior medial prefrontal cortex (pmPFC)) detects when errors occur and when decision strategies therefore need to be adjusted to maximize performance. Importantly, these systems do not act in a strictly hierarchical manner with a serial progression from perception to action. Rather, they interact in a heterarchical manner, with some of the processes happening in parallel. For example, premotor and motor regions represent sensory evidence during stimulus processing. Face image in part **b** reproduced, with permission, from REF. 46 © (2004) Macmillan Publishers Ltd.

In this Review, we propose an architecture for perceptual decision making that consists of at least four complementary, and in parts overlapping, systems. First, a system that accumulates and compares sensory evidence to compute a decision variable; second, a system that detects perceptual uncertainty or difficulty and signals when more attentional resources are required to process a task accurately; third, a system representing decision variables that extends to motor and premotor structures; and fourth, a system involved in performance monitoring that detects when errors occur and decision strategies need to be adjusted to maximize performance.

Certainly, some of these processes happen serially; for example, to determine if an error has occurred you have to have made a decision. However, these systems do not act in a strictly hierarchical manner with a serial progression from perception to action. Rather, they interact in a heterarchical manner in which at least some of the processes happen in parallel. For example, oculomotor regions represent sensory evidence during stimulus processing.

Heterarchy
A term used in social and information sciences that describes networks of elements in which each element has the same 'horizontal' position of power and authority and has a theoretically equal role. It is used here as an antonym to hierarchy.

Implications and future directions

The model sketched above might serve as a framework into which other important aspects of decision making could be incorporated.

We are beginning to understand the sub-processes that are involved in perceptual decision making; it will be important for future research to better characterize these components in both the spatial and the temporal domains. Furthermore, other factors are known to influence decision-making processes, and it will be important to specify on which neural mechanisms and systems these factors rely.

For example, the rewards that are associated with different options are an important factor in decision

Box 5 | **When perceptual decision making goes wrong**

Mistaking a face for a house

When visual information is limited — for example, at night or in a dark room — even healthy individuals sometimes report 'illusory percepts' (incorrect percepts with afferent sensory signals). A recent study by Summerfield *et al.* suggests that these so-called misperceptions might occur when higher-order visual regions incorrectly interpret weak sensory evidence arriving through feed-forward pathways from early visual regions[98]. The phenomenon of misperceiving one object as another occurs in several neuropsychiatric disorders, such as in patients with damage to posterior parts of the brain or patients with schizophrenia[99–101].

Seeing a face that is not there

Hallucinations (percepts that occur without sensory signals) might be due to a similar mechanism. It has been suggested that hallucinatory experiences in patients are the result of a mismatch between bottom-up (the representation of sensory evidence) and top-down (the integration of sensory evidence) processes[102,103]. Similar to misperceptions, hallucinations have been associated with many diseases, brain lesions and psychological states[103].

making. Recently, ideas about how the brain values different choices have been developed[69,75–77]; however, to date it is still unclear how the systems that are involved in perceptual decision making interact with the systems that are involved in valuation. Rewards might affect sensory representations, as well as motor planning or action selection; however, how this occurs in the human brain is still an open question. At the most basic level, future studies in this direction might provide information on how humans trade off speed and accuracy in decision making[78,79]. Beyond that, they will help us to understand whether the principles discussed here also hold for more complex decisions that are based on reward outcome, namely economic decisions[80,81].

The framework presented here might also prove useful for advancing our understanding of clinical disorders (BOX 5). For example, patients with obsessive–compulsive disorder (OCD) often show indecisiveness and inflexibility in regulating their behaviours. It has been suggested that altered function of frontostriatal circuits is involved in the pathophysiology of this disorder[82–84]. Because these frontostriatal brain regions are known to have an essential role in decision making, reward, performance monitoring and learning, it has even been suggested that OCD can be conceptualized as a disorder of decision making (for example, see REF. 85).

It is also tempting to speculate that the general principles derived from the studies of simple perceptual decision processes reviewed here extend to other settings — for example, the social domain[1,5,77,81]. In the context of social decision making, perceptual decision-making routines (for example, about facial expressions[58,86,87]) are likely to form the basis of more complex routines, such as inferences about the mental states of others[88]. These social decision-making routines might share their origins and neural mechanisms with those that are associated with the ability to simulate or imagine outcomes that would be expected from alternative actions that an individual can choose[81]. Ultimately, understanding how the human brain makes perceptual decisions will further our understanding of the neural mechanisms that are involved in the complex decisions that we repeatedly encounter in everyday life.

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