

# The neural bases of multistable perception

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**Multistable perception is the spontaneous alternation between two or more perceptual states that occurs when sensory information is ambiguous. Multistable phenomena permit dissociation of neural activity related to conscious perception from that related to sensory stimulation, and therefore have been used extensively to study the neural correlates of consciousness. Here, we review recent work on the neural mechanisms underlying multistable perception and how such work has contributed to understanding the neural correlates of consciousness. Particular emphasis is put on the role of high-level brain mechanisms that are involved in actively selecting and interpreting sensory information, and their interactions with lower-level processes that are more directly concerned with the processing of sensory stimulus properties.**

## Introduction

Multistable perception occurs when sensory information is ambiguous and consistent with two or more mutually exclusive interpretations. When no additional cues are available that allow perceptual synthesis to converge on one unique interpretation, perception alternates spontaneously every few seconds between two ('bistable') or more ('multistable') interpretations of the same sensory input. Well-known examples include the Necker cube, Rubin's face-vase illusion, bistable apparent motion and binocular rivalry (Figure 1). Interest in studying multistable perception in human observers has increased with the advent of modern non-invasive brain imaging techniques such as functional magnetic resonance imaging (fMRI) because multistable stimuli allow neural activity related to conscious perception to be distinguished from that related to physical stimulus properties. Moreover, multistable perception can help us understand the constructive neural processes that generate a unified and coherent subjective experience of the world even though the information available is often fragmentary, conflicting or even ambiguous.

A decade ago, a thought-provoking article on the neural basis of multistable perception was published in this journal [1]. Inspired by the first fMRI studies of bistable perception, (see Refs [1,2] for reviews) and contrasting with the traditional view that spontaneous perceptual

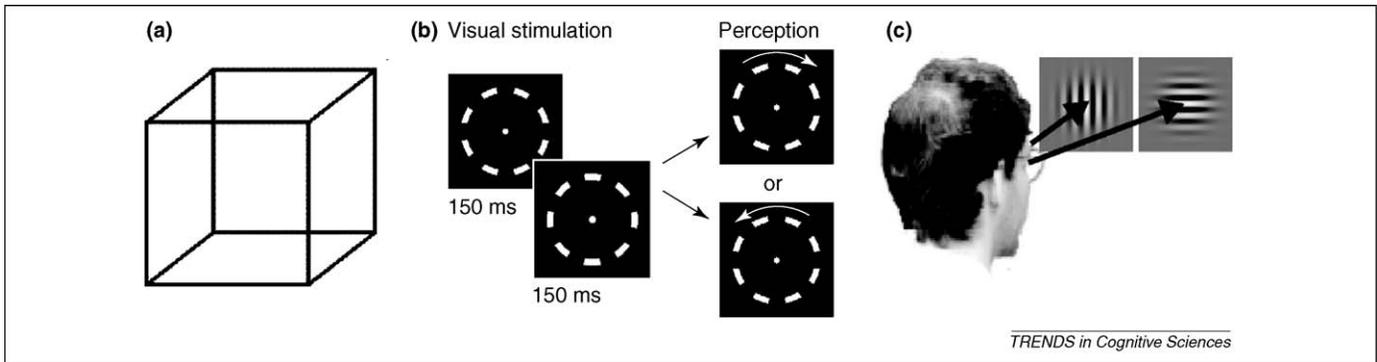
reversals are a consequence of antagonistic activity within the visual system (e.g. Refs [3,4]), the authors proposed that 'reorganizations of activity throughout the visual cortex, concurrent with perceptual reversals, are initiated by higher, largely non-sensory brain centers' [1]. Since then, hybrid theoretical proposals have emerged, on the basis of behavioural evidence, which conceptualise multistable perception as arising from interactions between low-level (sensory) and high-level (cognitive) processes [5]. In the last decade, the neural mechanisms of binocular rivalry, a special case of perceptual multistability, have been under intense investigation. Similar hybrid models of binocular rivalry that involve different visual processing levels have been proposed [6–8]. Finally, converging evidence from several recent lines of empirical neuroscience suggests a causal role of frontal and parietal cortex in generating perceptual switches in multistability, as previously proposed [1].

Here, we review recent findings addressing the neural mechanisms of different types of multistable perception, including but not limited to binocular rivalry. We incorporate these findings into an integrated view of how different neural processing levels, ranging from early sensory brain structures to non-sensory associative cortices, might interact to give rise to multistable perception, and how these processes are related to conscious perception in general. As most work has studied visual multistability, we focus on the visual system. However, there are striking behavioural similarities with comparable phenomena in other sensory domains (e.g. auditory [9,10] and tactile multistability [11]). The same or similar mechanisms involved in visual multistable perception might thus also have a role in other sensory domains (Box 1). Our review is structured according to the traditional hierarchical view of visual information processing, starting with subcortical and low-level cortical visual processing. After discussing intermediate processing stages at the level of extrastriate visual areas, we will focus on recent insights into higher-order mechanisms involving frontal and parietal cortices, and their interactions with lower-level sensory brain regions.

## Subcortical and early cortical visual processing

Several early electrophysiological studies concluded that neural activity at the anatomically earliest post-retinal visual processing stages, in the lateral geniculate nucleus (LGN) and primary visual cortex (V1), had little or no

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**Figure 1.** Examples of multistable visual phenomena. (a) The Necker cube is a wire-frame drawing of a cube in isometric perspective, which makes which plane is perceived as being in front ambiguous. This results in perceptual bistability with perception alternating between these two mutually exclusive interpretations of the sensory input. (b) The 'spinning wheel illusion' is an example of bistable apparent motion perception. Two frames showing dashed circles that are offset from each other by the dash length are shown in rapid alternation. This yields bistable perception of either clockwise or counter-clockwise rotation. (c) Binocular rivalry results from presentation of dissimilar images to each eye, leading to bistable perceptual alternations between the two images.

influence on the resolution of binocular rivalry (see Refs [1,2] for reviews). Subsequently, blood oxygenation level dependent (BOLD) fMRI studies in humans have repeatedly demonstrated strong effects of binocular rivalry on signals in V1 [12,13], with a close linkage between BOLD signals and the evolving spatiotemporal dynamics of rivalry perception [14]. Moreover, fluctuating perception during binocular rivalry can be predicted for extended periods of time from BOLD signals in human V1 alone

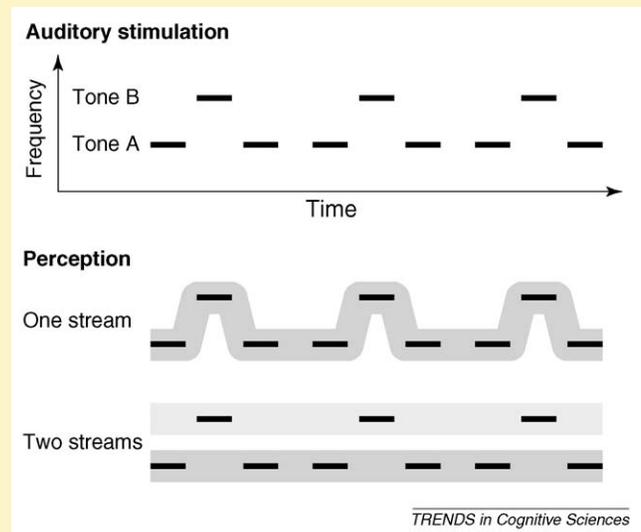
[15] when information is accumulated across voxels using multi-voxel pattern analysis [16,17] (Figure 2a). A recent magnetoencephalography (MEG) study showed that early visual cortex activity correlates with the perception not only in binocular rivalry but also with the figure-ground reversals underpinning Rubin's face-vase illusion [18] (Figure 2b). Transcranial magnetic stimulation over early visual cortex (V1) can induce perceptual alternations [19], suggesting a causal role for fluctuations in V1 activity in

### Box 1. Auditory multistable perception

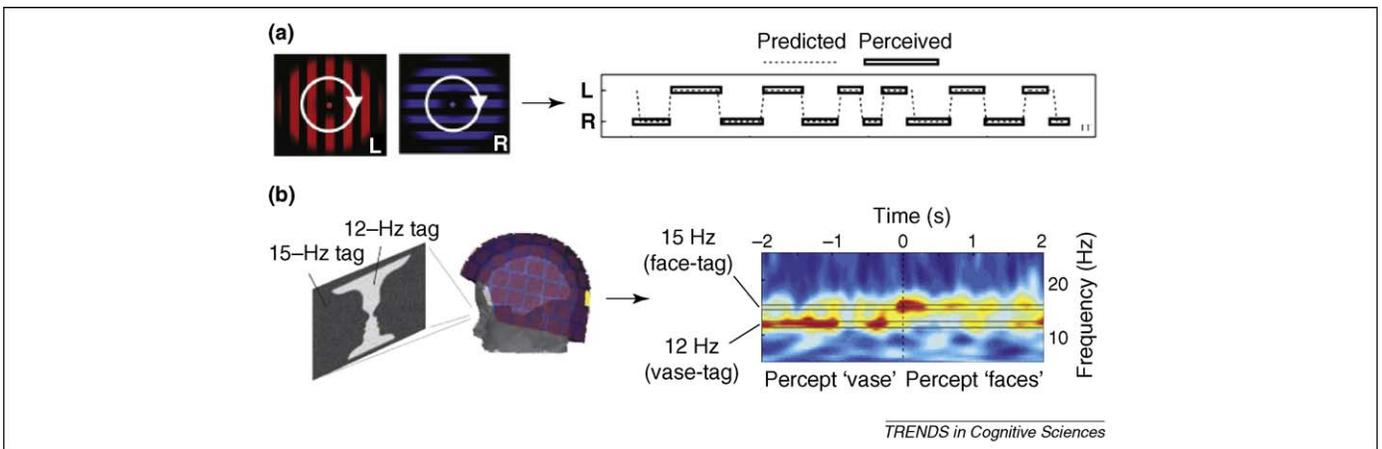
Two examples of perceptual multistability in the auditory modality are auditory stream segregation [79] and the verbal transformation effect [80]. Auditory stream segregation occurs when two tones are presented alternately or in another repeating temporal pattern (Figure 1). These sequences are perceived either as a single stream of fluctuating sounds or as two segregated streams, each comprising a single repeating sound. The temporal dynamics of perceptual alternations during auditory streaming are similar to those in bistable visual perception, and similarly susceptible to volitional control, indicating that auditory and visual multistable phenomena share common principles [10]. Interestingly, subject-specific biases do not show any correlation across sensory modalities, suggesting that the neural implementation of these common principles is at least partly independent for visual and auditory systems [10]. Neural correlates of auditory streaming have been observed at different levels of auditory processing. For example, electrophysiological recordings in monkeys show differential neural activity primary auditory cortex [81,82] and even in subcortical structures [83] when comparing the perception of one versus two auditory streams. In humans, fMRI and magnetoencephalography show increased activity during the perception of two rather than one stream in primary auditory cortex and surrounding non-primary auditory areas [84] and in the intraparietal sulcus [85].

The verbal transformation effect arises when a speech form is cycled in rapid and continuous repetition [80]. Initially, a percept matching the original form dominates, whereas at some point another percept takes over and then alternates with the original percept. For example, rapid repetitions of the word 'life' result in bistable alternation between the perceived words 'life' and 'fly'. Like other multistable phenomena, the timing of perceptual transitions for this verbal transformation effect conforms to gamma distributions [9]. In auditory cortex and prefrontal regions (left inferior frontal cortex and dorsal anterior cingulate cortex), activity increases during perceptual transitions. However, only prefrontal activations are specific for spontaneous changes in speech perception compared to a control condition where physical stimulus changes were reported. Although left inferior frontal activations correlate positively with the

number of perceptual transitions, the inverse relationship is found for cingulate activations, suggesting opposite influences of these two regions on perceptual alternations. An involvement of left inferior frontal cortex, in addition to left supramarginal gyrus, in bistable word perception is also suggested by an increase in gamma activity (>40 Hz) in these regions before perceptual transitions, as shown using intracerebral EEG recordings in epileptic patients with diagnostic electrode implants [86].



**Figure 1.** Auditory streaming as an example of auditory multistable perception. Two tones differing in frequency are presented alternately in a repeating temporal pattern. Listeners perceive the sequence as either one stream with fluctuating tones or as two segregated streams. The perceptual streams are indicated by the grey shading.



**Figure 2.** Neural correlates of multistable perception in human early visual cortex. (a) Functional magnetic resonance imaging BOLD contrast signal patterns from visual areas V1, V2 and V3 can accurately and blindly predict behavioural reports of perceptual alternations during binocular rivalry between rotating orthogonal gratings [15]. Behavioural reports of alternations between face and vase percepts in the Rubin's face-vase illusion correlate with activity in early visual cortex measured with magnetoencephalography (MEG). Specificity of the MEG signals for each percept is achieved by flickering the two components of the bistable image (the faces and the vase) at different frequencies. These frequency 'tags' can be identified in the MEG signal and used to examine neural activity correlating with each the two perceptual interpretations [18]. Reproduced from Refs [15,18] with permission from Cell Press and National Academy of Sciences, USA.

influencing the outcome of rivalry. Similar to the fMRI findings in V1, and contrasting with electrophysiological work (see Ref. [1] for a review), even BOLD signals in the LGN correlate with the perception of observers during rivalry [20,21]. Discrepancies between electrophysiological and fMRI studies can be related to the fact that neuronal spiking activity (as measured in earlier electrophysiological studies) is less closely related to perceptual awareness than local field potentials [22], which in turn correlate more strongly with fMRI BOLD signals than spiking activity [23], thus underlining the usefulness of fMRI for studying neural correlates of perception. Moreover, context-dependent differences in the coupling between fMRI and electrophysiological signals in visual cortex could have an important role [24], in addition to more general differences in methodologies and species.

fMRI studies in humans have thus established that signals from anatomically early visual processing stages including the LGN and V1, reflect the perceptual outcome of binocular rivalry (see Ref. [6] for a review). Together with earlier electrophysiological findings, they support the notion that neural activity at these earliest processing levels, although in itself not being sufficient for generating a conscious percept, is a prerequisite for visual information to reach consciousness [25–27]. Yet, although such findings provide information about which neuronal populations are involved in resolving binocular rivalry, they are less informative about how neuronal populations come to prefer just one perceptual interpretation of a multistable stimulus in the first place. One interpretative problem arises from the relatively poor temporal resolution of fMRI. For example, binocular rivalry itself might evoke different neural mechanisms, some primarily related to perceptual conflict, but others to inter-ocular competition. Changes in perception can, thus, arise as a by-product of low-level interactions at monocular processing stages. In this case, perception passively follows the resolution of 'inter-ocular' conflict. Alternatively, 'perceptual' conflict could drive processes of inference and interpretation that modulate neural activity throughout the visual hierarchy down to the lowest levels

(Box 2). For both scenarios, the role of LGN or V1 could be to gate visual information, either via local competitive interactions or through modulation by feedback signals from higher-order areas [27]. Evidence for the latter mechanism comes from fMRI studies of bistable apparent motion [28] and motion-induced blindness [29]. Whenever apparent motion is inconsistent with additional image cues (e.g. colour), early visual cortex activity is suppressed [28]. In motion-induced blindness, a bistable phenomenon where a target stimulus surrounded by a field of moving dots intermittently disappears from perceptual awareness, activity in visual areas V1 to V3 is globally reduced during target disappearance [29]. Such findings possibly reflect a gating mechanism whereby feedback from higher-order areas suppresses those features of input-related activity in early visual cortex that disagree with the perceptual outcome.

### Extrastriate visual cortex

A fairly congruent picture has emerged of the involvement of extrastriate visual areas, which lie beyond V1 in the visual pathway, in multistable perception. Both electrophysiological binocular rivalry experiments in human and monkey, plus fMRI experiments in humans reveal strong correlations between subjective perception and activity in functionally specialized extrastriate cortex (see Refs [1,2,30] for reviews). Recent studies have extended our understanding of the role of extrastriate visual cortex in conscious perception. The observation that the amplitudes of percept-related fMRI signal fluctuations during binocular rivalry in high-level extrastriate visual areas are similar to those during actual stimulus alternations (see Refs [1,2] for reviews) initially suggested that the conflict between incompatible interpretations of visual input had been fully resolved at this stage of processing, with no maintained representation of the suppressed stimulus. However, binocular rivalry is influenced by complex information contained in suppressed stimuli [31–34] (see also Refs [2,6] for reviews), indicating that information from binocularly suppressed stimuli still processed at suffi-

### Box 2. The ambiguous case of binocular rivalry - a rivalry of rivalries?

Binocular rivalry (Figure 1c in main text) has become a very popular tool for the investigation of the neural correlates of consciousness (see Refs [2,6] for reviews), perhaps because it is a particularly intriguing phenomenon. But more mundane factors such as practical feasibility and functional anatomy of the visual system can also affect the choice of experimental paradigm. For example, binocular rivalry is very flexible with regard to the stimulus material used. In principle, any stimulus class can be used in binocular rivalry – from simple grating stimuli optimal for the investigation of low-level processing, to complex object stimuli that are processed in higher-level visual areas. The use of object stimuli in binocular rivalry has the additional advantage that the processing of some object categories is to some degree spatially segregated in human visual cortex. Responses to two rivaling object categories (e.g. faces and houses) can therefore easily be dissociated using fMRI.

However, binocular rivalry potentially differs from other perceptual ambiguities because there is not only conflict between two interpretations of one sensory input pattern but also between two different patterns presented to the two eyes. Thus, in addition to competition between neural pattern representations, competition between eye-specific representations at early monocular stages of central visual processing can contribute to rivalry. Current models of binocular rivalry propose a multi-level process involving competitive neural interactions at both monocular stages (eye rivalry) and binocular stages (pattern

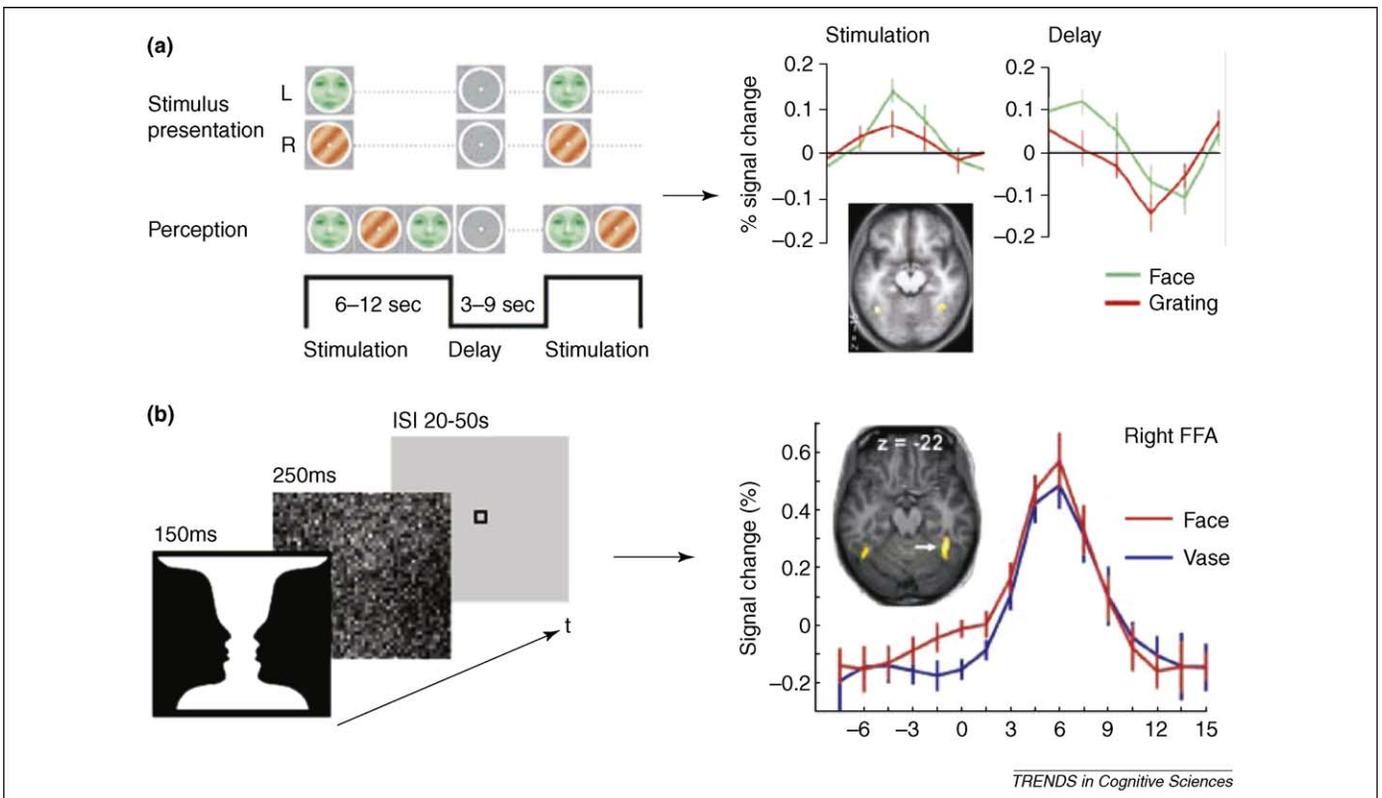
rivalry) of the visual processing hierarchy [6]. Involvement of perceptual (rather than purely inter-ocular) mechanisms is shown by persistence of rivalry when the monocular images are rapidly swapped between eyes, preventing interocular competition, and by the ability of complementary patchworks of intermingled images presented to each eye to drive rivalry (see Refs [1,2] for reviews). Neuroimaging studies have in general used binocular rivalry paradigms that do not explicitly tap one or other mechanism. Still, binocular rivalry has many behavioural similarities with other bistable percepts, such as the temporal characteristics of perceptual alternations. The effects of intermittent blank periods on rivalry and other forms of bistable perception are qualitatively identical [54], and the psychophysical relationships between stimulus strength and alternation dynamics are also comparable [87], suggesting common computational mechanisms. However, there are also important differences. With other types of multistability, different percepts are mutually exclusive, but this is not always the case in binocular rivalry. Briefly presented rivalry stimuli (<500 ms) can be perceived as superimposed on each other; and a patchy mixture of the two monocular images ('piecemeal rivalry') can occur, especially with large stimuli. Furthermore, unlike reversible figures, it is difficult to wilfully influence perceptual alternations in binocular rivalry [77]. A possible explanation for such differences is that the nature of conflict is different between binocular rivalry and other forms of multistable perception.

ciently advanced levels where this information can be extracted and represented. Indeed, areas outside the ventral visual pathway show responses to binocularly suppressed stimuli: the emotional content of suppressed stimuli, such as fearful faces, is associated with activity in the amygdala [35–37] and in the superior temporal sulcus [35]. Similarly, images of tools evoke activity in dorsal extrastriate areas, where this object category is preferentially processed, even during binocular suppression [38]. But these studies found no differences between responses to specific object categories (when interocularly suppressed) in 'ventral' extrastriate areas, such as the fusiform face area (FFA), parahippocampal place area (PPA) or lateral occipital complex (LOC). However, a recent high-resolution fMRI study used multi-voxel pattern analysis to show that fine-grained spatial activity patterns within FFA and PPA still contain information about the category of binocularly suppressed face and house stimuli [39], even though there were no significant differences in the mean response to suppressed faces and houses in these areas. Thus, the fine-grained spatial pattern of activity measured with fMRI encodes information about the identity of suppressed stimuli. Similarly, face-specific electromagnetic responses to binocularly suppressed stimuli are reduced in amplitude but still present in the human ventral visual pathway [40]. These results are consistent with more general findings of high-level processing for stimuli outside awareness in other paradigms (e.g. see Ref. [30]) and provide a possible neural basis for how complex stimulus features could contribute to the resolution of perceptual conflict even when suppressed.

Studies with reversible figures and ambiguous motion stimuli confirm that activity in extrastriate visual areas closely reflects conscious perception and, in addition, that these areas are directly involved in the resolution of visual ambiguities and conflict. Similar to binocular rivalry, BOLD signals measured using fMRI from human FFA are greater during face perception in Rubin's face-vase

illusion [41,42]. Similarly, viewing of an ambiguous stimulus whose elements can be perceived as either grouped or randomly arranged is associated with greater BOLD activity in the LOC during perception of a coherent shape [43]. Electrophysiological recordings in macaque monkeys show percept-specific activity also during bistable motion perception in motion-sensitive areas V5/MT [44], MST and parietal cortex [45]. BOLD contrast fMRI signals from human motion-sensitive extrastriate areas such as V5/MT allow accurate prediction of perceptual states during ambiguous structure-from-motion [46]; and stimuli ambiguous with respect to the type of motion or the perception of motion versus flicker evoke differential activity in human motion-sensitive cortex [47–49]. In contrast to the substantial evidence for an involvement of V5/MT in bistable motion perception, much less is known about the role of early extrastriate areas of the ventral visual stream, for example, V4, in multistable perception. This is because bistability between features such as colour is difficult to achieve experimentally. However, when colour or luminance cues are used to bias bistable apparent motion perception, activity in V4 is increased whenever perception is consistent with colour cues, suggesting that extrastriate colour processing is sensitive to perceptual dominance [28]. In motion-induced blindness, target visibility is associated with increased activity in the retinotopic representation of the target in V4, showing a close relationship between conscious perception and V4 activity [29].

In contrast to neural activity associated with different perceptual states, another line of research has focused on neural events associated with perceptual reversals. Reversal-related activity is consistently observed in extrastriate visual areas and is tuned to the visual feature or attribute that is perceived to change. Changes involving face or object percepts are accompanied by activations in object processing areas of the ventral stream (see Ref. [1] for a review), whereas perceived changes in motion direction or



**Figure 3.** The relationship between neuronal population activity in extrastriate visual areas and perceptual report in multistability. (a) When an ambiguous visual stimulus is removed after a few seconds of stimulation, the percept upon reappearance of the same ambiguous stimulus tends to be the one that was perceptually dominant when the stimulus initially disappeared. During removal of a face (versus grating) binocular rivalry stimulus ('delay'), activity in the fusiform face area (FFA), is greater after face than grating perception [53]. This percept-specific activity might contribute to the maintenance of a perceptual state across periods of stimulus removal. (b) When Rubin's face-vase figure is presented briefly, then masked, and repeated again at long and unpredictable intervals (ISI), perception of vase or face behaves stochastically over trials. Trials on which participants report a face percept are preceded by greater FFA activity than trials yielding the vase percept [60]. This suggests that the perceptual decision is determined by spontaneous activity fluctuations in extrastriate visual cortex that bias the outcome of perceptual competition between the mutually exclusive interpretations of the sensory input. Reproduced from Refs [53,60] with permission from MIT Press and National Academy of Sciences, USA.

motion type are associated with activations in motion-sensitive areas, most notably V5/MT [47,50–52].

Neural activity in functionally specialized extrastriate areas also has an important role in determining the perceptual choice at stimulus onset (e.g. during intermittent presentation of ambiguous stimuli [53]). When an ambiguous visual stimulus is removed for a few seconds, the percept upon stimulus reappearance tends to be the one that was dominant when the stimulus initially disappeared [54,55]. Such perceptual memory is proposed to reflect a consequence of sub-threshold elevation in the baseline activation of neurons that represent the last percept, thereby influencing the perceptual choice at stimulus reappearance [56]. A recent fMRI study tested whether perceptual memory during intermittent binocular rivalry is associated with percept-specific brain activity during temporary removal of a face (versus grating) binocular rivalry stimulus [53]. Activity in the FFA was greater during periods that were preceded by a face percept (and that were thus more likely to be followed by a face percept at the next stimulus onset) than during periods preceded by grating perception (Figure 3a). Thus, the perceptual choice at stimulus onset is influenced by the last conscious percept before stimulus removal, and extrastriate visual cortex seems to be involved in such perceptual memory (for a review see Ref. [55]). This is consistent with behavioural obser-

vation that perception of rivalrous stimuli can also be influenced by imagery [57], which enhances content-related activity in extrastriate visual cortex [58]. It should be noted that the perceptual choice at the onset of rivalrous stimuli is also subject to additional influences, such as low-level spatially localized factors, other than those governing perceptual alternations during ongoing rivalry [59].

But neural activity in extrastriate visual cortex can bias perceptual choice even when there is no measurable memory effect; that is, when ambiguous stimuli are briefly presented at long time intervals and perception shows stochastic behaviour [60]. Activity in the human FFA measured before presentation of Rubin's face-vase figure is higher when observers subsequently report perceiving a face instead of a vase, suggesting that endogenous variations in pre-stimulus neuronal activity bias subsequent perceptual inference (Figure 3b). A corresponding effect has been associated with visual motion perception, for the effect of spontaneous variations in pre-stimulus V5/MT activity on detection of near-threshold coherence in random dot motion kinematograms [61]. Such observations of apparently spontaneous baseline signal fluctuations and for carry-over between successive trials due to perceptual memory both suggest that ongoing activity before stimulus-driven processes contributes to how perceptual conflict is resolved by the human brain.

Taken together, recent studies have thus clarified how neural activity in functionally specialized extrastriate regions relates to conscious perception. It is now firmly established that neural activity in these areas shows strong modulations correlated with subjective perception of ambiguous or rivalrous stimuli. Together with a larger body of evidence from lesion or microstimulation studies, this suggests a key role of functionally specialized extrastriate areas in representing the contents of conscious visual perception (for a review see Ref. [30]). However, it should be noted that activity in functionally specialized areas is not always associated with a conscious percept, as demonstrated by the presence of stimulus-specific signals even when stimuli are made completely invisible (e.g. by binocular suppression). It is an intriguing question for future research how such unconscious representations of complex stimulus features can influence the dynamics of perceptual experience and, ultimately, behaviour.

### Parietal and prefrontal cortex

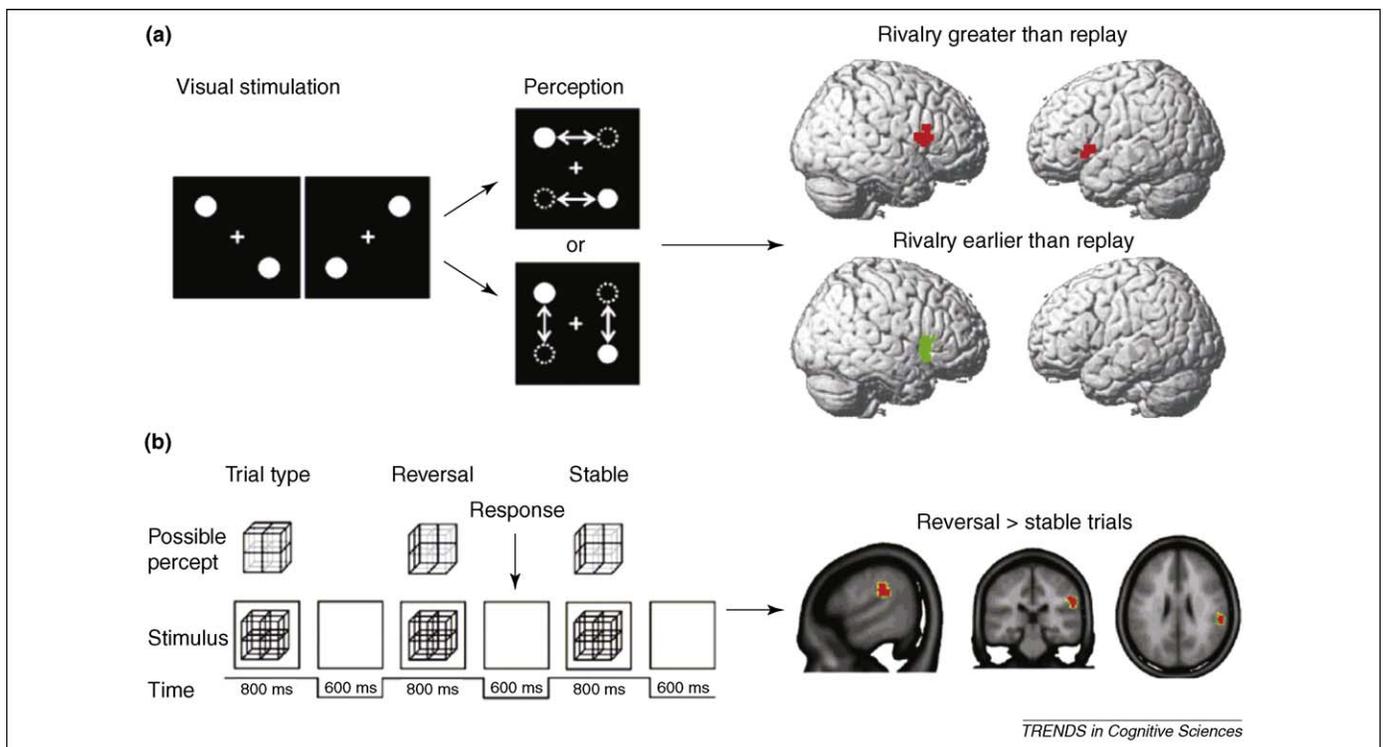
Multistable phenomena can identify neural correlates of conscious perception by characterizing neuronal populations that correlate with perception independently of physical stimulation. Although such studies can, thus, identify neural processes that reflect the contents of conscious perception, they cannot determine how the brain resolves conflict or ambiguities in the sensory input to settle on one of two (or more) mutually exclusive perceptual interpretations. Such an understanding touches upon the constructive nature of visual perception, which is not a passive mapping of visual input within the brain but an active interpretation involving inference. Natural visual scenes contain many ambiguities and conflicts that usually go unnoticed because the brain effectively disambiguates the information received [62]. In such a framework, multistable perception can be conceived of as a frequent re-evaluation of the current interpretation of the sensory input, which also occurs during normal vision but becomes particularly evident when ambiguities are maximised [1]. Such a theoretical account of multistable perception complements the traditional view of multistability as reflecting mutual inhibition between different representations of the sensory input. On the basis of behavioural observations, such as the stochastic nature of perceptual alternations and effects of high-level cognitive factors on the dynamics of multistable perception, it has been argued that an account solely based on mutual inhibition within sensory brain areas is unlikely [1]. Investigating neural activity that is associated with perceptual transitions rather than perceptual states during multistable perception should help to understand the inferential processes in visual perception.

Transient fMRI signal increases associated with perceptual reversals are not only observed in visual cortices (see earlier) but also in parietal and frontal regions [63] that have been implicated in visual attention [64] and in regulating access of sensory information to consciousness (see Refs. [30,65] for reviews). Although extrastriate areas are equally engaged by non-rivalrous perceptual changes, parietal and prefrontal regions show greater activation during rivalrous perceptual alternations [63]. Such fronto-

parietal activations could reflect top-down processes that initiate a reorganization of activity in visual cortex during perceptual reversals [1]. Alternatively, and according with the traditional view of multistability as a result of neural activity fluctuations in visual cortex (e.g. Refs [3,4]), frontoparietal activations could merely reflect the feed-forward communication of salient neural events from visual cortex to higher-order areas, similar to external stimulus changes. These two scenarios differ in the causal chain assumed to underlie changes in visual awareness, but it remains difficult to infer causality from correlative neurophysiological measures. Ideally, this question would be addressed by probing the causal role of frontal and parietal structures using experimental lesion and microstimulation techniques that have also been used in the study of perceptual decision making (see Ref. [66] for a review). However, no such studies have been reported to date, although investigations of multistable perception in patients with parietal and prefrontal damage after stroke provide suggestive evidence (see later). Alternatively, temporal precedence is usually considered good evidence in favour of a putative causal role [1,67].

Chronometric analyses of fMRI signals associated with spontaneous changes in apparent motion perception show that activation of right prefrontal cortex precedes that of V5/MT during bistable perception, relative to externally induced perceptual changes [68] (Figure 4a). It should be noted that conclusions from such chronometric analyses of BOLD contrast fMRI signals – even when appropriately grounded in demonstrating a region-by-condition interaction [68] that removes effects of local variations in neurovascular coupling – are still limited by our incomplete understanding of the relationship between neural activity and hemodynamic responses. However, the notion that the temporal precedence of BOLD activations might suggest a contribution of prefrontal structures to perceptual dynamics is supported by the finding that perceptual alternations are slowed in patients with focal damage to prefrontal [69] and parietal cortex [70] (see Ref. [1] for a review of earlier lesion studies with similar results). A similar conclusion was drawn from the electroencephalographic (EEG) finding that perceptual reversals during viewing of a Necker cube are preceded by neural activity in right parietal cortex [71] (Figure 4b), a region that exhibits stronger BOLD contrast fMRI signals during perceptual transitions in binocular rivalry compared to stimulus changes [63].

In addition to being associated with perceptual transitions during multistability, activity in frontal and parietal cortex can also contribute to percept stabilization. As mentioned earlier, perception can be stabilized by intermittently removing a multistable stimulus [54,55]. Intriguingly, the tendency of an individual observer to stabilize a percept across such periods of stimulus removal is strongly correlated with brain activity in frontal and parietal regions [53] previously associated with very different psychological processes of working memory and attentional selection [72]. Similar neural mechanisms might, thus, have a role in percept stabilization during multistable perception. The involvement of frontal and parietal regions in the regulation of percept stability is also



**Figure 4.** Involvement of frontal and parietal brain regions in multistable perception. **(a)** Alternating presentation of two frames showing two dots in diagonally opposite corners of a square results in bistable perception ('rivalry') of either horizontal or vertical apparent motion (in addition note that occasionally continuous clockwise or counter-clockwise motion can be perceived in association with these stimuli). Spontaneous perceptual switches between horizontal and vertical perceived directions of motion are associated with greater BOLD contrast fMRI signals in bilateral inferior prefrontal cortex (shown in red) compared to similar but stimulus-induced perceptual changes in a control condition where the perceptual sequence during rivalry is replayed using unambiguous stimuli ('replay'). Right inferior prefrontal activations associated with spontaneous perceptual changes occur earlier (shown in green) than those associated with stimulus-induced changes, whereas such a difference is absent in other brain regions, including visual cortex [68]. **(b)** During intermittent presentation of ambiguous figures with short stimulus durations (<1 s), perceptual reversals mostly occur at stimulus onsets. This allows analysis of brain activity time-locked to perceptual reversals. Measurements of brain activity with electroencephalography (EEG) during intermittent presentation of a complex Necker cube show that perceptual reversals are preceded by greater activity in right inferior parietal cortex, compared to stable perception [71]. Reproduced from Refs [68,71] with permission from National Academy of Sciences, USA, and Oxford University Press.

suggested by the correlation of activity in these regions with the tendency to maintain a percept during intermittent bistable motion perception [73].

Although there is a growing body of evidence for involvement of frontal and parietal cortices, their exact role in multistable perception and the implications for the understanding of conscious perception is still subject to speculation (Box 3). Signals associated with perceptual reversals are seen in frontal and parietal areas previously implicated in cognitive processes such as attention and working memory. Perhaps most striking is the similarity between brain regions implicated in directing attention to salient events [64] and those activated by spontaneous perceptual reversals [52,63,68,71]. Recent observations that activations in frontal [68] and parietal [71] cortices precede activity associated with the sensory processing of perceptual switches suggest that feedback signals from frontoparietal regions can modulate visual processing even in the absence of triggering sensory events. These studies investigated spontaneously alternating perception, without any instruction to wilfully influence perception or to attend to particular stimulus features. Although it is possible to voluntarily control multistable perception to some extent, this control seems to be limited [74–78]. Reversal-related activations found in neuroimaging studies are thus unlikely to reflect voluntary attention, even though they occur in similar brain regions. One possibility is that regions involved in voluntary attention also generate feedback signals spontaneously and

automatically. Such feedback signals, if occurring iteratively, could serve the frequent re-evaluation of the current perceptual interpretation [1]. They could, thus, initiate perceptual reorganizations whenever the 'balance of power' between neuronal populations coding for different multistable percepts in sensory cortices destabilizes due to adaptation or mutual inhibition. An alternative possibility, which would also account for temporal precedence of frontoparietal activations, is that such putative destabilization in sensory cortices might serve as a salient event that

### Box 3. Outstanding questions

- Is frontal and parietal activity during spontaneous perceptual reorganizations directly related to cognitive processes that these brain regions have been implicated in, such as reorienting of attention?
- What is the neural basis for the effects of cognitive processes like attention, working memory or intentions and expectations, on multistable perception?
- Under which conditions do signals from other senses affect multistable perception in a single modality [88,89], and how might such influences be mediated neurally?
- Which neural processes mediate the resolution of local ambiguities in visual scenes by contextual information?
- How do emotions, motivation and volition influence the resolution of perceptual ambiguities?
- How does sensory information that is perceptually suppressed influence behaviour?

activates frontoparietal regions in a feed-forward manner. Frontoparietal regions could in turn work to re-direct attention to the sensory input and initiate a re-evaluation of its current interpretation, eventually leading to a perceptual reversal. Whether frontoparietal cortices are involved spontaneously or as a consequence of sensory destabilization, it seems likely that their functional role is not restricted to the detection of salient external events, but rather that it extends into a constructive process of evaluating sensory input for its perceptual significance. These regions could thus take an active part in inferential processes that give rise to the subjectively unitary and unambiguous conscious perception of the sensory input. To more closely characterize the causal relationships between different processing levels in the brain and how they interact to generate conscious awareness is an intriguing challenge for future research. Possible experimental approaches include methods with greater temporal resolution and experimental lesion or microstimulation techniques in the context of multistable perception.

### Conclusions

Multistable phenomena have not only helped to elucidate the neural processes underlying perceptual awareness of sensory stimuli but also to shape our view on the constructive nature of visual processing that provides us with unitary perceptual experiences despite many inconsistencies and ambiguities in the sensory input. In contrast to previous models that explicitly contrast 'low-level' (e.g. Refs [3,4]) or 'high-level' mechanisms [1], we and many others (e.g. Refs [1,5]) now consider multistable perception to be the product of continuous interactions between 'low-level' (sensory) and 'high-level' (frontal and parietal) brain regions. There is now unequivocal evidence that fluctuations in neuronal population activity at both anatomically early and later stages of visual processing are strongly correlated with perception. Such activity fluctuations can arise from different sources, including top-down modulation, mnemonic processes, adaptation and spontaneous fluctuations. Conversely, there is an increasing body of evidence supporting the hypothesis that high-level frontoparietal processes continuously re-evaluate the current interpretation of the sensory input and initiate changes in subjective perception [1]. Such a causal role of higher-order processes in initiating perceptual reorganizations is not irreconcilable with the notion that activity fluctuations in sensory brain areas have a role in determining perception. Rather, perceptual alternations could be determined by the joint effect of local processes embedded into a more global process. That is, whenever local processes act to destabilize activity that underpins the currently dominant percept, higher-order evaluative processes can take effect and initiate a perceptual reorganization. Future research using multistable perception and related phenomena should seek to provide a more detailed account of how these processes contribute to human consciousness.

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