Multistable phenomena: changing views in perception

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Traditional explanations of multistable visual phenomena (e.g. ambiguous figures, perceptual rivalry) suggest that the basis for spontaneous reversals in perception lies in antagonistic connectivity within the visual system. In this review, we suggest an alternative, albeit speculative, explanation for visual multistability – that spontaneous alternations reflect responses to active, programmed events initiated by brain areas that integrate sensory and non-sensory information to coordinate a diversity of behaviors. Much evidence suggests that perceptual reversals are themselves more closely related to the expression of a behavior than to passive sensory responses: (1) they are initiated spontaneously, often voluntarily, and are influenced by subjective variables such as attention and mood; (2) the alternation process is greatly facilitated with practice and compromised by lesions in non-visual cortical areas; (3) the alternation process has temporal dynamics similar to those of spontaneously initiated behaviors; (4) functional imaging reveals that brain areas associated with a variety of cognitive behaviors are specifically activated when vision becomes unstable. In this scheme, reorganizations of activity throughout the visual cortex, concurrent with perceptual reversals, are initiated by higher, largely non-sensory brain centers. Such direct intervention in the processing of the sensory input by brain structures associated with planning and motor programming might serve an important role in perceptual organization, particularly in aspects related to selective attention.

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$\mathbf{W}$hen viewed continuously, certain visual patterns, such as those shown in Fig. 1, initiate a sequence of subjective changes that continue as long as the pattern is seen. Such multistability in perception can arise from a variety of stimulus types, involving alterations in a pattern's perceived depth, direction of motion, or visibility[1–4], and have been used extensively in the visual sciences as a tool for investigating mechanisms of perceptual organization[5–7]. Theoretical accounts of multistability commonly postulate a mechanism of reciprocal inhibition among visually responsive neurons[6,8–10], where perceptual dominance of one stimulus derives from the activation of a subset of neurons encoding that stimulus and the simultaneous suppression of those encoding competing representations. Over time, fatigue or 'satiation' causes the balance in the sensory network, and ultimately the subjective state, to reverse[11]. According to this view, perceptual alternations derive from the autonomous oscillations of a circuit within the visual areas.

In this review we have gathered evidence from the literature that we believe suggests an alternative to traditional models of multistable vision (or multistable perception in general). Based on this evidence we propose that the perceptual changes are the accidental manifestation of a general mechanism that mediates a number of apparently different behaviors, including exploratory eye movements and shifts of attention. We also propose that while the different perceptions of ambiguous stimuli ultimately depend upon activity in the 'sensory' visual areas, this activity is continually steered and modified by central brain structures involved in planning and generating behavioral actions. We draw upon evidence from psychophysical and physiological experiments in humans and monkeys, many of which exploit the multistable visual phenomenon of binocular rivalry. The first section describes electrophysiological and neuroimaging studies of activity patterns inside and outside the visual cortex in relation to perceptual reversals. The second section outlines the striking phenomenological similarities between the reversals in perception and spontaneous behaviors associated with cognitive or visuo–exploratory behaviors. From this we build the argument that not only might the neural mechanisms underlying these phenomena be closely related, but that multistable perception might itself be viewed

as a sort of behavior – originating in sensorimotor association areas and acting upon representations in the visual cortex. Finally, the last section speculates why multistability in perception exists at all, and what its existence might reveal about fundamental mechanisms of perceptual organization in normal vision.

Activity in the brain during multistable vision

A number of recent neurophysiological and imaging experiments in monkeys and humans, respectively, have shed light on cortical activity during multistable perception. Most of these studies have used binocular rivalry, a psychophysical paradigm in which perception can be destabilized simply by showing sufficiently dissimilar images to the two eyes (see Fig. 1D; for reviews see Refs 10,12). During rivalry, perception is wholly dominated by one pattern while that presented to the other eye is rendered invisible. In past decades, explanations of this phenomenon have attributed the complete dominance of one eye's pattern to the elimination of a monocular stimulus representation when or before information from the two eyes is combined in primary visual cortex. However, a number of psychophysical studies suggest that rivalry represents a more general competition in the visual system – between central stimulus representations rather than between eyes. For this reason, rivalry has lately been considered to be more closely related to other forms of multistable perception than was previously thought (see Box 1). The hypothesis presented here postulates generalized mechanisms of multistable perception and considers binocular rivalry to be but a single example. Wherever possible, we draw upon evidence both from rivalry and a second form of multistable perception in order to emphasize further their similar phenomenology.

What might one expect from neural activity in the visual system during multistable perception? Would activity continually change in accordance with the perceived stimulus, or would it maintain a constant level of activity in line with the fact that the input is unchanging? For binocular rivalry, the extreme views offer opposite predictions. Proponents of the 'monocular blockade' theories of binocular rivalry would predict that nearly all neurons in the visual system would change during a perceptual change. This is because the representations of each of the two stimuli would be alternately 'erased' at a very early stage of visual processing (at or before the stage when information from the two eyes comes together in primary visual cortex) whenever the percept changes. On the other hand, rivalry and other forms of multistable perception could theoretically also represent high-level 'cognitive' processes that are wholly unrelated to explicit sensory-stimulus representations. In this case, one might expect that neurons in the visual system would be oblivious to the perceptual changes, and continue to respond based only on
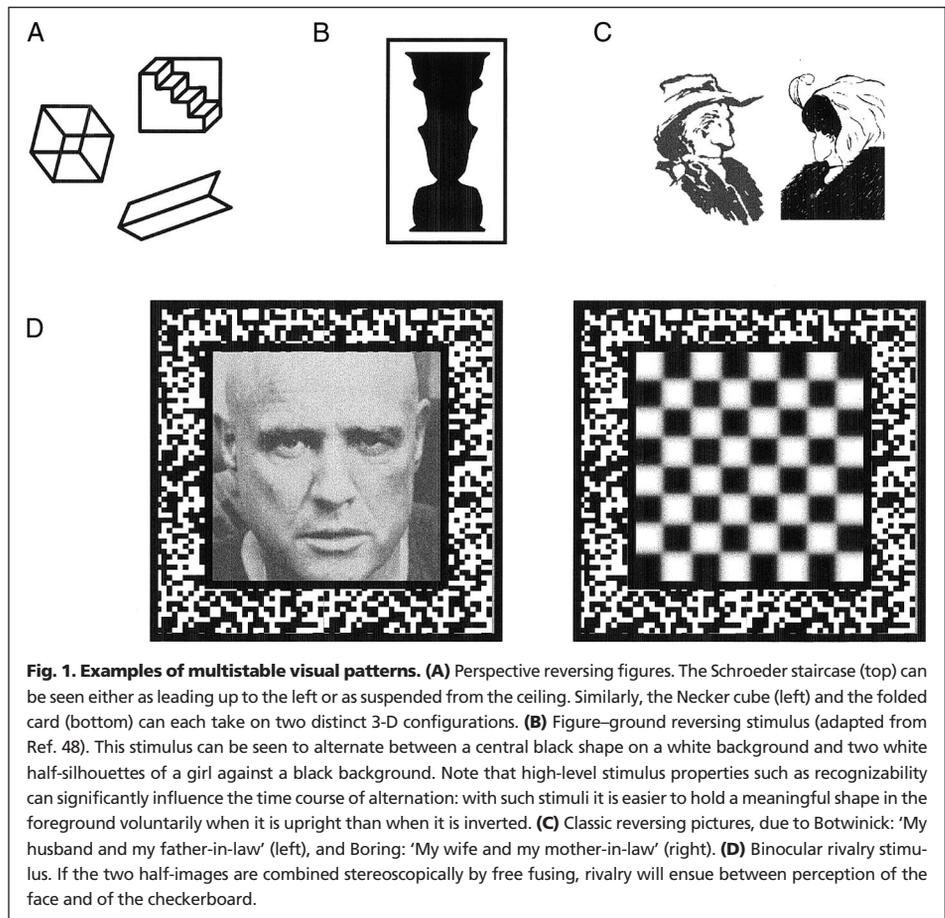
Fig. 1. Examples of multistable visual patterns. (A) Perspective reversing figures. The Schroeder staircase (top) can be seen either as leading up to the left or as suspended from the ceiling. Similarly, the Necker cube (left) and the folded card (bottom) can each take on two distinct 3-D configurations. **(B)** Figure–ground reversing stimulus (adapted from Ref. 48). This stimulus can be seen to alternate between a central black shape on a white background and two white half-silhouettes of a girl against a black background. Note that high-level stimulus properties such as recognizability can significantly influence the time course of alternation: with such stimuli it is easier to hold a meaningful shape in the foreground voluntarily when it is upright than when it is inverted. **(C)** Classic reversing pictures, due to Botwinick: 'My husband and my father-in-law' (left), and Boring: 'My wife and my mother-in-law' (right). **(D)** Binocular rivalry stimulus. If the two half-images are combined stereoscopically by free fusing, rivalry will ensue between perception of the face and of the checkerboard.

the retinal input. We believe that understanding how neurons behave under these conditions provides insights not only into the neural basis of these interesting phenomena, but also into fundamental mechanisms of visual perception.

Animal studies

In our laboratory we have recorded from isolated neurons in numerous visual areas of monkeys that were experiencing and reporting upon binocular rivalry. We found a subset of cells throughout the visual system that was strongly modulated during perceptual alternations (see Box 2). In addition we identified an even larger number of neurons, including nearly all the monocular neurons, that was largely unaffected during perceptual transitions, and continued to fire based solely on the patterns entering the eyes. Thus neurophysiology suggests that neither extreme account of rivalry outlined above can be correct. Rivalry does not involve the elimination of a monocular stimulus representation, as many neurons throughout the visual system, both monocular and binocular, continue to respond to a stimulus even when it is perceptually suppressed. At the same time, sensory processing is not independent of rivalry either, because a large fraction of visual neurons consistently change their activity according to the subjectively perceived pattern. What then is the nature of the perception-related modulation observed in these studies? Additional clues to this question may emerge from the temporal patterning of neural responses during rivalry.

One might imagine that neurons participating in the subjective changes would alternate their firing rates between 'state A' and 'state B', matching the alternating visibility of the two

Box 1. Binocular rivalry

Binocular rivalry is a conceptually simple example of multistable perception that can be initiated simply by showing dissimilar images to the two eyes. The perceptual impression under such conditions is not the spatial sum or average of the two monocular images, but rather a sequence of subjective reversals in which each of the stimuli, in turn, dominates perception while the other entirely disappears from view. A century ago, it was thought that binocular rivalry was mediated by shifts of attention (Refs a,b). However in the past few decades much evidence has suggested that it represents a form of interocular competition that arises when patterns in the two eyes cannot be stereoscopically fused. According to some theories, singleness of vision in rivalry results from the sequential blockade of each monocular channel, initiated by an interocular mismatch (Ref. c; but see Ref. d).

Although this extreme view of rivalry accounts well for some of its properties, such as the apparent non-selectivity with respect to stimulus features of its suppression (e.g. dominance of an achromatic, moving stimulus can entail the complete suppression of a stationary colored stimulus), it is inconsistent with a number of old and new psychophysical experiments. First, it is known that adaptational aftereffects generated by prolonged viewing of a stimulus are not weakened or curtailed if the adapting stimulus is perceived only a fraction of the time because of binocular rivalry (Refs e,f). This is particularly significant for interocular transfer of aftereffects, which is also unaffected (Ref. g). If rivalry involved the inhibition of a monocular channel, one might expect that suppressed stimuli would make no impact on the visual system and thus generate no aftereffects. Second, several stimuli demonstrate that normal rivalry can proceed under conditions in which competing stimuli are not assigned to different eyes. This is true, for example, in monocular rivalry (Ref. h), where competing stimuli are both presented to the same eye, 'switch' rivalry (Ref. i), where competing stimuli are continually switched between the eyes, and 'interocular grouping' rivalry (Refs j–l), where competing stimuli are divided spatially between the two eyes. The study on switch rivalry (Ref. i) excluded the possibility that eye-based models could account for the perceptual alternations. It should be noted that in contrast to recent claims (Ref. m) the stimulus spatiotemporal characteristics and luminance contrast in this study were equally effective in instigating switching and traditional binocular rivalry.

These results (together with the electrophysiology results described in Box 2), have suggested to us and others that mechanisms of binocular rivalry do not involve specialized interocular inhibitory processes, but rather represent a competition between central stimulus representations. Thus, rivalry is likely to be closely related to other forms of multistable perception, a view that is further supported by evidence regarding their common temporal dynamics, effects of attention, practice and a variety of other factors presented in this review.

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patterns. However, in our recordings such strict adherence to the enduring percept appeared in only a subset of neurons. Most modulating neurons exhibited changes in their spiking rate that were short-lived, and more closely associated with transitions than with lasting perceptual states (see Fig. 2). Only in the inferotemporal cortex (IT) was elevation or suppression activity commonly sustained throughout a period of perceptual dominance. These results suggested that not only did the 'early' and 'late' visual areas participate to different degrees in the perceptual changes, but that they had significantly different roles as well. In the context of the current hypothesis, a transient signal observed in the earlier areas could represent the response to a discrete 'command' signal involved in *initiating* a reorganization, while the state changes seen in the temporal areas might better reflect the enduring perceptual state *resulting* from a reorganization.
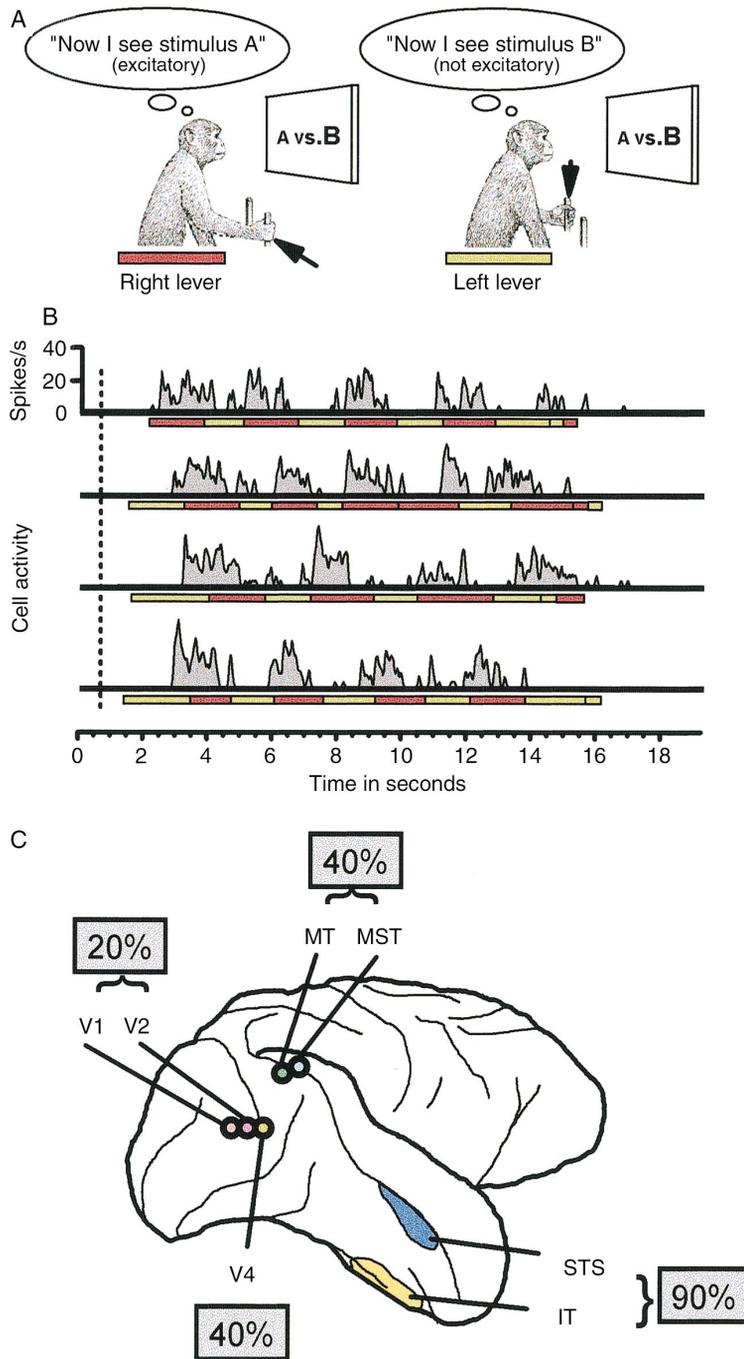
However, according to several studies, the absence of firing-rate changes does not necessarily imply the absence of state changes, as populations of neurons can increase and decrease the *coherence* in their firing as a function of time. Recent work has demonstrated that the synchrony between neurons, rather than the spiking of any individual neuron, can best represent the prolonged perception of a stimulus[13]. Synchronized firing has been speculated to underlie perceptual dominance during rivalry[14], a prediction that appears to gain support from a recent study in awake cats[15]. However, the cats in this study suffered from strabismic amblyopia and showed no spontaneous perceptual alternations, leaving unclear the implications of this result for multistable perception. Given that the temporal coordination between neurons can be influenced by a diversity of factors, including stimulus structure[16], generalized cortical activation[17], and discrete events such as microsaccadic eye movements[18], it is possible that top-down events similarly impact the interaction between neurons, rather than simply the activity of single neurons.

Human studies

Recent results using functional magnetic resonance imaging (fMRI) in humans have added further evidence for the active role of extrastriate visual areas in ambiguous vision, and have suggested that areas outside the visual cortex might have an important role in alternation as well. In the most relevant of these studies, Lumer *et al.* traced event-related hemodynamic responses and found that activity in the extrastriate areas of the fusiform gyrus, but not in the striate cortex, was related to the subjects' perceptual transitions during binocular rivalry[19]. But most interestingly, the activity

Box 2. Multistable perception in the monkey brain

A

"Now I see stimulus A"
(excitatory)

"Now I see stimulus B"
(not excitatory)

A vs. B

A vs. B

Right lever

Left lever

B

Spikes/s

Cell activity

Time in seconds

C

In a series of experiments in our laboratory (Refs a–c), neural activity was monitored in the visual cortex of monkeys reporting their percepts during binocular rivalry. The animals were taught to pull one of two levers to indicate which of a pair of patterns was perceived at each point in time (Fig. IA). During this task single neurons were monitored in many cortical areas, including the striate cortex (area V1), as well as the extrastriate areas V2, V4, the middle temporal area (MT), the medial superior temporal sulcus (MST), the inferotemporal cortex (IT), and the upper and lower bank of the superior temporal sulcus (STS). The rivalry stimuli were tailored to the preferences of the neuron being monitored, and an excitatory (preferred) stimulus was shown to one eye and a non-excitatory (null) stimulus to the other. The recordings revealed that despite the unchanging retinal input, a subset of neurons throughout the visual system was consistently modulated in accordance with the monkeys' internally generated perceptual changes.

An example of recordings from such a neuron in area V4 is shown in Fig. IB. For this cell, activity was sharply increased when the rightward stimulus became visible (just before the response), despite the unchanging visual input. In general, such cells increased their firing when the preferred pattern became subjectively visible to the animal, although the opposite pattern was observed for some neurons in areas MT, MST, and V4.
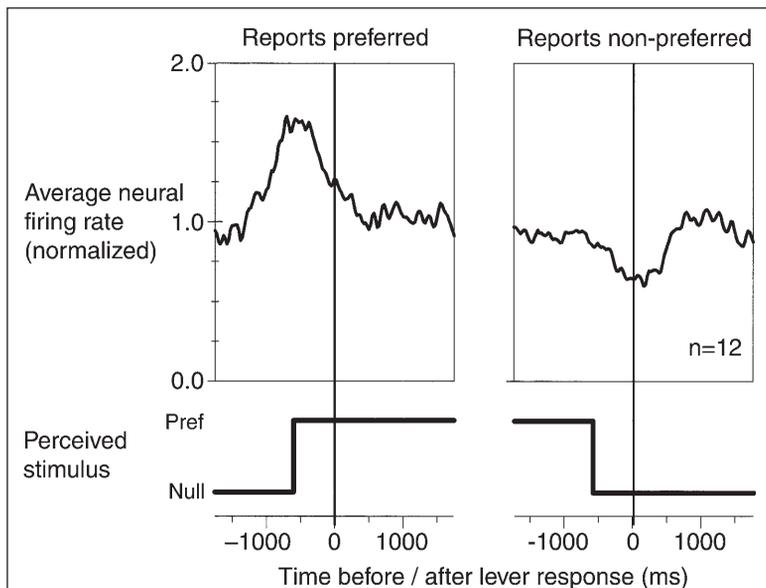
While many neurons in the visual cortex exhibited activity correlated with the monkey's subjective perception, an even larger fraction maintained a relatively constant level of activity regardless of which stimulus was seen, as if the pattern falling on the retina were the only factor determining their firing. The percentage of percept-related cells differed significantly in the different areas (Fig. IC). Only a small fraction in the earliest cortical areas V1 and V2 responded in concert with the rivalry alternations, while the percentage was considerably higher in the extrastriate areas V4, MT, and MST. Finally, the activity of nearly all visually responsive neurons in areas IT and STS closely matched the animal's perceptual state. This cortical modulation contrasts with the activity in the lateral geniculate nucleus (LGN) of awake monkeys, which does not show any modulation during binocular rivalry (Ref. d).

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Fig. I. Recording multistable perception in the monkey brain. (A) The task learned by the monkey while viewing a rivaling stimulus. The right lever was pulled when the animal was perceiving one percept (e.g. a right-oriented grating patch), and the left lever was pulled when the alternative percept was seen (e.g. a left-oriented grating patch). **(B)** The four horizontal panels represent individual observation periods in which the monkey viewed the bistable stimulus, the onset of which is shown by the vertical dotted line. The activity of the cell (between 0 and 50 spikes/s) is portrayed as a function of time in the gray shaded area. The animal's responses are shown as the colored bars below each panel, where red corresponds to the animal pulling the right lever (in response to seeing stimulus A, right-oriented grating patch) and green to pulling the left lever (in response to stimulus B, left-oriented grating patch). For this cell, activity was sharply increased when the rightward stimulus became visible (just before the response), despite the unchanging visual input. **(C)** The brain areas that contained cells whose activity correlated with the monkey's subjective perception. The percentage of percept-related cells increases in the 'higher' visual centers.

associated with the perceptual transitions was not restricted to the visual system, but included several frontal and parietal areas normally associated with various cognitive behaviors. This study demonstrated for the first time that fronto–parietal cortical areas are actively involved in binocular rivalry, and furthermore that their participation was specific to multistable viewing, as they were not active in a control passive-viewing condition (see Box 3).

Reports preferred   Reports non-preferred

Average neural firing rate (normalized)

2.0

1.0

0.0

n=12

Perceived stimulus

Pref

Null

−1000   0   1000   -1000   0   1000

Time before / after lever response (ms)

Fig. 2. Averaged cell responses of several representative V4 neurons during binocular rivalry. The monkey's approximate subjective experience is represented in the lower half of the figure, and is based upon the mean reaction time during a non-rivalrous discrimination. Note that shortly before the monkey responded to the subjective appearance of an excitatory stimulus by pressing a lever (vertical line, left panel) the activity of the cells increased sharply. However, this increase was not maintained throughout the perception of the preferred stimulus, but returned abruptly to its previous level, even though it was still perceived (as shown below). In contrast, many neurons in the temporal lobe displayed elevated or depressed activity during rivalry that often lasted throughout the entire phase of perceptual dominance (not shown). This difference was even more pronounced during 'flash suppression' rivalry, a paradigm in which a change in perception can be induced exogenously by presenting the rivaling stimuli with a time offset of a couple of seconds (Refs 100,101 and D.A. Leopold, PhD dissertation, Baylor College of Medicine, 1997).

In another fMRI study, Tong *et al.* examined rivalry between classes of stimuli that are known to activate distinct high-level extrastriate visual areas, and found that activity in these areas during perceptual dominance of a pattern was indistinguishable from that seen when the patterns were presented in isolation[20]. Finally, a recent study demonstrated that event-related hemodynamic activity during perceptual reversals of classical ambiguous figures was strong in the fusiform and intraparietal extrastriate areas but, interestingly, that the thalamus and striate cortex were specifically *deactivated* during visual instability[21].

Taken together, the electrophysiological and imaging results suggest that the instability in perception experienced during binocular rivalry entails widespread changes in the neural representation of the sensory input, and further suggests the possibility that these changes are in some way coordinated with brain activity lying outside the visual system. In the next section, we review some aspects of the phenomenology of multistable vision and build the argument that perceptual reversals are closely related to programmed behavioral actions. We propose that the reorganizations themselves might best be considered as the expression of a very special type of behavior – one whose output does not effect a motor response, but rather a perceptual change.

The nature of perceptual reversals
Temporal dynamics
A strong line of evidence in support of the present hypothesis is the very similar temporal dynamics for perceptual

reversals and a variety of spontaneously generated visuomotor behaviors. For example, periods of dominance and suppression in ambiguous vision are characterized by sequential stochastic independence[8,22–24]. This empirical observation has presented difficulties for reciprocal-inhibition models of bistable perception in which fatigue initiates perceptual reversals, for such models predict a correlation between the period in which a percept is suppressed and the following period in which it is dominant. The longer neurons involved in the competition remain inactive, the stronger they should compete in the next cycle[25] (but see Ref. 9), a relationship that is never observed in multistable perception. Similar randomness characterizes many exploratory behaviors that draw upon the integration of a large number of sensory and internal variables. For example, during free viewing, intervals between successive saccades (i.e. fixation durations) are stochastic[26]; that is, the duration of one fixation has no significant effect on that of the next. Eye movements during cognitive tasks such as the solving of arithmetic problems are similarly characterized by a lack of memory in their time course (successive fixation positions and durations do not have significant first-order of higher-order correlations), reflecting a random exploration rather than a stimulus-driven behavior[27]. In fact, it is possible that the stochastic time course in multistable perception bears the 'signature' of exploratory behaviors, which operate randomly by default, and become more deterministic only when constrained either by the sensory input or voluntary control. It is interesting to note that similar patterns are even observed during the initiation of spontaneous behaviors in species as primitive as the fly[28], suggesting that such a strategy might have deep roots in evolution.

Further similarities between perceptual reversals and certain types of behavioral actions are revealed by statistical analysis of their temporal dynamics. In contrast to the alternation process itself, the *distribution* of dominance phases for a given ambiguous image is predictable and consistent, and similar for nearly all multistable phenomena. Distributions of dominance times are unimodal and asymmetric, with fast growth and a long tail, and are often (but not always) modeled as a gamma distribution[29–33]. Closely related distributions are observed in sequences of goal-oriented behaviors involving target selection and perceptual integration, such as free-viewing fixation times in infants and naïve adults[34], fixation durations in cognitive tasks[35], and look durations in young infants viewing a stimulus[36].

The average timing of perceptual reversals can be largely influenced by the low- and high-level physical properties of the competing stimuli. The Gestalt psychologists, for example, described holistic stimulus properties, such as symmetry, closure, and element proximity, that influence the average time spent perceiving each stimulus during reversible perspective illusions, figure–ground illusions, and ambiguous motion[37–39]. In rivalry, first- and second-order stimulus attributes, such as brightness, contrast and spatial-frequency content can serve to strongly influence the balance of dominance and suppression[10]. Many multistable stimuli can also be influenced by high-level properties of the stimuli, including recognizability and even semantic content[40]. For example, the inversion of a recognizable figure can significantly affect

Box 3. Multistable perception in the human brain

Using fMRI, Lumer and colleagues showed that the roles of various cortical areas could be differentiated by comparing the hemodynamic responses under two perceptually equivalent conditions – normal rivalry, and a monocular 'emulation' of normal rivalry (Ref. a). The emulation consisted of perceptual conditions matched as closely as possible to that experienced by the subjects during normal rivalry, both in the time course as well as the spatial quality. This was achieved by 'replaying' the time course of a rivalrous sequence by switching the identity of the non-rivalrous stimulus back and forth, and blending the stimuli at the transition times to best simulate the subjective impression during normal rivalry. This emulation was not for the purpose of fooling or training subjects, as has been its role in previous animal studies (Refs b,c), but rather to provide an ideal subtraction condition for functional imaging. Given that the perceptual experience and motor responses were nearly identical in the two conditions, the subtraction of the monocular 're-play' condition from the rivalry condition provided a map of brain areas whose activity was specific to binocular rivalry.

The subtraction revealed that the primary visual cortex was activated only during the passive viewing condition, in which the stimuli were actually changing (and not during rivalry, in which the physical stimuli were constant). Moreover, and most relevant to this review, activation of several areas in the frontal and parietal cortex was found to be specific to the binocular rivalry condition, and was not present during the 'replay' condition. This activity showed was consistently lateralized to the right hemisphere in each of the subjects tested. In a follow-up study, Lumer and Rees measured the covariation in the hemodynamic responses between different brain areas while subjects experienced rivalry without being required to give manual responses (Ref. d). They found reliable covariation between the extrastriate areas and several frontoparietal areas, including Brodmann's area 46 in the lateral prefrontal cortex. From these results the authors concluded that the fronto–parietal areas might play a critical role in multistable perception, and that interactions between the prefrontal and visual cortices are likely to be important in perceptual awareness.

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its perceptual dominance in both figure/ground stimuli[41] (Fig. 1B) and binocular rivalry[42,43] (Fig. 1D). Although stimulus influences have generally been considered to act upon the same sensory circuits that initiate the alternation process itself, it is also possible that their influence is more indirect. In the present hypothesis, stimulus structure represents one of many factors that provide input to the cognitive machinery that eventually initiates a perceptual transition.

Voluntary control

Like many cognitive and non-cognitive behaviors, the reversal of perception during ambiguous vision is subject to a great degree of voluntary control. Just as voluntary processes can initiate a motor output (e.g. a finger movement) or influence a stimulus-contingent behavior (e.g. the likelihood of an express saccade[44]), they can also control to a large degree which of two competing stimuli is seen. In the case of reversible figures, the intention of the observer plays a critical role in perceptual alternation[45,46], a fact that is exploited in paradigms that use bistable stimuli to study perceptual organization[47,48]. Although voluntary control is somewhat weaker in binocular rivalry than with other multistable stimuli[49], several studies put forward evidence that the subject's intention nonetheless plays a large role in the pattern of perceptual dominance[50–52]. Naïve observers, for example, can nearly achieve a three-fold increase in their alternation rate if they consciously attempt to see 'fast' alternations rather than 'slow' alternations. Such control is not attributable to eye movements, as it does not disappear when stimuli are presented as afterimages[53] or stabilized on the retina by some other means[54]. Moreover, like most voluntary behaviors, control over perceptual reversals improves significantly with practice. In one study, for instance, control over the rivalry alternation rate was found to improve by three- to eight-fold after a training period of 10 days[50]. Other multistable phenomena show similar improvements[55], and evidence suggests that in many cases, ambiguous stimuli do not automatically generate perceptual multistability until reversals are 'learned'[56,57].

Apart from the structure of the competing stimuli, a wide variety of other factors can strongly influence the alternation process, many of which might affect cognitive mechanisms but have nothing to do with the processing of sensory stimuli *per se*. For example, the rate of perceptual alternation is correlated with intelligence[58], personality variables[59], and even mood disorders[60,61] (see Ref. 40 for a review). Among normal individuals the rate of alternation varies by as much as a whole order of magnitude from one person to the next[62,63]. Pharmacological agents that affect cognitive variables, such as caffeine and sodium amytal, can also significantly influence the rate of alternation during both binocular rivalry and the viewing of other reversible figures[49]. In a mechanistic, sensory model of multistable perception it is difficult to establish how any of these factors could affect the sequence of alternating perceptual dominance; however, in the present account these factors would act upon perception only indirectly by influencing the programming of planned events.

Finally, like many other cognitive or behavioral acts, perceptual reversals can be impaired by frontal brain damage. Ricci and Blundo[64] investigated 40 patients with unilateral frontal or posterior cortical lesions, assessing their ability to perceive ambiguous figures. In agreement with previous reports[65], patients with frontal lobe damage were

severely impaired in their ability to switch from one subjective view of an ambiguous figure to the other. Remarkably, those patients with posterior lesions only, where the visual system itself was damaged, were no worse at perceiving alternations than control subjects. A more recent study suggests that difficulty in shifting perspective is restricted to patients with lesions in the right frontal areas[66], a result that is consistent with the lateralized activity pattern observed by Lumer *et al.* in binocular rivalry[19] (see Box 3). The fact that damage to the structures involved in the initiation of behavioral actions specifically impairs the capacity to alternate between perceptual representations strongly supports the present hypothesis.

Similarities to selective attention

Stimulus selection during multistable perception is similar to, albeit more dramatic than, that made when attending to one stimulus at the expense of another. In fact, some accounts of selective attention employ the concept of 'biased competition', in which visual processing is restricted to a particular location or stimulus feature by top-down influences[67]. The interplay between non-visual and visual areas in selective attention might indeed be similar to that proposed for multistable perception, given that theories of attention often stress its close relationship to motor processes, and because its influence on neural responses in the visual system is ubiquitous.

Attention, like multistable perception, is an active process subject to voluntary control. The directing of attention takes the form of discrete and spontaneous actions that frequently occur 'covertly', that is, in the absence of any movement or gesture. Attentional shifts are associated with latencies and refractory periods that limit the speed at which the focus of attention can be redirected from object to object. Studies with serial search paradigms suggest that this refractory time is in the order of tens of milliseconds[68], whereas direct measurements suggest it to be one order of magnitude longer[69]. Although attentional shifts can be covert, they are often closely associated with saccadic eye movements. Experiments have demonstrated an obligatory coupling of the destination target of attentional shifts with that of voluntary saccades, suggesting that attentional shifts automatically accompany saccade programming[70–72], a hypothesis that has been supported by experiments examining the responses of single neurons in the superior colliculus[73]. It has even been suggested that both overt and covert shifts in attention involve premotor programming, and that covert orienting can only occur when movement is voluntarily prevented[74]. Corbetta and colleagues recently reported a large cortical overlap between neural networks associated with attentional shifts and those associated with making saccadic eye movements, further suggesting that the two processes are tightly linked[75,76]. Interestingly, several areas in common with this overlap were also activated during binocular rivalry[19].

The processing of sensory input can be strongly influenced by the attention directed toward a stimulus. This is suggested by psychophysical experiments in which improvements in sensitivity are brought about by orienting attention towards a particular object or location. Attention improves the capacity to analyse and discriminate objects, particularly in cluttered environments, an effect that has been shown to result from a modification of sensory processing rather than of short-term memory storage or response capability[67,77]. Single-unit neurophysiology in monkeys has verified that neurons throughout the visual cortical and subcortical areas show enhanced responses when a target stimulus is attended to because it is behaviorally relevant[78–82] (see Ref. 67 for a review). fMRI studies in humans similarly found widespread activation that was associated with spatially directed attention, activation that included the extrastriate visual areas[75,83].

Thus, mechanisms of selective attention and multistability might indeed be closely related; however, there are some key differences that suggest they are not one and the same. First, voluntary control in orienting attention is generally greater than in multistable vision. Second, in multistability top-down influences are not limited simply to enhancing the visual processing of a particular object or spatial location, but instead spur organizational mechanisms to change perception completely, possibly by shifting the balance between mutually exclusive neural representations in the visual system itself (see next section). Finally, attentional shifts can proceed with a speed that is considerably faster than even the most rapid perceptual reversals[69]. Although the specific relationship between attention and multistable perception remains to be clarified, the notion that activity in the visual cortex is continually punctuated with intervening signals from central, non-visual areas during both unstable and normal vision has important implications for deciphering the activity patterns of 'sensory' neurons.

Why might perception alternate?

The view of multistable perception presented here invites the question: Why does the brain continually reorganize an ambiguous sensory input? Although an observer can have significant voluntary control over dominance and suppression (as discussed above), it is clear that this influence is not the driving force for alternation, which continues in the absence of any particular intent on the part of the observer and can never be stopped entirely. By and large, any events leading to perceptual reversals take place unconsciously.

There are at least three fundamental properties that are common to all forms of multistable alternation: *exclusivity*, *inevitability* and *randomness*. Although these attributes are not entirely independent, they are worth considering one at a time, as they may provide insights into why perception becomes unstable.

Exclusivity, or uniqueness, ensures that conflicting visual representations are never simultaneously present. That only a single perceptual solution can exist at once is likely to have its origins in the structure of the sensory machinery itself; that is, uniqueness is a fundamental encoding principle among neurons in the visual cortex. Such a neural arrangement, shaped by evolutionary and developmental experience, might account for the fact that perceptual reversals, when they do occur, are most often global and sudden, reflecting a switch in the visual system between two equally likely organizations of the input. This occurs either when stimulus information is ambiguous (as in Fig. 1A–C) or conflicting (as in rivalry, Fig. 1D).

Inevitability in perceptual alternation has often been taken as evidence for alternation being a passive and automatic process; however, it could suggest nearly the opposite – that active, 'top-down' mechanisms impact persistently, and perhaps even iteratively, upon activity in the sensory areas. This might be true even for normal vision, where persistence in perceptual mechanisms can be important for survival in the environment, especially under challenging visual conditions. Figure 3 illustrates this point with two stimuli that, when first seen, often require several seconds of reorganizing or 'searching' before a target is successfully identified. During this process, 'binding' based on image properties very often leads to wrong Gestalt solutions, so that the visual system needs to overcome the conjunctions dictated by its own functional anatomy. When the embedded object finally appears, the accompanying subjective change is often sudden and dramatic, resulting in a permanent difference in how the pattern is interpreted. The unconscious processes that ultimately provide the correct solution in this case almost certainly involve input from brain areas outside the visual cortex, because the perception of such stimuli can be facilitated by high-level information about a stimulus, such as object-class[84–86]. Thus, arriving at a correct perceptual solution might rely upon persistently changing perceptual hypotheses about a particular sensory pattern. Multistable perception might represent an extreme manifestation of this strategy, arising when stimuli are truly ambiguous and perception can never become 'locked' onto a single solution.

Randomness is the third characteristic that is common to all forms of multistable vision. We discussed in the previous section how randomness might represent a 'signature' for exploratory behaviors. This view is consistent with that of Carpenter, who has recently suggested that the brain purposefully introduces randomness in the timing of its active events, such as saccadic eye movements, to achieve a desirable variability in the interaction of the organism with its environment[87]. Perception might benefit from such randomness by constantly 'shaking-up' the organization of the input to allow for solutions that are not the most probable given the functional–anatomical constraints imposed by the visual pathways. In the case of saccade generation, such variability appears to have its roots in the trial-to-trial behavior of individual neurons in the frontal eye fields[88]. If multistable perception has similar underlying processes to the generation of eye movements, similar neural mechanisms could account for the randomness observed in its time course.

Given these fundamental aspects of multistable perception, we suggest that perceptual reversals arise not from satiation, nor from a specialized mechanism of any sort. We suggest, rather, that they are likely to stem from intervention by central, sensorimotor areas upon the visual system, which is present continually in normal vision, but only reaches conscious perception when there is ambiguity in the visual input. This might take the form of an iterative and random system of 'checks and balances', whereby higher integrative centers periodically force perception to reorganize or 'refresh'. During normal vision this process is likely to proceed completely unnoticed, delivering only a stable and reliable subjective depiction of the surrounding world.
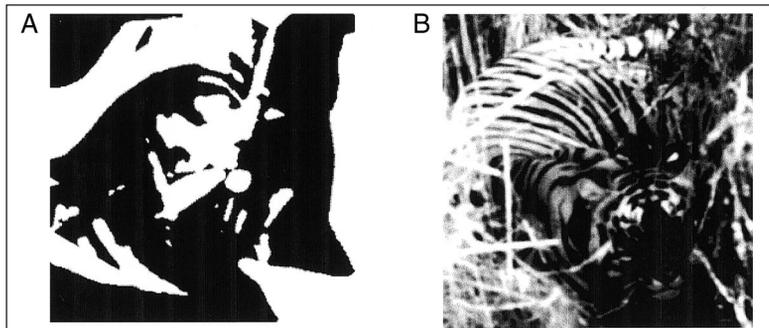
Fig. 3. Figures that challenge perceptual mechanisms. Threshold images such as those in **(A)** have often been used to investigate perceptual closure or the capacity to subjectively 'complete' a pattern given insufficient visual information. Such images often require several seconds of inspection before perceptual mechanisms lock onto a meaningful structure, a process which can be greatly aided by high-level information – in this case the clue 'Star Wars'. The camouflaged tiger shown in **(B)** presents similar difficulties for vision, and illustrates that perseverance in perceptual organization can be important for the survival of an organism.

It is important to re-emphasize that in the current framework such reorganizations are not initiated by areas involved primarily in sensory processing or memory, but rather in those that ultimately *use* and *act upon* the perceptual representations. Such areas are likely to be central cortical structures, such as the fronto–parietal areas that are neither purely sensory nor purely motor in nature, but which integrate sensory information to coordinate a variety of cognitive and non-cognitive behaviors. By continually issuing reorganizations of perception, such central areas could maintain a particular 'tone' (similar in a sense to muscle tone) that would ensure that the perceptual representation is both accurate and robust. The same areas might also be responsible for dispatching commands to motor structures that could aid perception, such as a saccade to a visual target. Such sensorimotor coordination is likely to be critical for perceptual awareness of the environment.

It is perhaps then not surprising that some perceptual actions are tightly coupled with motor responses. The obligatory coupling between saccades and attentional shifts mentioned above serves as one clear example. In addition, there are other phenomena in which the relationship between motor actions and perceptual experience is unclear. For example, the role of small saccades in multistable perception has long been poorly understood. Measurements of eye position often confirms subjects' intuition that perceptual transitions are strongly correlated with eye movements[89,90]. Yet experiments in which bistable stimuli were presented as afterimages or stabilized on the retina by other means have made it clear that gaze adjustments themselves are neither the primary cause of perceptual alternation, nor are they responsible for its temporal dynamics[91–94]. In the current framework, gaze adjustments and perceptual transitions might best be conceived as behaviors that work together to achieve a common goal – namely, the meaningful perceptual organization of a challenging stimulus. As the eye moves to scrutinize a new portion of the ambiguous or rivalrous pattern a perceptual transition is executed to test the competing perceptual hypothesis in the context of the new eye position. From this viewpoint, motor-directed and perception-directed actions are coordinated to achieve,

in combination, the best possible analysis of the visual environment.

As a final point, the notion that central, integrative brain areas can impact upon activity in the visual areas could have important implications for the interpretation of neural responses in these areas, beyond the modulation provided by attention already mentioned. Such top-down influences might, for example, be important for the evaluation of a noisy or subthreshold stimulus for which there is *no* 'correct answer'. Viewing patterns of 'noise' often lead to the spontaneous perception of meaningful patterns, based entirely on top-down processing. In such cases a perceptual solution may be 'forced' in a way similar to that during multistable vision. Data from monkeys reveal that under such conditions, where judgments must be made about the net motion of random dot patterns, the activity of visual neurons in the extrastriate areas is often correlated with the animal's perceptual judgments on a trial-by-trial basis. This is true when there is no 'correct' direction of motion, and occurs even when the same stimulus produces different judgments during different trials[95–97]. Thiele and Hoffmann[97] have attributed such correlation not to the monkey's basing his decisions on a noisy signal, but rather to his 'imagining' one or the other correct solution, a perceptual effect that could be mediated by the types of top-down influences described here.

Conclusions

The hypothesis presented in this article can be restated as follows: the complex analysis of sensory information ultimately leading to visual perception is continually steered and modified by sequences of planned interventions emerging from areas lying outside the visual system. Such intervention is most apparent when perception is unstable, as in ambiguous vision, but is likely to be a general property of active perception that is closely related to selective attention. If the brain's planning centers have reign over basic sensory processing, there are implications not only for perceptual organization, but also for conscious awareness. For example, Crick and Koch recently proposed that visual awareness relies on frontal cortical centers having direct access to visual representations constructed largely in the extrastriate visual cortex[98,99]. The present hypothesis adds to

this the notion that the frontal areas must, in turn, act upon these representations according to high-level contextual and motivational states in order to guide perceptual organization. Phenomena like binocular rivalry demonstrate that, although our brain can simultaneously analyse two conflicting representations, a selection process – perhaps even a high-level 'executive decision' – ensures that we are only aware of one. Further investigations, particularly those in which several brain regions are simultaneously monitored during multistable vision, are needed to test the merits of this hypothesis and to better identify the role of planning areas in visual perception.

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Mechanisms of selection for the control of hand action

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Most attention research has viewed selection as essentially a perceptual problem, with attentional mechanisms required to protect the senses from overload. Although this might indeed be one of several functions that attention serves, the need for selection also arises when one considers the requirement of actions rather than perception. This review examines recent attempts to determine the role played by selective mechanisms in the control of action. Recent studies looking at reach-to-grasp responses to target objects in the presence of distracting objects within a three-dimensional space are discussed. The manner in which motor aspects of the reach-to-grasp response might be influenced by distractors is also highlighted, rather than merely addressing the perceptual consequences of distractors. The studies reviewed here emphasize several factors highlighting the importance of studying selective processes within three-dimensional environments from which attention and action have evolved.

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Visual attention is one mechanism that enables us to select relevant objects and spatial locations over less important ones. Visual attention has been the target of extensive research, but despite this large amount of interest our understanding of some aspects of selective behaviour remains unclear. For instance, little is known about the limits governing the brain's ability to process information presented in parallel for the control of action towards three-dimensional (3D) stimuli.

Traditionally, selective attention research in cognitive psychology has been based on very brief presentations of two-dimensional (2D) stimuli (alphanumeric characters) on computer screens or tachistoscopes. This form of testing typically restricts attentional measurement to arbitrary and indirect responses such as key-presses or verbal naming[1,2]. However, the emergence of more powerful methods for the investigation of these mechanisms within 3D environments