

a0005

Bistable Perception and Consciousness

P Sterzer, Charité Campus Mitte, Berlin, Germany

G Rees, University College London, London, UK

© 2009 Elsevier Inc. All rights reserved.

Glossary

- g0005 **Ambiguous figures** – Images that can be interpreted as representing two objects or scenes, or two versions of an object.
- g0010 **Binocular rivalry** – A phenomenon of visual perception that is characterized by perceptual alternations between different images presented to each eye.
- g0015 **Bistability** – The ability of a system to exist in either of two steady states.
- g0020 **Extrastriate cortex** – A belt of visually responsive areas of cortex surrounding the primary visual cortex.
- g0025 **Functional magnetic resonance imaging (fMRI)** – A brain imaging technique that measures the hemodynamic responses related to neural activity in the brain.
- g0030 **Gamma distribution** – A probability density function that plays an important role in statistics; the exponential distribution and chi-square distribution are special cases of the gamma distribution.
- g0035 **Neural correlate** – A neurobiological state whose presence regularly correlates with a specific content of experience.
- g0040 **Parietal cortex** – Superior posterior part of the human brain, the most important function of which is the integration of sensory information from different modalities.
- g0045 **Prefrontal cortex** – The most anterior part of the frontal lobes of the brain. It has been implicated in planning complex cognitive behaviors, personality expression, and regulation of social behavior.
- g0050 **Primary visual cortex** – The first cortical area to receive inputs from the eye via the geniculostriate pathway; also referred to as V1, area 17, and striate cortex.

Introduction

s0005

Bistable perception is a perceptual phenomenon characterized by changes in subjective perception while sensory input remains constant. Usually, perception alternates spontaneously between two mutually exclusive interpretations of the same sensory input. Rarely, more than two interpretations are possible, in which case the term multistable perception is used.

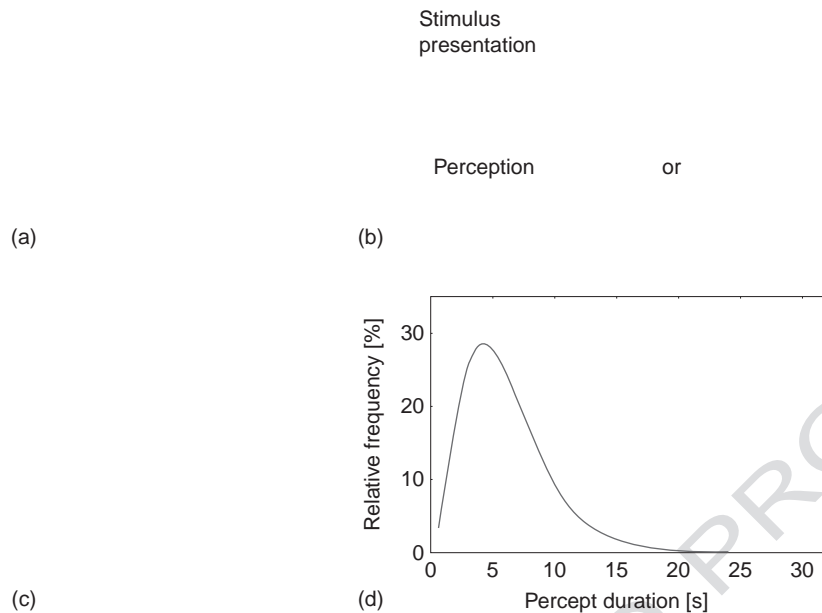
p0005

While bistability is also known for auditory stimuli, it is best known and has been most extensively studied in the visual domain. Bistable perception occurs when incoming sensory information is ambiguous or conflicting and when no additional cues are available that allow the visual system to converge on one unique interpretation. Typically, one interpretation remains stable for a few seconds until perception switches spontaneously and unpredictably to the alternative interpretation and then switches back again after another few seconds, and so forth. Famous examples include the Necker cube, Rubin's face-vase illusion, bistable apparent motion, and binocular rivalry (Figures 1(a)–1(c)).

p0010

Human fascination with such phenomena can be traced back to antiquity, but interest in bistable perception has recently been boosted by the advent of modern brain imaging techniques such as functional magnetic resonance imaging (fMRI). Such techniques can be used to measure brain activity in humans noninvasively, and therefore offer the opportunity to study the neural correlates of con-

p0015



10005 Figure 1 (a) Rubin's face/vase illusion, a figure-ground reversing stimulus that can be seen to alternate between a central white shape on a black background and two black profiles of a face against a white background. (b) The apparent motion quartet: Two dots are flashed in diagonally opposite corners of an implicit square in rapid alternation with two dots appearing in the other two corners, typically yielding bistable perception of two dots moving either horizontally or vertically. (c) Binocular rivalry: different images are presented to the two eyes, resulting in spontaneous perceptual alternations between each monocular view. (d) The distribution of perceptual phase durations during bistable perception typically follows a gamma distribution.

stimulation remains constant, is an elegant experimental approach to distinguish neural activity related to conscious perception from that related to enabling physical stimulus properties. Over the past decade, a number of studies have chosen this approach to investigate various aspects of conscious perception. This article summarizes the evidence that something (e.g., an object in the environment) has been derived from the neuroscientific study of the neural correlates of consciousness using bistable perception.

s0010 Theoretical Considerations

s0015 Types of Consciousness and the Question of Causality

p0020 When we talk about neural correlates of consciousness, we first have to define what we mean by consciousness. One fundamental and widely accepted distinction is between level of consciousness and the contents of consciousness. Level of consciousness refers to the state of being conscious

consciousness has used bistable phenomena to characterize the neural states that are associated with the specific contents of consciousness.

A second important theoretical consideration is the need to clarify the relationship between subjective phenomenal experience of consciousness and the neural states associated with that experience that can be measured. Importantly, it is not clear how any physical process, such as neural activity, can give rise to a subjective phenomenon such as conscious awareness of something, and even the possibility of such a causal relationship is controversial. It must be kept in mind that

empirical research on the neural correlates of consciousness should be neutral to the question of causality. Instead, this research can identify and characterize patterns of neural activity that specifically correlate with conscious as opposed to unconscious perception.

s0020 **Anatomical-Location versus State-Change Theories of Consciousness**

p0030 What kind of information can we expect from identifying neural correlates of conscious visual perception? Most of the studies that used bistable perception to investigate the neural correlates of conscious visual perception sought to characterize neural information processing that leads to awareness in contradistinction to processing that proceeds unconsciously. One popular approach is based on the general idea of anatomical location. Such anatomical location theories, also referred to as localizationism, propose that there is one neural structure (or a set of neural structures) in the brain that can generate conscious awareness by virtue of its activity. Information may be processed unconsciously through several stages of the brain but will only reach consciousness through processing in a particular structure of the brain. The most extreme form of an anatomical location theory postulates the existence of one single structure in the brain that is necessary for any information to become conscious. Alternatively, a certain class of neurons or brain regions that share some critical functional properties may equally be able to generate consciousness, but which exactly is critical for consciousness depends on the type of information that is processed. The most advanced anatomical location theories are known as global workspace theories and propose a common functional arrangement, but place the crucial anatomical locus (or loci) in various sites. Most studies investigating bistable perception with fMRI in humans, or electrophysiological recordings in monkeys, are based on such anatomical location theories as they have tried to localize brain activity associated with conscious states or with changes in conscious perception.

p0035 In contrast to anatomical location theories, so-called state-change theories postulate a special state of neural activity resulting from a particular

way of processing that gives rise to consciousness. The most influential theory of this type proposes that oscillations in neuronal firing and their exact synchrony are the crucial features for conscious awareness. Some studies using electrophysiological measurements in humans or nonhuman primates have used bistable perception to elucidate the role of synchronous oscillations in consciousness, while the fMRI signal is too slow to measure these temporal aspects of neural processing at a sufficiently high resolution. It is important to note that anatomical-location and state-change theories, fundamentally different though they appear, are not mutually exclusive. On the contrary, it is plausible that both aspects of neural activity, location and oscillatory synchrony, may be important aspects of the neural correlates of consciousness.

Bistable Perception and the Neural Correlates of Consciousness

s0025
p0040 What can we learn from bistable perception about the neural correlates of consciousness? It could be argued that the visual ambiguity that gives rise to bistable perception may be a special case, a situation that can be generated under laboratory conditions but is rarely encountered in natural scenes. What we can learn from the investigation of a special case such as bistable perception may thus be very limited and tell us little, if anything, about the neural mechanisms associated with conscious experience under normal conditions. However, the observation that we usually do not experience ambiguities in natural scenes is misleading. In fact, human vision is routinely faced with conflicting or ambiguous information that necessarily requires active interpretation guided by contextual information, prior experience, and intentions. Accordingly, bistable perception can be seen as a patent manifestation of vision as an active, interpretive process that under normal circumstances is so efficient and effortless that one seldom becomes aware of its inherent difficulty. The study of bistable perception can therefore help understand the interpretive processes that most of the time go unnoticed but give rise to visual consciousness in the form of unified, coherent, and unambiguous percepts. These interpretive processes include the integration of prior expectations that are based on

experience and of contextual information in the visual scene. Moreover, visual processing may also play an active role in continuously reevaluating the current interpretation of the visual input, in stabilizing perception and in weighing and selecting the information available according to its behavioral relevance.

s0030 **Visual Stimuli Evoking Bistable Perception**

p0045 Bistable perception can arise from a wide variety of different visual stimulus types. The common denominator of all bistable phenomena is that, while the visual input pattern remains the same, perception changes spontaneously and unpredictably between two states that typically remain stable for a few seconds. All bistable phenomena have in common that periods of dominance and suppression are characterized by sequential stochastic independence, i.e., the timing of the next perceptual switch cannot be predicted from the history of previous switches. Another feature that is shared by all types of bistable perception and, in fact, is so typical that it is sometimes used as a criterion for bistability, is the characteristic gamma distribution of phase durations (see Figure 1(d)). This distribution is typically skewed toward shorter durations. Depending on the stimulus type, changes can occur for various types of visual features, including object category and identity, depth, direction of motion, and visibility. Stimulus types that are known to evoke bistable perception can be classified into reversible figures, ambiguous motion stimuli, and binocular rivalry.

s0035 **Reversible Figures**

p0050 Reversible figures include the most famous examples of bistable perception, such as the Necker cube and Rubin's face/vase illusion. The Necker cube is a perspective-reversing wire-frame figure of a cube that can take on two distinct 3D configurations. Further examples for perspective-reversing figures are the Schroeder staircase and the folded card. Rubin's face/vase illusion is a figure-ground reversing stimulus, which can be seen to alternate between a central white shape

on a black background and two black profiles of a face against a white background (Figure 1(a)). An interesting feature of figure-ground reversing figures is that high-level stimulus properties such as recognizability can strongly influence the time-course of alternation. For example, with such stimuli it is easier to hold a meaningful shape in the foreground voluntarily when it is upright than when it is inverted. Yet another group of ambiguous stimuli are the classic reversing pictures, the most famous example being Boring's classic illusion "My wife and my mother-in-law," a drawing that can be seen as depicting a young or an old woman. Reversing pictures of this type are usually complex drawings that accommodate two different images by containing ambiguous image-defining features.

Ambiguous Motion

Bistable motion phenomena were first described by German Gestalt psychologists in the first half of the twentieth century. A typical example is the so-called *Stroboskopische Alternativbewegung* (strobe-4621.6possibility8.6(es62(6le)-294.1(is)stingly13of)s-10.1(62(altrf)-

s0040

p0055

principle no categorical differences between the two percepts. An example for bistable motion perception that involves changes between two different types of motion are plaid stimuli. They are composed of two orthogonal diagonal gratings that are superimposed in the same display. Observers can perceptually segregate these surfaces and perceive the gratings sliding on top of one another in opposite directions (component motion); or the two components can be integrated perceptually into a single surface that moves in a direction intermediate to the motion directions of the component gratings (pattern motion).

to both eyes and the ambiguity of the pattern gives rise to perceptual conflict between two possible interpretations. While perceptual conflict between two images or patterns is also likely to be relevant in binocular rivalry, conflict between monocular signals that are processed separately at the lowest levels of the visual system is also thought to play a significant role in the resolution of binocular rivalry. It is important to keep the differences between binocular rivalry in mind when comparing the results of studies investigating binocular rivalry and those of involved in other forms of bistable perception.

s0045 **Binocular Rivalry**

p0065 When dissimilar images are presented to the two eyes, instead of the two images being seen as superimposed or blended, perception alternates spontaneously between each monocular view (Figure 1(c)). Binocular rivalry has many similarities with other bistable percepts. For example, the temporal characteristics of perceptual alternations in binocular rivalry are similar to those in other forms of bistability. Alternations are largely stochastic and percept durations typically follow a gamma distribution (Figure 1(d)), and are similar to other bistable phenomena. However, there are also important differences. With other types of bistable stimuli, different percepts are mutually exclusive. However, this is not always the case in binocular rivalry. For example, when rivalrous stimuli are presented very briefly (<500 ms), the two images can be perceived as superimposed on each other. Piecemeal rivalry can also occur, especially with large stimuli, when a patchy mixture of the two monocular images is perceived. Furthermore, unlike reversible figures, it is very difficult to willfully influence the perceptual alternations in binocular rivalry. For example, perception of reversible figures can be strongly biased by focusing attention on one of the two percepts or on a particular image feature, while such attentional affects are considerably weaker in binocular rivalry. One possible explanation for such differences is that the nature of conflict is quite different between binocular rivalry and other forms of bistable perception.

p0070 In the case of reversible figures or ambiguous motion stimuli, the same information is presented

Theoretical Models of Bistable Perception and Behavioral Evidence

p0075 What are the neural processes that govern the timecourse of perceptual alternations in bistable perception? The emerging view is that the neural correlates of bistable perception are dispersed throughout many areas of the visual cortex and beyond. However, different researchers have put different emphasis on the involvement of low-level and high-level processes, respectively.

Low-Level Theories of Bistable Perception

p0080 Proponents of low-level theories argue that bistability results from neural activity fluctuations at the sensory processing level (Figure 2(a)). Neuronal populations that code for the two possible perceptual interpretations of the visual input are thought to be in dynamic competition. Spontaneous fluctuations and adaptation of percept-related neural activity are two mechanisms that could contribute to perceptual dominance of either percept during ongoing rivalry. In bistable motion stimuli, for instance, different subsets of direction-selective neurons responding to visual motion (e.g., in motion-sensitive area V5/MT in the lateral occipitotemporal cortex, see below) code for the two alternative percepts. The neuronal population that codes for the currently dominant percept will exhibit adaptation over time, with the firing rate of these cells waning. Such adaptation will change the competitive equilibrium between the

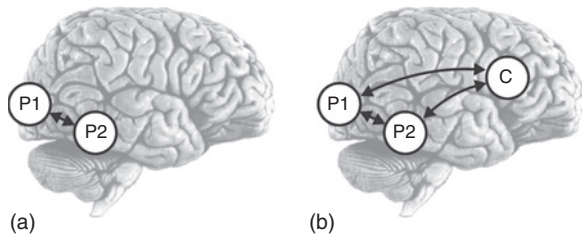


Figure 2 (a) Low-level theory of bistable perception: spontaneous alternations of perceptual states are explained by activity changes of neuronal populations ('P1' and 'P2') in visual cortex that code for the two possible percepts. Possible sources of neural activity changes are adaptation to the currently dominant percept, spontaneous fluctuations, and direct competitive interactions between the two neuronal populations P1 and P2. (b) High-level theory of bistable perception: Perceptual alternations are governed by a central process ('C') involving, for example, frontal brain regions. This central process is thought to evaluate the sensory input and to modify activity in sensory areas via feedback connections. Whenever processes in visual cortex (e.g., adaptation or competitive interactions) act to destabilize activity that underpins the currently dominating percept, higher-order evaluative processes can take effect and initiate a perceptual reorganization.

sensory representations of the two alternative percepts. This could in turn result in the currently dominant neuronal population, and hence the subjective perceptual state, to reverse.

Spontaneous fluctuations of neural activity may additionally affect the dynamics of perceptual alternations. Especially after adaptation of activity coding for the currently dominant percept, spontaneous increases in neuronal activity that codes for the nondominant percept could contribute to a perceptual reversal. In addition to adaptation and spontaneous fluctuations, competitive interactions between neurons coding for rivaling percepts may be an important factor in perceptual bistability. Direct inhibition of neural activity representing the suppressed percept by neurons that code for the currently dominant percept has been implemented in computational models for binocular rivalry, but might also play a role in other forms of bistability.

There is ample evidence to support the idea that adaptation plays an important role in bistable perception. For instance, after prolonged presentation of an unambiguous version of one of the

possible interpretations of an ambiguous stimulus, the previously adapted percept is less likely to occur upon subsequent viewing of the ambiguous stimulus. Similarly, prior adaptation of a monocular stimulus presented to one eye increases the likelihood of perceiving the stimulus presented to the other eye during subsequent binocular viewing. The phase duration of a percept can also be influenced by changing the position of ambiguous and binocular rivalry stimuli in the visual field. Perceptual alternation rates are slowed when binocular rivalry or ambiguous stimuli move within the visual field, thereby avoiding local adaptation. Alternation rates can also be dramatically reduced by showing bistable stimuli intermittently, which can be interpreted along similar lines, implying that intermittent removal of the stimulus prevents adaptation. It should be noted, however, that some features of this stabilizing effect of intermittent stimulus removal are difficult to explain with adaptation alone. For example, even if the stimulus is removed for 30 s or more, observers tend to have the same percept when the stimulus reappears as they had before it disappeared. It is not clear why the neuronal populations coding for the two possible percepts should stay in the same firing state over such prolonged periods of stimulus absence.

Another empirical observation that is difficult to accommodate within models relying on adaptation and competitive interactions at the sensory level alone is that periods of dominance and suppression in bistable vision are characterized by sequential stochastic independence. This means that the longer one percept is suppressed, the more strongly it should compete for dominance in the next cycle, if adaptation was the major determinant of bistability. However, such a relationship between sequential dominance phases is never observed in bistable perception. This has led to the suggestion that other processes in addition to those described at the level of sensory processing should be involved in bistable perception.

High-Level Theories of Bistable Perception

Such an alternative view proposes that perceptual alternations are influenced by a central process

that is involved in the evaluation of sensory input and planning behavioral actions, and that can modify activity in sensory areas via feedback connections (Figure 2(b)). A strong argument in favor of this view is based on the observation that the temporal dynamics of bistability are similar to other exploratory behaviors, such as spontaneous exploratory eye movements, and might therefore reflect a general process serving the continuous automatic exploration and reevaluation of the sensory environment. Accordingly, perceptual alternations may not be the consequence of a specialized mechanism limited to situations of extreme sensory ambiguity. Rather, they could reflect a general mechanism that only becomes evident in cases of extreme ambiguity in the sensory input, but is present continually in normal vision and serves an iterative reevaluation of hypotheses or inferences about the perceptual significance of the current sensory input pattern. The general notion that bistable perception is influenced by higher-level, or at least nonsensory, processes is supported by a number of observations. It is a well established finding that voluntary control can strongly influence the temporal dynamics of bistable perception. Observers can not only willfully increase the probability of one percept over the other but it is also possible to change the rate of alternations voluntarily. The latter effect cannot be attributed to retinal shifts due to eye movements (which can also cause perceptual changes), as it is still present when visual stimuli are presented as afterimages or are stabilized on the retina by other means. Other examples for nonsensory influences on the dynamics of bistable perception include expectations, intelligence, mood disorders, laughter, and meditation.

The Special Case of Binocular Rivalry

As mentioned above, binocular rivalry needs special consideration because of the fundamental difference from other types of bistability that there is not only conflict between two interpretations of one sensory input pattern, but between two different patterns presented to the two eyes. Thus, in addition to competition between the neural pattern representations, competition between eye-specific representations at early stages of central visual information processing may contribute to

rivalry. Current models of binocular rivalry propose a multilevel process involving competitive neural interactions at both monocular stages (eye rivalry) and binocular stages (pattern rivalry) of the visual processing hierarchy. The degree to which eye rivalry and pattern rivalry are involved in the resolution of binocular rivalry depends on a variety of factors, including the exact timing parameters of stimulus presentation and the type of information contained in the rivaling input patterns. Complex object stimuli are more likely to involve rivalry between high-level pattern representations than simple grating stimuli, where competition at monocular processing levels may play a more decisive role.

Neural Correlates of Bistable Perception

A variety of methodologies have been used to study the neural correlates of bistable perception in humans as well as nonhuman primates, including invasive electrophysiological recordings, electroencephalography (EEG), magnetoencephalography (MEG), and fMRI. For a better understanding of the empirical observations made with these techniques, they are briefly described in the following section.

Measuring the Neural Correlates of Bistable Perception

Using invasive electrophysiological techniques to record the spiking activity of neurons is often considered to be the gold standard that is necessary for a quantitative explanation of perception and behavior in terms of its underlying constitutive elements. However, it requires electrodes to be inserted through the skull into the brain, which puts subjects at risk of injury and infection. With the exception of the rare case that electrodes are implanted in humans for diagnostic reasons, e.g., for presurgical mapping in epilepsy, such measurements are limited to nonhuman primates or other animals for ethical reasons. In principle, such electrodes can be used to measure single-unit activity, multiunit activity, and local field potentials (LFP). Single- and multiunit activity reflects

s0065

p0105

s0070

p0110

s0075

p0115

the action potentials (the basic electrical signals required for information processing in the nervous system) recorded from one or more neurons in the vicinity of an electrode. LFPs represent the aggregate activity of a population of neurons located close to the electrode and are thought to reflect mainly synaptic activity associated with both input to and output from a cortical area.

p0120 In human subjects, fMRI has become a popular tool to study the neural correlates of bistable perception. fMRI is based on the measurement of a blood-oxygen level dependent (BOLD) signal, which is a component of the hemodynamic response that is associated with local neural activity. The BOLD signal is essentially linearly correlated with multiunit activity and even more strongly with LFPs. It might therefore reflect pre- and postsynaptic activity and hence the processing in an area more closely than multiunit activity. One drawback of fMRI is that it does not measure neural activity directly and that it has a limited temporal resolution (in the range of seconds) due to the sluggishness of the hemodynamic response. Despite great technical improvements over the last years, fMRI has also limited spatial resolution (in the range of millimeters) and can therefore only measure signals that are generated by relatively large populations of neurons. However, the spatial resolution is still considerably better than that of other noninvasive methods as EEG and MEG. The greatest strength of fMRI is its capacity to record activity from the entire brain essentially simultaneously. In contrast to single- or multiunit recordings, fMRI, therefore, in principle does not require prior assumptions as to where activity is expected to occur.

p0125 EEG and MEG measure the electric activity of the brain by recording from electrodes placed on the scalp and the magnetic fields produced by electrical activity in the brain, respectively. EEG and MEG responses to external stimuli, so-called event-related potentials (ERPs) are also thought to reflect the summed electrical effects of synaptic neurotransmission in large neuronal populations. Similar to the association between the BOLD signal and LFPs, there is also a nearly linear relationship between ERP amplitude measured with EEG and BOLD signal measured with fMRI in sensory cortices. While EEG and MEG have a much

higher temporal resolution than fMRI, their spatial resolution is inferior to fMRI and especially EEG, is limited to recording only electrical activity that is generated in superficial cortical regions within the reach of scalp electrodes.

Taken together, there seems to be an overall good agreement between these various measures of neural activity, but it is important to bear in mind that the noninvasive methods available (fMRI, EEG, and MEG) measure neural activity associated with populations of neurons only indirectly and therefore need to be interpreted with caution. On the other hand, single cell measures have – in addition to the fact that they are usually only available from nonhuman primates and can therefore not easily be extrapolated to humans – the disadvantage that the number of neurons that can be recorded simultaneously is limited.

Choosing the Bistable Stimulus Paradigm

The majority of studies have investigated binocular rivalry rather than other forms of bistability. This tendency is most pronounced in electrophysiological studies in animals, which may be due to the fact that bistable perception is easier to achieve and to validate in nonhuman subjects using binocular rivalry stimuli than with reversible figures, the ambiguity of which may rely more on higher cognitive functions. But also in human studies binocular rivalry has been a very popular paradigm. One reason for this may be that binocular rivalry is a particularly intriguing phenomenon, but more mundane factors such as practical feasibility and functional anatomy of the visual system can also bias 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 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 (see below). Responses to two rivaling object categories (e.g., faces and houses) can therefore easily be dissociated using fMRI. To a limited degree, this

p0130

s0080

p0135

may also be possible with selected reversible figures involving complex objects, but is much more difficult with geometrical stimuli like the Necker cube or bistable motion stimuli, where responses to the two alternative percepts are not so clearly segregated. As noted above, however, it should be kept in mind that the interpretation of binocular rivalry studies with regard to the neural correlates of consciousness is complicated by the involvement of mechanisms specifically operating at the monocular levels of stimulus processing.

s0085 **Subcortical and Early Cortical Processing**

p0140 The first stage of central visual processing is the lateral geniculate nucleus (LGN) of the thalamus. The retinal projections from each eye terminate in different laminae of the LGN, so that they remain segregated and processing is hence strictly monocular. Some monocular processing is still preserved at the lowest level of cortical visual processing, in the ocular dominance columns of primary visual cortex (V1). Beyond V1 visual processing is essentially binocular. That is, input from corresponding retinotopic locations from the two eyes is processed together and information about the eye of origin appears not to be preserved at these higher levels.

p0145 The role of the earliest stages of visual processing in the brain, the LGN and V1, in bistable perception is controversial. This is because studies using different methodologies (single unit recordings and fMRI) in different species (monkeys and humans) have yielded diverging results. Single unit recordings in the LGN of awake monkeys during binocular rivalry provide no evidence for a correlate of rivalry in the LGN, whereas fMRI studies in humans found that BOLD responses in the LGN reflect eye-specific dominance and suppression. A similarly incongruent picture has emerged from studies investigating the role of V1 in binocular rivalry. In electrophysiological recordings in awake monkeys, only a small percentage of cells showed activity that reflected dominance and suppression in binocular rivalry, while human fMRI studies have demonstrated strong effects of binocular rivalry in V1. Differences between methodologies and species may contribute to such divergent findings, which await further clarification. With regard to consciousness, it has been proposed that

the evidence from human fMRI studies indicates an important role for early visual processing, at least in V1, for conscious awareness. However, activity in LGN and V1 may merely reflect the dominance of one monocular processing channel over the other, thus gating what information reaches higher-level visual areas rather than being directly related to conscious perception. A similar role for early visual cortex is suggested by fMRI findings in bistable apparent motion perception. Whenever apparent motion is inconsistent with additional image cues (e.g., color), early visual cortex activity is suppressed, which may reflect regulatory mechanisms that flexibly gate early visual feature processing in accord with an overriding perceptual decision.

Intermediate Levels of Visual Processing

Beyond V1, the primate visual system is organized in a distributed fashion, with different aspects of the visual scene being analyzed in different cortical areas. Visual areas beyond V1 (striate cortex) are at large called extrastriate visual cortex. Extrastriate processing is divided in two major pathways, the dorsal and ventral streams. The dorsal stream is associated with motion processing and representations of object locations. It extends from V1 through areas V2, V3A, and V5/MT to the inferior parietal lobe. Area V5/MT is in humans located in the lateral occipitotemporal junction and plays a prominent role in the processing of motion signals (Figure 3). The ventral stream passes from V1 through V2 and V4 to inferotemporal cortex. V4 is located in the ventral occipital cortex anterior to V2 and is thought to preferentially process color information. The inferotemporal cortex has an essential role in higher visual functions, such as object recognition. In humans, inferotemporal cortex accommodates various functionally characterized areas that are associated with certain object categories, most notably the fusiform face area and the parahippocampal place area.

Electrophysiological recordings in early extrastriate areas (V4 and V5/MT) of awake macaque monkeys reporting rivalry showed activity modulations that were stronger than in V1 but still modest compared with the perceptual changes experienced during rivalry. In contrast, responses were markedly different in inferotemporal cortex.

s0090

p0150

p0155

Recordings showed that most of the inferotemporal neurons were active only when their preferred stimulus was perceived and showed essentially no activity during the perceptual suppression of the stimulus, indicating that inferotemporal cortex represents a stage of processing beyond the resolution of perceptual conflict. In humans, invasive electrophysiological recordings were made from the temporal lobes of patients in whom electrodes had been implanted for diagnostic reasons and showed results compatible with those obtained from monkeys. During binocular rivalry, medial temporal lobe neurons tuned to a specific stimulus category fired selectively when their preferred stimulus was perceived, but not when it was perceptually suppressed and invisible. Findings from fMRI studies in humans experiencing binocular rivalry support the notion that binocular conflict is fully resolved at higher levels of the visual processing hierarchy. During rivalry, fMRI responses that are recorded in the fusiform face area to face stimuli – and in the parahippocampal place area to images of places – are large and equal in amplitude to responses evoked by nonrivalrous stimuli. Interestingly, temporary removal of binocular rivalry stimuli, when the stimulus perceived on reappearance tends to be the one in awareness as they disappeared, is accompanied by persistent activity in functionally specialized regions of human visual cortex representing the last percept before stimulus removal. Such activity during stimulus absence is not measurable during removal of nonrivalrous stimuli, suggesting a role for specialized extrastriate

cortex in stabilizing perception in situations of perceptual conflict.

Studies with reversible figures and ambiguous motion stimuli support the notion that intermediate levels of visual processing are involved in the resolution of visual ambiguities and conflict. In parallel with the observation in binocular rivalry using house and face stimuli, fMRI activity in the fusiform face area is greater during face perception during viewing of Rubin's face/vase illusion (Figure 1(a)). Percept specific activity in extrastriate visual areas can also be found during bistable motion perception. Electrophysiological recordings in monkeys showed that during viewing of a bistable random-dot kinematogram, neuronal firing in area V5/MT correlates with the reported direction of rotation. Distinguishing activity associated with different directions of motion is more difficult with fMRI because there is no spatial segregation between cells selective of different motion directions that could easily be resolved on the basis of fMRI signals. However, motion stimuli that are ambiguous with respect to the type of motion have shown differential activity in human motion-sensitive extrastriate cortex. During viewing of ambiguous plaid stimuli where perception alternates between global motion and component motion, stronger activity in V5/MT is found during component-motion perception. Similarly, the comparison of object-motion with illusory self-motion during large-field stimulation with a rotating stimulus is accompanied by differential activation in V5/MT and also in area V3A. Finally, when a simple apparent motion stimulus composed of two dots shown in alternation in different visual fMRI(ot)20.2(ic47TD5(ul)19.2(s)11.9(t)20.3(i)0)-329.5(

with color cues, suggesting that extrastriate color processing influences the resolution of perceptual ambiguities.

p0170 While the work mentioned so far has capitalized on identifying differences in activity associated with different perceptual states, another line of research has been primarily concerned with the neural events associated with and time-locked to perceptual reversals. fMRI studies investigating reversal-related activity have used a variety of bistable paradigms including binocular rivalry, reversible figures, and ambiguous motion stimuli. In addition to distributed activations in frontal and parietal brain regions (see below), these studies have consistently found transient activity increases in extrastriate visual areas in association with perceptual reversals. These activations are tuned to the visual feature or attribute that is perceived to change. While changes involving face or object percepts are accompanied by activations in object processing areas of the ventral stream, perceived changes in motion direction or motion type are associated with activations in motion-sensitive areas, most notably V5/MT (Figure 3).

p0175 Taken together, electrophysiological and fMRI studies have established that neural activity in functionally specialized extrastriate cortex correlates with subjective perception during bistability. While it is difficult to make strong quantitative statements on the basis of fMRI measurements, single-cell recordings in monkeys suggest that the degree of correlation increases at successive stages of the visual processing hierarchy. While the exact role of LGN and V1 is still controversial, it seems now firmly established that high-level areas in inferotemporal cortex represent a stage of processing beyond the resolution of perceptual conflict. These findings have often been taken as evidence for a crucial role of higher-level visual cortex in consciousness. It has been argued that if neurons in these areas show such strong modulations in accord with perception, neural activity in these areas should be a prerequisite for visual information to gain access to consciousness.

s0095 **Parietal and Prefrontal Cortex**

p0180 The possible role of brain regions outside the visual system has been investigated almost entirely in human subjects. Neuroimaging investigations into

the neural correlates of bistable perception have indicated that activity in the parietal and prefrontal cortices might be associated with conscious perception in normal subjects. As mentioned in the section titled 'Intermediate levels of visual processing,' these studies measured brain activity time-locked to spontaneous perceptual reversals both during binocular rivalry and for other bistable stimuli. In addition to reversal-related activations in extrastriate visual areas, cortical regions with activity that reflects perceptual transitions include inferior parietal and inferior frontal cortex, regions previously implicated in regulating access of sensory information to consciousness. While extrastriate areas are equally engaged by nonrivalrous perceptual changes, parietal and prefrontal regions show significantly greater activation associated with perceptual alternations during viewing of rivalrous or ambiguous stimuli.

The attempt to define in more detail the functional significance of reversal-related activations in higher-order brain structures inevitably leads into a primacy debate resembling the chicken-and-egg problem. In one view, changes in perception are caused by neural activity fluctuations in visual cortex (the low-level theory propounded above, see Figure 2(a)). Whenever a perceptual change occurs, the underlying neural event in visual cortex is communicated to higher-order areas and entrains their activation in a feed-forward fashion, similar to external stimulus changes. An alternative view also proposes that visual cortical areas house the competing perceptual representations and that perceptual dominance is ultimately underpinned by their relative degree of activity. However, in this view, the reorganization of activity in visual cortex during perceptual reversals is initiated and instructed by frontal and parietal brain structures (the high-level theory described above, see Figure 2(b)). 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. Still, temporal precedence is generally considered good evidence in favor of a putative causal role. Invasive neurophysiological recordings would therefore appear ideally suited to resolve this question but suffer from the uncertainty of where exactly to place recording electrodes for instance in the frontal lobe.

p0185

Recent analytical approaches have made it possible to resolve latency differences between fMRI responses in the range of a couple of hundreds of milliseconds. Indeed, chronometric analyses of fMRI activations in association with spontaneous changes on apparent motion perception showed that activations in right inferior frontal cortex occur earlier during bistable perception than during externally induced perceptual changes, while such temporal precedence is absent in extrastriate visual cortex. This suggests that prefrontal structures may participate in initiating spontaneous reversals during bistable perception. In line with this notion, studies in patients with brain lesions have shown that spontaneous perceptual alternations are slowed down in cases of focal damage to the right prefrontal cortex. The low-level theory that adaptation of percept-related neural activity plays an important role in perceptual bistability is not irreconcilable with a causal role of higher-order processes in initiating perceptual changes. The actual alternations of perception could be determined by the joint effect of local processes embedded into a more global process. That is, whenever local processes (e.g., adaptation) act to destabilize activity that underpins the currently dominating percept, higher-order evaluative processes can take effect and initiate a perceptual reorganization (Figure 2(b)).

In addition to participating in the initiation of perceptual changes, higher-order brain structures may also contribute to the stabilization of perception. As mentioned above, perception can be stabilized by intermittently removing a bistable stimulus, and this effect is still present when the stimulus disappears for intervals in the range of tens of seconds. An individual observer's tendency to stabilize a percept across such periods of stimulus removal strongly correlates with brain activity in frontal and parietal regions previously implicated in working memory. This suggests that higher-order brain structures in prefrontal and parietal cortices may not only play a role in the initiation of perceptual reversals but also in the stabilization of perception.

The Role of Neural Synchronization

This account of the neural underpinnings of bistable perception has so far almost exclusively been concerned with their anatomical location.

Relatively few studies have addressed the question of whether bistable perception may be related to neural synchronization, an approach based on state-change theories of consciousness. The role of neural synchronization in binocular rivalry was studied in awake cats viewing dichoptically presented drifting gratings with orthogonal orientations. Electrophysiological recordings from visual cortex show that neurons representing the dominant stimulus increase their synchrony, whereas cells that process the suppressed pattern decrease their temporal correlation. In contrast to neural synchrony, however, the firing rates of cells responding to the dominant and the suppressed stimulus did not differ. This finding may provide a link between the divergent results from electrophysiological recordings and fMRI measurements of early visual processing, especially as the fMRI signal also correlates with the degree of neural synchronization.

In humans, MEG was used to identify synchronization in neural activity between spatially distributed cortical areas with dominance phases in binocular rivalry. Rival gratings flickering at different frequencies were used to tag the MEG signals associated with the two gratings. Over a wide array of sensor locations encompassing the occipital, parietal, temporal, and frontal lobes, the amplitudes of the MEG responses correlated with observers' reports of dominance and suppression. Dominance phases of rivalry were also associated with marked increases in synchronization of MEG signals recorded from widely distributed sensors, with the most prominent examples of synchronization arising in frontal areas of the brain.

Taken together, there is thus evidence demonstrating that neural synchronization, both locally within visual cortex and globally among spatially remote brain regions, may contribute to the resolution of visual conflict in bistable perception.

Conclusions

What have we learned from bistable perception with regard to the neural correlates of consciousness? Quite apart from the findings from electrophysiological and neuroimaging studies, bistable perception is an impressive illustration of the constructive nature of perception. The fact that visual

perception can change while the physical input remains constant clearly demonstrates that visual perception results from active interpretive processes in the brain. While this general argument is historically important, empirical studies of bistable perception over the last decade have yielded the following insights:

- Bistable perception is a multilevel process. Neural correlates of bistable perception are measurable throughout the visual system and beyond.
- Neural activity fluctuations in neuronal populations representing the competing percepts are involved in determining the perceptual outcome and hence influence conscious awareness.
- High-level visual areas play a key role in consciousness. Activity in these areas reflects the actual perceptual outcome of the processes involved in the resolution of visual ambiguity and conflict.
- Central processes involving prefrontal and parietal brain regions can exert an influence on bistable perception by stabilizing the current percept or by initiating perceptual reversals. Conscious perception is therefore a result of local sensory processes embedded into more global evaluative and interpretive processes.
- Neural synchronizations are likely to be involved in generating a coherent conscious percept.

We conclude that bistable perception has proven a valuable tool for neuroscientific research and yielded important insights into the neural correlates of conscious vision. Some aspects, such as the prominent role of high-level extrastriate visual areas in conscious vision, are supported by a significant number of studies using very different paradigms and methodologies and therefore appear to be firmly established. Research into the neural mechanisms of bistable perception has also shed light on the role of early visual processing, which may be more important for conscious vision than previously thought. However, more research is needed to resolve controversies that have arisen from seemingly contradictory results, and to provide a more detailed account of the role that low-level processing, especially in V1, plays in consciousness. Similarly, fascinating new insights were gained about interactions between higher-order frontoparietal regions and visual cortex and about the role of neural synchronizations in conscious

vision. Future research using bistable perception and related phenomena should try to provide a more detailed account of how these processes contribute to human consciousness.

See also: Neural Basis of Perceptual Awareness (00054); Perception: Unconscious Influences on Perceptual Interpretation (00060); Visual Imagery and Consciousness (00083).

Suggested Readings

- Alais D and Blake R (2005) *Binocular Rivalry*. Cambridge, MA: MIT Press.
- Blake R and Logothetis NK (2002) Visual competition. *Nature Review, Neuroscience* 3: 13–21.
- Haynes JD, Deichmann R, and Rees G (2005) Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* 438: 496–499.
- Kleinschmidt A, Büchel C, Zeki S, and Frackowiak RSJ (1998) Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society of London, Series B* 265: 2427–2433.
- Leopold DA and Logothetis NK (1999) Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences* 3: 254–264.
- Leopold DA, Maier A, Wilke M, and Logothetis NK (2005) Binocular rivalry and the illusion of monocular vision. In: Alais D and Blake R (eds.) *Binocular Rivalry*, pp. 231–258. Cambridge, MA: MIT Press.
- Long GM and Toppino TC (2004) Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin* 130: 748–768.
- Lumer ED, Friston KJ, and Rees G (1998) Neural correlates of perceptual rivalry in the human brain. *Science* 280: 1930–1933.
- Parker AJ and Krug K (2003) Neuronal mechanisms for the perception of ambiguous stimuli. *Current Opinion in Neurobiology* 13: 433–439.
- Rees G (2007) Neural correlates of the contents of visual awareness in humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Science* 362: 877–886.
- Sheinberg DL and Logothetis NK (1997) The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences of the United States of America* 94: 3408–3413.
- Sterzer P and Kleinschmidt A (2007) A neural basis for inference in perceptual ambiguity. *Proceedings of the National Academy of Sciences of the United States of America* 104: 323–328.
- Tong F, Meng M, and Blake R (2006) Neural bases of binocular rivalry. *Trends in Cognitive Sciences* 10: 502–511.
- Tong F, Nakayama K, Vaughan JT, and Kanwisher N (1998) Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21: 753–759.
- Tononi G, Srinivasan R, Russell DP, and Edelman GM (1998) Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proceedings of the National Academy of Sciences of the United States of America* 95: 3198–3203.

Biographical Sketch



Philipp Sterzer (born 1970, Germany) is a supervising psychiatrist and the head of the Visual Perception Laboratory at the Department of Psychiatry, Charité University Hospital, Berlin. After medical training at Ludwig Maximilian University in Munich and Harvard Medical School in Boston, USA, he obtained his MD under the supervision of Florian Holsboer at the Max-Planck Institute of Psychiatry in Munich. He completed his training in clinical neurology at Johann-Wolfgang-Goethe University in Frankfurt am Main, where he also worked as a postdoctoral research fellow in the laboratory of Andreas Kleinschmidt. He then worked as a postdoctoral fellow in Geraint Rees's group at the Wellcome Trust Centre for Neuroimaging, University College London, before moving to Berlin in 2006 to work as a clinical psychiatrist. In 2008, he became a group leader with the award of an Emmy Noether junior research group from Deutsche Forschungsgemeinschaft. His main research interests include the neural basis of visual awareness, the interactions of emotion and motivation with visual awareness, and alterations of these processes in mental diseases.



Geraint Rees (born 1967, the United Kingdom) is a professor of cognitive neurology and Wellcome Trust Senior Clinical Fellow at the Institute of Cognitive Neuroscience and Wellcome Trust Centre for Neuroimaging, University College London. After medical training in Cambridge, Oxford, and London, he completed his PhD under the supervision of Chris Frith at University College London's Functional Imaging Laboratory. He then worked as a postdoctoral fellow in Christof Koch's laboratory at the California Institute of Technology for two years before returning to the Institute of Cognitive Neuroscience at University College London in 2001. In 2002, he became a group leader with the award of a senior fellowship from the Wellcome Trust. His work has been internationally recognized with the award in 2003 of the Young Investigator Medal of The Organization for Human Brain Mapping. In 2007, he was awarded the Experimental Psychology Society prize and gave the Royal Society Francis Crick lecture. His research seeks to understand the neural basis of human consciousness.