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Multistable Perception and the Role of the Frontoparietal Cortex in Perceptual Inference

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Abstract

A given pattern of optical stimulation can arise from countless possible real-world sources, creating a dilemma for vision: What in the world actually gives rise to the current pattern? This dilemma was pointed out centuries ago by the astronomer and mathematician Ibn Al-Haytham and was forcefully restated 150 years ago when von Helmholtz characterized perception as unconscious inference. To buttress his contention, von Helmholtz cited multistable perception: recurring changes in perception despite unchanging sensory input. Recent neuroscientific studies have exploited multistable perception to identify brain areas uniquely activated in association with these perceptual changes, but the specific roles of those activations remain controversial. This article provides an overview of theoretical models of multistable perception, a review of recent neuroimaging and brain stimulation studies focused on mechanisms associated with these perceptual changes, and a synthesis of available evidence within the context of current notions about Bayesian inference that find their historical roots in von Helmholtz's work.



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Contents

INTRODUCTION	78
MECHANISMS CAUSING PERCEPTUAL TRANSITIONS	
IN MULTISTABLE PERCEPTION	81
PERCEPTUAL STATE TRANSITIONS AS A WINDOW ONTO	
PERCEPTUAL INFERENCE	84
META-ANALYSIS OF CORTICAL TOPOGRAPHY OF FUNCTIONAL	
MAGNETIC RESONANCE IMAGING AND TRANSCRANIAL	
MAGNETIC STIMULATION FINDINGS	86
FUNCTIONAL NEUROIMAGING OF MULTISTABLE PERCEPTION	87
BRAIN STIMULATION	91
FUNCTIONAL ROLES OF FRONTAL AND PARIETAL SUBREGIONS	93
DISCUSSION	95

INTRODUCTION

The year 2017 marks the 150th anniversary of the publication of the third volume of Herrmann von Helmholtz’s monumental three-volume *Handbuch der physiologischen Optik* (von Helmholtz 1867), one of the most important, comprehensive books in the history of sensory physiology. Among the book’s many credits is von Helmholtz’s explication of the idea that perception entails unconscious inference. The origin of this idea can be traced back almost 1,000 years to the polymath Ibn Al-Haytham, also known as Alhazen (Al-Haytham 1989, Cavanagh 2011, Howard 1996). Centuries later, as pointed out by Wade & Ono (1985), intimations of that idea resurfaced in Wheatstone’s famous essay on binocular stereopsis (Wheatstone 1838). But it is von Helmholtz who is credited with resurrecting the idea of unconscious inference with a clarity that ensured its endurance to this day. Specifically, visual perception perforce comprises an inferential process carried out at an unconscious level, the aim being to identify what in the world one is looking at (a challenge dubbed inverse optics in contemporary parlance). This process of “unconscious inference” is essential, so goes the argument, because optical images formed on the retina provide ambiguous information about the specific objects and events that constitute the sources of those retinal images. To resolve those ambiguities, the nervous system must rely on information embodied in prior experience, in expectations, in context, and in the motor activities of the person faced with the challenge of seeing. In other words, the nervous system must make a perceptual decision regarding the most likely state of the world given the evidence from these different sources of information.

The notion that vision entails inference has continued to reverberate throughout the century and a half since von Helmholtz gave new life to Alhazen’s idea. Thus, one encounters an appeal to inference-like processes in the writings of Brunswik (1943), Gregory (1980), MacKay (1956), Rock (1983), Neisser (1967), Barlow (Barlow et al. 1972), and Knill & Richards (1996), to name just a few. Besides unconscious inference, various other terms have been used to characterize this process, including analysis by synthesis, hypothesis testing, probabilistic functionalism, cognitive agency, and Bayesian inference. In recent years, the idea has gained substantial traction within computational neuroscience (e.g., Friston 2005, Petrovici et al. 2016, Summerfield & de Lange 2014) with the development of so-called predictive coding models that frame perception as the culmination of dynamical neural activity within a hierarchical predictive system (an idea we return to in our Discussion).

Not only did von Helmholtz champion Alhazen's idea that perception must be an inference-based decision-making process, he also buttressed his conviction with reference to viewing situations where the culmination of this inferential process is laid bare in the viewer's experience. As von Helmholtz (1867, pp. 15–16) put it:

SFM:
structure-from-motion

Without any change of the retinal images, the same observer [in these situations] may see in front of him various perceptual images in succession, in which case the variation is easy to recognize . . . in a case of this sort various perceptual images may be developed; and we should seek . . . to discover what circumstances are responsible for the decision one way or the other.

In this quote, von Helmholtz discusses viewing situations that give rise to multistable perception: situations where what an individual is looking at remains invariant but what the individual sees fluctuates over time between alternative, incompatible perceptual interpretations. Von Helmholtz may have been primed for this line of reasoning by reading section 10 of Wheatstone's (1838, pp. 381–82) essay on binocular vision, where Wheatstone comments on viewing situations where "indetermination" of perceptual judgment arises in viewing situations permitting "double interpretation." As one such example, Wheatstone explicitly points to the reversible figure popularly known as the Necker cube. An example of that figure and other classic examples of viewing situations that promote multistable perception are shown in **Figure 1**.

At face value, multistable perception does indeed seem to provide an excellent means for testing theories built around the notion of perception as inference: Metaphorically speaking, when faced with ambiguity or visual conflict, the brain weighs evidence favoring different, alternative hypotheses about what is being viewed, and when that evidence is insufficiently compelling to reject all but one interpretation, the brain vacillates between the alternatives (**Figure 1**, *bottom row*). Indeed, several characteristics of multistable perception comport well with the idea of perception as inference based on multiple information sources. To give some examples:

- When the fidelity of the evidence that favors one interpretation during multistable perception is higher than that of the evidence that favors another, perception is biased toward that former interpretation. Thus during binocular rivalry, a form of multistable perception evoked when the two eyes view dissimilar monocular stimuli (**Figure 1c**), a well-focused monocular stimulus enjoys greater predominance in the observer's perceptual experience than does a blurred one (Arnold et al. 2007, Levelt 1966). Similarly, an ambiguous structure-from-motion (SFM) animation (**Figure 1d**) is more frequently seen to rotate in a given direction when supplementary visual information (e.g., luminance disparity) consistent with that direction is added to the display (Doshier et al. 1986).
- When the ecological likelihood of one perceptual outcome is higher than that of a competing outcome, the more plausible interpretation predominates. Thus, when viewing an ambiguous SFM stimulus, perceived rotational motion tends to be resolved in favor of the rotational direction implied by friction, in obedience to physical principles (Gilroy & Blake 2004). In a similar vein, a visual stimulus portraying a ground surface dominates in binocular rivalry over a stimulus portraying a ceiling surface, presumably reflecting the ground-plane perspective's salience for humans, who spend nearly all our time navigating on ground surfaces (Ozkan & Braunstein 2009).
- When stimulus information from another, nonvisual sensory modality accompanies viewing of a multistable display, that auxiliary information can boost predominance in favor of the visual interpretation that is consistent with the nonvisual input. These kinds of ancillary multisensory interactions have been reported for multistability elicited by an ambiguous face picture (i.e., old woman/young girl figure) accompanied by unambiguous voices (Hsiao

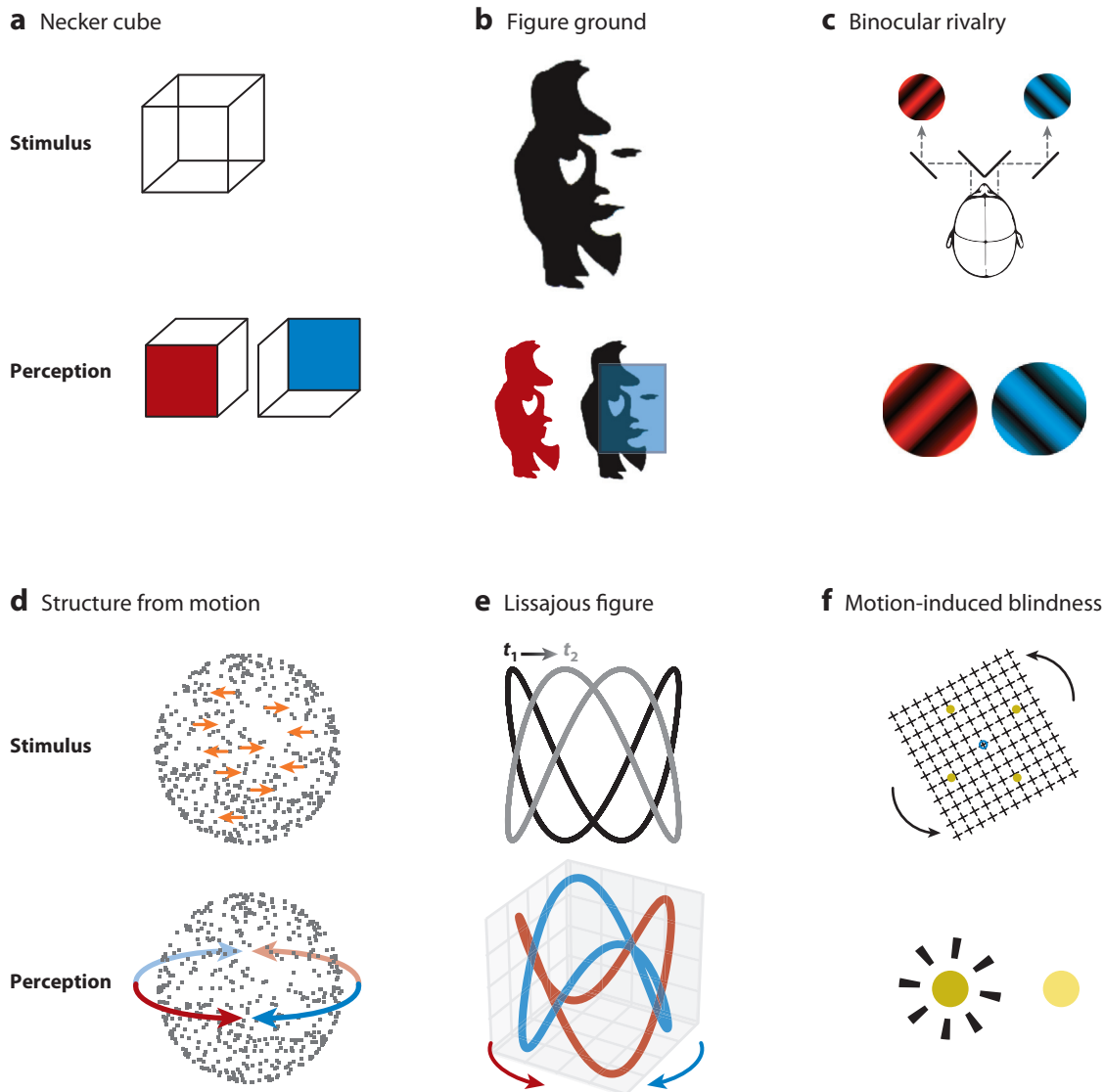


Figure 1

Examples of multistable stimuli (*top rows*) and their associated perceptual interpretations, schematically indicated in red and blue (*bottom rows*). (*a*) The Necker cube is ambiguous in terms of the three-dimensional geometry it pictorially represents. Two different cube faces can be perceived as the forward-facing side of the cube. (*b*) Ambiguities in figure–ground assignment promote alternative interpretations of the pictorial content, which, in this stimulus, can correspond to either a saxophone player or a woman’s face. (*c*) Binocular rivalry takes place when the two eyes view dissimilar monocular images, presented in this case through a stereoscope. At any given moment, the dominant percept corresponds to one of the two eyes’ images. (*d*) Motion is a potent visual cue to spatial structure, leading to the perceptual phenomenon of structure-from-motion or the kinetic depth effect. When the projection of a sphere of dots is presented orthographically, depth order is ambiguous, and the sphere can be seen to rotate with the front-surface dots moving either leftward or rightward. (*e*) Lissajous figures are also ambiguous structure-from-motion stimuli. When viewing this stimulus, transitions between the perceptual interpretations of the nearest line segment moving left or right are temporally confined to moments of self-occlusion. (*f*) Motion-induced blindness occurs when static stimuli (*yellow circles*) are presented near a moving surface. The static stimuli periodically disappear from the viewer’s awareness. Panel *b* is reproduced with the kind permission of Roger Shepard, the copyright holder of this image (Shepard 1990).

et al. 2012) and by ambiguous apparent motion stimuli paired with tactile motion (Conrad et al. 2012). In the case of binocular rivalry, there are multiple examples of auxiliary, nonvisual influences, such as rivalry involving visual musical notation accompanied by melodic sound (Lee et al. 2015), visual gratings paired with tactile stimulation by a grooved surface (Lunghi et al. 2010), or pictures of familiar objects accompanied by distinct odors (Zhou et al. 2012).

- When a given visual interpretation is more consistent than a competing interpretation with the current behavioral context, perceptual dominance favors the interpretation implied by the context (Sundareswara & Schrater 2008). Thus, for example, a self-controlled, rotating globe dominates in binocular rivalry compared to the same globe rotating in the same manner but not under the viewer's control (Maruya et al. 2007).
- Multistable perception is influenced by prior experience and expectations. When observers are repeatedly exposed to the same ambiguous stimulus, perception upon each new stimulus presentation strongly tends to be the same as the percept during the preceding presentation (Leopold et al. 2002, Orbach et al. 1963, Pearson & Brascamp 2008). Similarly, perception of ambiguous stimuli can also be strongly biased by prior exposure to an unambiguous stimulus (priming) (Pearson et al. 2008, Schmack et al. 2016). Moreover, it is also well documented that learned expectations—both implicit and explicit—can bias the interpretation of perceptually ambiguous stimuli (Di Luca et al. 2010; Schmack et al. 2013a, 2016; Sterzer et al. 2008).

Scientific interest in multistable perception has endured since the time of von Helmholtz, but different eras have had different emphases and angles on the subject. During the past few decades, much research has been concerned with the search for neural processes that bring about the spontaneous perceptual alternations that characterize multistable perception. For instance, functional magnetic resonance imaging (fMRI) research has focused on neural events that specifically accompany the transitions between perceptual states, hoping that those events could provide insights into the inference processes that govern the dynamics of multistable perception. In this article, we review this body of work and evaluate it in the light of von Helmholtz's and Alhazen's ideas. In particular, we first give an overview of theoretical models of multistable perception and their implications for perceptual inference. We then review recent neuroimaging and brain stimulation work that has focused on the mechanisms underlying transitions in multistable perception, also touching on an ongoing controversy regarding the involvement of frontal and parietal brain regions in this context. Finally, we attempt to provide a synthesis of the available empirical evidence within current models of perceptual inference.

Methodologically, the focus of our review is primarily psychophysical observations combined with transcranial magnetic stimulation (TMS) and fMRI—these are the approaches that, in our view, have promoted the substantial progress witnessed in recent years. This means that our discussions do not touch on related work involving approaches such as electroencephalography (EEG; reviewed in Kornmeier & Bach 2012) or assessment of multistable perception in lesion patients (e.g., Ricci & Blundo 1990, Valle-Inclan & Gallego 2006). Nevertheless, some of our more general points are likely to be relevant to that work as well.

MECHANISMS CAUSING PERCEPTUAL TRANSITIONS IN MULTISTABLE PERCEPTION

Although it makes sense to focus on the time period surrounding perceptual transitions when trying to understand their cause, the neural processes that lead to transitions are not necessarily confined to this time period alone. Existing attempts to model the dynamics of multistable perception posit rapid neural changes at the time of the transition, as well as gradual changes during quiescent

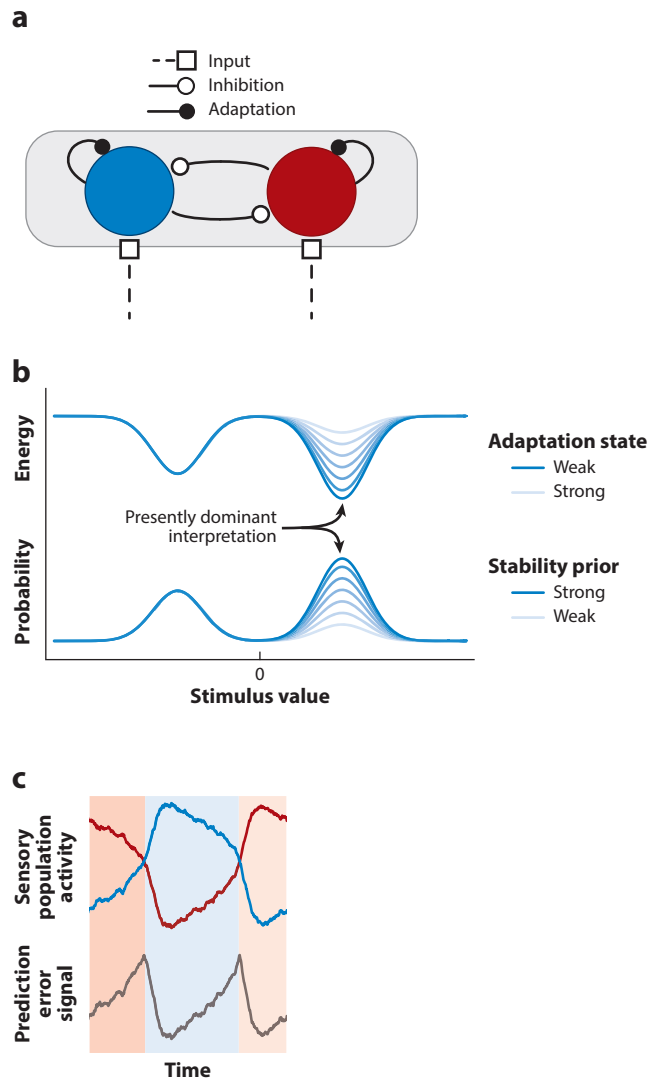
fMRI: functional magnetic resonance imaging

TMS: transcranial magnetic stimulation

EEG: electroencephalography

periods when perception remains stable between transitions. In this section, we review and link two dominant classes of such models and illustrate the relevant concepts in **Figure 2**.

Traditionally, dynamical systems accounts of multistable perception assume three neurally plausible ingredients shaping the time course of multistable perception: inhibition, adaptation, and neural noise (Hock et al. 2003, Kalarickal & Marshall 2000, Laing & Chow 2002, McDougall 1903). Under such accounts, separate pools of neurons, each representing the information pertaining to one of the two perceptual interpretations, exert mutual inhibition on one another. It is this inhibition that allows one interpretation's neuronal pool to suppress activity in the neuronal pool representing the other interpretation, thus temporarily promoting coherent perceptual dominance of one of the two alternatives (**Figure 2a**). During these dominance periods, activity in the dominant pool diminishes as a result of adaptation (**Figure 2b, top**); the dominant pool thereby slowly relinquishes its suppressive grip on the other until the balance of power tips and a rapid transition



occurs (**Figure 2c, top**). When multiple cycles of alternating dominance are allowed, the process will further involve recovery from adaptation of the now-suppressed pool. Thus, in this view, the relative activations of the perceptual interpretations are continually modulated by adaptation and those activations change rapidly during the transition. Additionally, various sources of noise combine to introduce variability in the time elapsing between successive transitions (Kang & Blake 2011, Moreno-Bote et al. 2007). Evidence from psychophysics, brain imaging, and neuropharmacology supports the involvement of each of these three ingredients (Alais et al. 2010, Blake et al. 2003, Pastukhov & Braun 2011, van Loon et al. 2013; although see Sandberg et al. 2016), and simulations of dynamical systems models that employ these ingredients capture hallmark temporal characteristics of multistability (Brascamp et al. 2006, Noest et al. 2007, Wilson 2007).

This traditional conceptualization has recently been supplemented by conceptualizations that frame perceptual multistability in terms of the Bayesian principle of predictive coding (Gershman et al. 2012, Hohwy et al. 2008, Kanai et al. 2011, Megumi et al. 2015, Schmack et al. 2016, Schrater & Sundaeswara 2006, Weinhhammer et al. 2017). On the face of it, predictive coding theories are more closely related to von Helmholtz's and Alhazen's ideas, in the sense that they are explicitly phrased in terms of inference. In particular, under these theories, perception results from hierarchical Bayesian inference, in which each level of the processing hierarchy forms a hypothesis to predict, in a feedback fashion, the input received by the level below it. This lower level, in turn, sends upward a so-called prediction-error signal that codes the discrepancy between this prediction and the actual input, and the predictive model is then adjusted on the basis of this discrepancy (Friston 2005, Hohwy 2012, Lee & Mumford 2003). Perception, in this framework, is the result of iterative adjustments across all levels of the hierarchy, mirroring von Helmholtz's conceptual notion that perception would involve a neural reconstruction of the hypothesized cause of input. According to one model of multistable perception that conforms to this predictive coding view (Hohwy et al. 2008), a stimulus that gives rise to multistable perception provides equally strong sensory evidence (Bayesian likelihood) for two (or more) different percepts, but the currently dominant percept establishes an implicit prediction (prior) that perception will remain similar in the near future. This stabilizing prediction would be implemented as feedback from higher to lower hierarchical levels. The application of Bayes' rule combines the sensory evidence

←

Figure 2

Mechanisms of multistable perception. (a) In the dynamical systems account, multistable perception results from mutual inhibition between, and adaptation of, distinct neural populations that correspond to the alternative perceptual states. (b) (top) The dynamical system can be represented by means of an energy landscape in which the system state tends to occupy the lowest point in the landscape (the bottom of a so-called well). During the dominance period of a perceptual interpretation, adaptation decreases the depth of the presently occupied well and leads to the occurrence of a transition to the other, now deeper, well. (b) (bottom) In the predictive coding account of multistable perception, the presently dominant state remains dominant as a result of a stability prior, thought to reflect learned temporal characteristics of the world. The fact that sensory input of the suppressed interpretation is unexplained leads to prediction errors that gradually decrease the strength of the stability prior, eventually ushering in a transition between perceptual interpretations. (c) Results of a simulation using a dynamical systems model. Red and blue shaded regions indicate periods of perceptual dominance of the two alternative interpretations. The top part of the panel depicts neural activations of two sensory neuronal pools evolving antagonistically (each color corresponds to one neuronal pool). The bottom part of the panel depicts one potential component of the predictive coding account, i.e., a prediction error-type signal, which can be modeled as the relative amount of suppressed sensory activation at different points in time. This signal, in this case constructed by taking the negative value of the square of the difference between sensory activations, slowly builds up during a perceptual dominance period and peaks at the time of the transition.

with the stability prior into a posterior that represents stronger evidence for the dominant percept but still contains residual evidence for the suppressed percept. This residual evidence, in turn, is tantamount to a prediction error that percolates through the hierarchy in a feed-forward fashion, and this leads to the update of the stability prior. This progressive updating of the prior based on the unexplained sensory information draws the posterior toward the suppressed percept and eventually results in a perceptual transition (**Figure 2b**, *bottom*).

Conceptual differences notwithstanding, the dynamical systems and predictive coding accounts of multistable perception are strikingly similar in terms of the dynamics of the processes they portray, as illustrated by **Figures 2b** (*bottom*) and **2c** (*bottom*). For example, accumulation of unexplained prediction error in the predictive coding account parallels the buildup of adaptation in the traditional dynamical systems account (**Figure 2c**, *bottom*), and one might consider whether adaptation is simply a description, in the context of dynamical systems, of the changing stability prior of the predictive coding account. Of note, conceptual connections between adaptation and predictions have been drawn by researchers working on problems quite different from multistable perception (Grotheer & Kovács 2016, Srinivasan et al. 1982, Stefanics et al. 2014). Even though both accounts of multistable perception suggest similar dynamic properties, a potentially important difference is that dynamical systems models are usually interpreted in terms of local neural circuits at sensory processing stages, whereas the inherent hierarchical structure of predictive coding models can naturally incorporate higher levels of processing such as those putatively mediated by frontal and parietal brain regions. This difference becomes particularly relevant as our review of the literature on perceptual transitions unfolds because much debate regarding that topic centers on the putative involvement of frontal and parietal brain regions.

It should be noted that there are other theories about perceptual alternations that have little to do with inference or with low-level neural adaptation, a prime example being the interhemispheric switching hypothesis. Advocates of this position, like many theorists, focus on the paradigm of binocular rivalry (Miller et al. 2000, Pettigrew & Miller 1998); according to them, binocular rivalry involves competition between alternative perceptual representations embodied in neural activity within the separate brain hemispheres, and the switching itself is governed by signals originating in bistable, subcortical oscillators. This provocative idea puts a very different twist on the account of transition-related neural activity, and it seems incompatible with the empirical evidence as presented in the following sections. Still, the oscillator model has parsimony on its side when it comes to explaining the correlation in alternation frequencies for different kinds of multistable phenomena (Carter & Pettigrew 2003; see also the sidebar titled Varieties of Multistable Perception: Different yet Fundamentally the Same?).

PERCEPTUAL STATE TRANSITIONS AS A WINDOW ONTO PERCEPTUAL INFERENCE

As previewed in the Introduction, multistable perception provides a potentially revealing means for studying the inferential processes implicated in perception. Our aim is to review work that centers on the perceptual transitions during multistable perception, events that provide clearly demarcated, measurable time stamps signifying a neural state change in the putative inference process. Specifically, our emphasis is on neural events, identified through neuroimaging, that accompany transitions, as well as on changes in alternation frequency that are brought about by neurostimulation. In recent years, considerable empirical evidence on both of these topics has emerged, and our review identifies the common findings across studies. In addition, uncertainty and controversy exist regarding the interpretation of the empirical data, and we also provide a tentative synthesis that ties multistability to the more general notion of perceptual inference.

VARIETIES OF MULTISTABLE PERCEPTION: DIFFERENT YET FUNDAMENTALLY THE SAME?

Do various instances of multistable perception arise from a single neural network or mechanism, or from neural events implemented within different networks varying not only in anatomical location but also in the underlying mechanism? Consider the configurations in **Figure 1**. The source of conflict in these configurations varies: Conflict arises from ambiguity about border ownership in **Figure 1b**, from eye-of-origin competition in **Figure 1c**, and from underspecification of 3D structure in **Figure 1d**. Moreover, multistability perceptually manifests itself in diverse ways: In some instances, perceived stimulus organization fluctuates (**Figure 1a,b,d,e**), whereas in others, salient stimulus components perceptually disappear and then reappear (**Figure 1c,f**). Still, these distinct forms of multistable perception share common properties, including statistical characteristics of the durations of perceptual dominance and dependence on stimulus characteristics such as salience (Brascamp et al. 2015b, Klink et al. 2008). Moreover, the rate at which perception fluctuates [a stable trait within a given individual (Schmack et al. 2013b)] correlates significantly across different stimuli (Carter & Pettigrew 2003). Perhaps, then, fluctuations in perceptual state result from canonical computations performed by different neural substrates. For that matter, the neural substrates promoting multistability may vary depending on an observer's task and the larger behavioral context in which that task is performed, an idea explored in this review.

The chapter of scientific history reviewed in this article starts in 1998. In one of the first, highly influential fMRI studies on multistable perception, Lumer et al. (1998) measured blood-oxygen-level dependent (BOLD) signals associated with perceptual transitions during binocular rivalry. To dissociate the specific neural processes involved in spontaneous perceptual transitions from those evoked by actual changes in visual stimulation, they used a version of the replay condition devised by Blake & Fox (1974) (see also the sidebar titled *Replaying Multistable Perception*). To implement this replay condition, Lumer and colleagues first recorded the sequence of perceptual transitions indicated by the participants during binocular rivalry and then mimicked this sequence by physically presenting two stimuli in alternation. Lumer et al. found that activity in a number of brain regions was greater during spontaneous perceptual transitions than during these replayed transitions. These regions included a right-lateralized network of brain areas in the frontal and parietal cortices, and several of these regions overlapped with those identified in a second study performed in the same year, in which multistability was elicited using ambiguous images (Kleinschmidt et al. 1998). The apparent involvement of this frontoparietal brain network could be construed to imply a literal relation between reasoning and perceptual inference, as regions in this network are thought to be involved in high-level, cognitive operations such as visual working memory (Todd & Marois 2004), perceptual decision making (Heekeren et al. 2004), and inhibitory control (Aron et al. 2004), as well as in shifting spatial attention (Silver et al. 2006, Yantis et al. 2002) and guiding eye movements (Corbetta et al. 1998). Moreover, the right hemisphere lateralization bias is reminiscent of the dominant role of right hemisphere parietal regions in spatial attention (Corbetta & Shulman 2002, Sheremata & Silver 2015, Sheremata et al. 2010), and rightward lateralization is also observed in the distribution of noradrenergic locus coeruleus terminals to frontoparietal regions (Corbetta et al. 2008) that change the dynamics of the cognitive processes these brain regions perform (Aston-Jones & Cohen 2005, Eldar et al. 2013). Lumer et al. (1998, p. 1933) themselves proposed a close association between multistable perception and attention (fully concordant with von Helmholtz's views on that matter, incidentally) and suggested that both "call upon a common neural machinery in frontoparietal cortex, involved in the selection of neuronal events leading to visual awareness."

BOLD:
blood-oxygen-level
dependent

REPLAYING MULTISTABLE PERCEPTION

To isolate the unique neural source of endogenous perceptual transitions, some neuroimaging studies have contrasted transition-related activations with those associated with on-screen, animated, replay transitions. However, any perceptual difference between these two event types could also contribute to the signal revealed by this contrast (Knapen et al. 2011). Formal analyses of perceptual equivalence are rare and, when performed, confined to certain aspects of the transition, such as its duration (Weilnhammer et al. 2013). It is, furthermore, our personal impression that replay transitions are often easily perceptually distinguishable from endogenous transitions, at least for trained observers. Perhaps, then, analysis contrasts involving conventional replay conditions do not effectively isolate the inferential neural processes of interest in the present context. Thus, researchers would have to create replay transitions that better approximate the real perceptual experience (Knapen et al. 2011, Weilnhammer et al. 2013), so that, in the limit of perceptual indistinguishability, this type of replay contrast finds the neural processes genuinely involved in the perceptual inference process. Interestingly, recent paradigms that render transitions perceptually indistinct (Brascamp et al. 2015a, Zou et al. 2016) can thus also be thought of as involving replay: Any successful attempt to render transitions perceptually indistinguishable from periods during which no transition happens makes those periods a perfect replay of sorts.

The putative link with high-level cognition was subsequently elaborated in an influential review article by Leopold & Logothetis (1999). In that article, the authors endorsed a causal role for frontoparietal activations in perceptual multistability by proposing an “iterative and random system of ‘checks and balances’, whereby higher integrative centers periodically force perception to reorganize or ‘refresh’” (Leopold & Logothetis 1999, p. 261). In the decades following these seminal papers, a number of brain imaging studies have, by and large, replicated the finding of greater right-lateralized frontoparietal activations during spontaneous than during stimulus-induced perceptual transitions (as reviewed in more detail in the section Functional Neuroimaging of Multistable Perception), regardless of the stimulus paradigm used to evoke multistability. Lumer et al.’s (1998) interpretation of the data, however, remains just one of several proposed alternatives, which are reviewed in the Discussion section.

Around the same time, there began to appear studies using transcranial magnetic stimulation (TMS) to transiently influence neural processing in areas of the right parietal and frontal cortices and, then, to assess resulting changes in the cycle of perceptual transitions. Although both categories of studies—fMRI and TMS—tended to highlight the right frontal and parietal cortices, upon closer inspection, there are differences in the functional anatomies implicated by results derived from these two different methodologies. To make explicit which frontoparietal regions are most relevant to this review, we first provide a meta-analysis that shows which brain areas have been implicated most commonly, without reference to interpretation. After that, we provide a historical overview that also touches on potential interpretations that have competed in the literature.

META-ANALYSIS OF CORTICAL TOPOGRAPHY OF FUNCTIONAL MAGNETIC RESONANCE IMAGING AND TRANSCRANIAL MAGNETIC STIMULATION FINDINGS

Figure 3 shows the results of a meta-analysis across 10 neuroimaging studies, as well as the two loci targeted in the majority of relevant TMS studies. Although methodologies varied across the neuroimaging studies summarized in this section, in each case the included analysis derived something

akin to the difference maps between spontaneous perceptual transitions and replayed transitions produced by Lumer et al. (1998). Our meta-analysis confirms that the areas showing differential BOLD activations in such comparisons are located predominantly in the right hemisphere. Focusing on this hemisphere, several hotspots that consistently crop up are highlighted using a color scale that ranges from red to yellow. The most consistently reported region is located in the inferior frontal cortex (IFC) and encompasses the anterior insula and the inferior frontal gyrus (sometimes termed the inferior frontal junction or inferior precentral sulcus, which forms the posterior boundary of the inferior frontal gyrus). Another focus of activation in the frontal cortex is in the superior precentral sulcus [also termed the frontal eye field (FEF)]. There are also activations in a more anterior lateral region, which we refer to as the dorsolateral prefrontal cortex (DLPFC), but these are less consistent than those in the other two loci. In the parietal lobe, the main locus of transition-related activation straddles the intraparietal sulcus (IPS), extending more extensively into the superior parts of the anterior parietal lobe (i.e., into the superior parietal lobule) than into the inferior parts (inferior parietal lobule). The second focus of parietal activation lies in a more anterior and lateral direction, in the temporoparietal junction (TPJ). Interestingly, most if not all of these regions are known to be organized retinotopically: Within these regions, the anatomical distances between neurons that respond to stimulation of different visual field locations mirror those locations' relative positions in visual space, resulting in orderly representations of visual space along the cortical surface, known as retinotopic maps (Jerde et al. 2012, Silver & Kastner 2009, Silver et al. 2005, Swisher et al. 2007).

The blue disks in **Figure 3** mark the two parietal loci that are most commonly targeted in TMS studies. Although imaging and neurostimulation results can be conveniently construed as two sides of the same coin when it comes to parietal involvement in multistability, it is noteworthy that the main locus of parietal BOLD activation in this meta-analysis does not coincide with either of the TMS loci. We discuss this in detail when reviewing TMS results in the section Brain Stimulation.

In the Discussion, we speculate about the roles played in multistability by the five areas identified by this meta-analysis. For now, we want to reiterate what others have noted (e.g., Leopold & Logothetis 1999, Sterzer et al. 2009), namely, the extensive overlap between this set of areas and those that compose the dorsal and ventral attention-related networks identified by Corbetta and colleagues (Corbetta & Shulman 2002, Corbetta et al. 2008). The dorsal attention system includes the anterior IPS and FEF bilaterally and is thought to be involved in preparing and applying goal-directed (top-down) selection for stimuli and responses. The ventral attention system comprises the right TPJ and IFC and is thought to be specialized for the detection of behaviorally relevant stimuli, particularly when they are salient or unexpected. This ventral system has been hypothesized to work as a circuit breaker for the dorsal system, directing attention to salient events. Such a division of labor between ventral and dorsal regions may also play a role in the context of multistable perception, subserving different aspects of the perceptual inference process.

Having identified the overall anatomical pattern that emerges from the body of work reviewed in this section, we proceed in the next section to an overview, organized roughly chronologically, of the specific questions asked by various authors and of the interpretations and discussions that have emerged. We start with work using fMRI and then turn to studies that have used TMS.

FUNCTIONAL NEUROIMAGING OF MULTISTABLE PERCEPTION

The central question running throughout this literature is not whether the frontoparietal areas highlighted in **Figure 3** show transition-related, endogenous BOLD activations, as this pattern of activations is consistent across studies. Rather, the question is what function those activations reflect. Although the BOLD activations may reflect inferential processes that give rise to the new

IFC: inferior frontal cortex

FEF: frontal eye field

DLPFC: dorsolateral prefrontal cortex

IPS: intraparietal sulcus

TPJ: temporoparietal junction

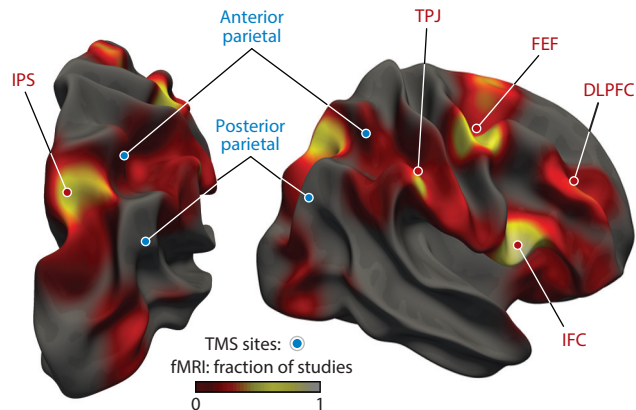


Figure 3

Results of fMRI and TMS meta-analysis. Posterior (*left*) and lateral (*right*) views on the inflated standard-brain right cortical hemisphere. For each included fMRI study, we took the MNI locations of peak activations from reported analyses that were conceptually similar to the “endogenous transitions > replay” contrast in Lumer et al. (1998). In other words, these analyses were designed to incorporate a basic control for nonspecific activations such as those associated with key presses. Studies without such analyses were not included, nor were some recent analyses that were designed to be more restrictive. In cases where Talairach coordinates were reported, these were converted to MNI coordinates using the transform proposed by Lancaster et al. (2007; see also <http://sdmproject.com/utilities/?show=Coordinates>). MNI coordinates were converted to vertex locations on an average surface using FreeSurfer, after which we smoothed these locations with a 15 mm Gaussian window on the surface. Thus, for the fMRI results, the red and yellow shading represents, for each vertex, the fraction of evaluated fMRI studies on multistable perception that report a peak activation in an approximately 15 mm vicinity on the surface. For the TMS data, the markers correspond to the MNI coordinates of the two locations most commonly targeted by TMS studies: (36, -45, 51) and (38, -64, 32) (Kanai et al. 2011). The included literature for the fMRI data, along with the analysis used in each case, is as follows: Brascamp et al. (2015a), transition without key press > no transition, “different colors” condition; Frässle et al. (2014), transition with key press > replay transition with key press; Kleinschmidt et al. (1998), transition with key press > key press without transition; Knaben et al. (2011), transition with key press > “instantaneous” replay transition with key press; Lumer et al. (1998), transition with key press > replay transition with key press; Lumer & Rees (1999), time-series correlation with Brodmann area 18/19 during rivalry without key presses > during replay without key presses; Megumi et al. (2015), transition with key press > replay transition with key press; Sterzer & Kleinschmidt (2007), transition with key press > replay transition with key press; Weilhammer et al. (2013), transition with key press > replay transition with key press; Zaretskaya et al. (2010), transition with key press > replay transition with key press. Abbreviations: DLPFC, dorsolateral prefrontal cortex; FEF, frontal eye field; fMRI, functional magnetic resonance imaging; IFC, inferior frontal cortex; IPS, intraparietal sulcus; MNI, Montreal Neurological Institute; TMS, transcranial magnetic stimulation; TPJ, temporoparietal junction.

perceptual interpretation, the broad range of cognitive functions supported by these areas (Todd & Marois 2004) suggests a second, alternative interpretation: Perhaps the activations in these areas reflect elevated cognitive demands that result from the occurrence of a perceptual transition. For instance, the unpredictable transitions may capture an observer’s attention or may require heightened scrutiny when the observer is required to report them. This ambiguity in interpreting the origins of these activations has been acknowledged from the beginning: It motivated Lumer and colleagues (1998) to employ the replay condition and has since motivated other design choices in this field.

One of the earliest studies to follow up on Lumer and colleagues’ work was performed by Sterzer & Kleinschmidt (2007). In an experiment involving ambiguous apparent motion, these investigators confirmed that activation in IFC was greater during spontaneous perceptual transitions

than during replay. As noted above, the IFC in the right hemisphere is also the region that most consistently appears in the studies covered in our meta-analysis (**Figure 3**). To explore whether this IFC activation reflects a causal role or an ancillary consequence of perceptual transitions, Sterzer & Kleinschmidt performed chronometric analyses of the transition-related BOLD signal time courses. They found an earlier onset of the BOLD response in the right IFC associated with spontaneous transitions, as compared to replayed transitions, and no such onset difference in any other brain region, including occipital and parietal regions. The earlier onset of transition-related activation in the right IFC was interpreted as indicating a role for this brain region in inducing perceptual reorganizations, an idea advanced earlier by Leopold & Logothetis (1999). However, it should be noted that conclusions from such chronometric analyses of fMRI signals—even when appropriately grounded in demonstrating a region-by-condition interaction that removes effects of local variations in neurovascular coupling (Sterzer & Kleinschmidt 2007)—are still limited by our incomplete understanding of the relationship between neural activity and hemodynamic responses.

Knapen et al. (2011) raised concerns regarding the approaches of Lumer et al. and Sterzer & Kleinschmidt. These authors focused on the unique character of perceptual transitions originating endogenously, noting that such transitions are often not instantaneous and, instead, take time to unfold, unlike the exogenously created transitions used in studies up until that time, i.e., transitions involving instantaneous changes from one on-screen stimulus to the other. This difference between endogenous and exogenous transitions introduces two potential concerns. First, the subtle but real timing differences between these two conditions are relevant for chronometric analyses, which rely on small temporal differences. Second, any imperfection in the perceptual match between spontaneous and replayed transitions can contribute to a BOLD signal difference between the two types of transitions. To quantify the duration of perceptual transitions, Knapen and colleagues required participants to report both the onset and the offset of transitions during binocular rivalry, as well as during ambiguous motion perception. They then devised two distinct replay conditions: a traditional one with near-instantaneous transitions and a modified replay condition, in which on-screen simulations of transitions were matched in visual complexity and duration to those recorded during rivalry. In the condition with traditional replay, this study replicated the finding of greater transition-related activations during multistable perception in much the same regions as had been implicated in previous studies (Lumer et al. 1998, Sterzer & Kleinschmidt 2007), but, when using the duration-matched replay, no difference between conditions was observed. This observation suggested that greater transition-related activation during multistable perception may be explained by a mismatch in perceptual properties between multistable perception and replay, rather than by neural activity that corresponds to the causal origin of perceptual transitions (see also the sidebar titled *Replaying Multistable Perception*).

The role of transition duration was also addressed by Weilhhammer et al. (2013) using a type of SFM stimulus called a Lissajous figure (**Figure 1e**). Using careful behavioral assessment, Weilhhammer and colleagues established that perceptual transitions generated by this stimulus are reliably abrupt and are thus equivalent temporally to those in an unambiguous replay version. In other words, when comparing brain activation associated with the two conditions, transition duration can be ruled out as a confounding factor. Still, Weilhhammer and colleagues observed greater activation in a right-lateralized frontoparietal network resembling the network identified in earlier studies, which rendered it unlikely that differences in transition duration were the sole explanation for these activations. Moreover, analyses of effective connectivity using dynamic causal modeling (Friston et al. 2003) showed that enhanced activity accompanying perceptual transitions was associated with a modulation of connectivity from the IFC to the visual cortex, arguing for a top-down effect of the IFC on visual processing in association with perceptual transitions.

NO-REPORT PARADIGMS

To eliminate neural signals related to report rather than perception, two approaches have been used to infer the occurrence of perceptual transitions without report (Tsuchiya et al. 2015). One approach does involve reports but dissociates them from transitions by requesting them at predetermined time points. At these times, participants report perceptual state (Brascamp et al. 2015a, Mamassian & Goutcher 2005) or, alternatively, other judgments that correlate with perceptual state (Alais et al. 2014, Wilbertz et al. 2014, Yu & Blake 1992). Alternations can then be inferred, albeit with coarser temporal resolution compared to direct reports. Another approach omits reports altogether and tracks perceptual alternations using signals from the eyes (Fox et al. 1975, Frässle et al. 2014, Naber et al. 2011) or the brain (Brouwer & van Ee 2007, Brown & Norcia 1997, Haynes & Rees 2005, Schmack et al. 2013b). Brain signals, however, have mostly been used to confirm, rather than replace, perceptual reports (Zhang et al. 2011). An important difference between approaches with (cued) report and ones without is that the former still require attentive focus on the stimulus, which is relevant when aiming to eliminate signals related to factors like reorienting or arousal in addition to report-related signals.

Another question arises when interpreting the traditional frontoparietal activations accompanying perceptual transitions: Are these activations dependent on the task being performed by the participant (Knapen et al. 2011)? One possibility is that frontal and parietal regions play a role in the act of reporting perceptual events. In a recent study, Frässle et al. (2014) directly addressed this question by inferring participants' perceptual transitions from objective ocular-motor data rather than relying on manual report (see also Tsuchiya et al. 2015; see the sidebar titled No-Report Paradigms). In this study, binocular rivalry was induced between two gratings that had a particularly large spatial extent and that differed in either mean luminance or motion direction, thus allowing the investigators to distinguish between the two possible perceptual states by analyzing pupil size and optokinetic nystagmus, respectively. In this no-report condition, as compared to the traditional condition, the contrast between spontaneous and replayed perceptual transitions yielded a weaker signal in some frontoparietal regions. The result was most pronounced in the right DLPFC, where any remaining signal did not reach statistical significance in the no-report condition. The FEF and IFC, however, still showed significant activations even without report, echoing earlier findings (Weilhammer et al. 2013). This suggests differential functional roles for frontal subregions in multistable perception, with the right DLPFC being specifically involved in registering and reporting perceptual transitions, but with responses in the other regions also reflecting additional aspects that are unrelated to active report. The notion that some frontoparietal signals persist even without manual report is consistent with results from an early study that also involved a no-report paradigm (Lumer & Rees 1999).

Brascamp et al. (2015a) recently employed a different tactic to distinguish various influences on frontoparietal involvement around the time of transitions. Given that factors such as task relevance and salience of the perceptual transition play a role in the work reviewed above, Brascamp and colleagues asked whether frontoparietal regions still show elevated BOLD responses when perceptual transitions go unnoticed. They developed a binocular rivalry procedure in which the two eyes were presented with different visual motion stimuli and perception demonstrably switched between these two inputs. However, the stimuli were designed in such a way that the transitions were so inconspicuous as to become unreportable. Interestingly, transition-related frontoparietal activations were minimized by this procedure. This suggests that frontoparietal regions may not be involved in rivalry transitions that are not consciously registered, implying that transitions

prompted by conflicting input do not necessarily require the involvement of higher-level brain circuits, at least in situations where the transitions are not consciously registered.

This tentative interpretation received further support from a study by Zou et al. (2016), who induced binocular rivalry between two color-modulated gratings that were rendered invisible by means of rapid counter-phase flicker and the onset of which produced no detectable BOLD activations in frontal and parietal areas. These invisible gratings produced rivalry dynamics similar to those of visible gratings, further strengthening the notion that higher-level brain circuits are unnecessary for eliciting transitions during binocular rivalry (see also Giles et al. 2016).

Studies such as those by Brascamp et al. (2015a) and Zou et al. (2016) contribute to the incremental deconstruction of the cascade of perceptual and cognitive events that surround transitions in multistable perception and thereby help elucidate the functional nature of frontal and parietal involvement. However, this type of result, which pivots on invisibility or unreportability, cannot easily be translated from binocular rivalry to other forms of multistable perception, such as that arising from ambiguous figures (**Figure 1**), which inherently and inevitably involve transitions between perceptually distinct states. Thus, the role of certain brain areas in perceptual transitions may vary depending on the nature of the sensory conflict and perceptual experience. Although the visual system may be able to resolve the conflict between competing monocular inputs at a local level (see also Xu et al. 2016), integration of a broader range of information, coded by a broader set of brain areas, may be involved when the alternating states evoke distinguishable perceptual experiences and when transitions between these states are behaviorally relevant.

The studies reviewed above were all designed to disambiguate the specifics of the role of frontoparietal involvement in perceptual transitions. Several other fMRI studies have also replicated Lumer and colleagues' empirical result, yet without the specific aim of arbitrating between alternative hypotheses. In particular, in a study investigating the effect of TMS on the transition rate in binocular rivalry, Zaretskaya et al. (2010) performed an fMRI experiment to determine, in each participant, the regions that showed greater activation in association with perceptual transitions during standard reported binocular rivalry relative to a conventional replay condition; this experiment replicated Lumer and colleagues' result. A further replication using ambiguous SFM was provided by Megumi et al. (2015) (as discussed in more detail in the section Functional Roles of Frontal and Parietal Subregions). Other studies have performed more advanced analyses on patterns of frontoparietal BOLD data collected during multistable perception, again without the specific objective of disambiguating various causal explanations (e.g., Wang et al. 2013, Watanabe et al. 2014).

Rather than having to rely on particular design features of an fMRI study, a more direct strategy to infer causal involvement of particular brain regions in perceptual transitions is via TMS. In particular, several studies have used TMS to interfere temporarily with the function of various brain regions during perceptual multistability and, thus, to assess the effect of such virtual lesions on perceptual transitions. This work has focused mostly on the parietal cortex, so when thinking roughly in terms of frontoparietal involvement, such work would seem to address the same questions as the fMRI studies discussed above. But the links between results from these two types of methods deserve closer examination, and in the next section, we review existing TMS work with a special focus on these links (see Ngo et al. 2013 for a review with a different focus).

BRAIN STIMULATION

The earliest work using brain stimulation in the context of perceptual multistability was not explicitly guided by functional imaging results. In a pioneering study, Miller et al. (2000) found

that single TMS pulses applied to the left hemisphere of observers experiencing binocular rivalry hastened a transition in dominance from the currently dominant stimulus to the other, currently suppressed monocular stimulus. This finding was interpreted as supporting the interhemispheric switching hypothesis mentioned above (Miller et al. 2000, Pettigrew & Miller 1998). Follow-up work showed a similar effect during motion-induced blindness (**Figure 1f**), this time with single pulses delivered to either the left or the right hemisphere (Funk & Pettigrew 2003). TMS coil placement in both of these studies was guided by scalp landmarks and, consequently, the specific brain structures receiving maximal TMS are unknown, but it is plausible that the parietal cortex was among the brain areas impacted by TMS in both cases. A later study observed that TMS to the occipital cortex also can prompt the occurrence of a perceptual transition in binocular rivalry (Pearson et al. 2007).

In a number of more recent TMS studies, coil placement was guided by high-resolution anatomical images obtained using MRI, making it easier to draw explicit parallels between those results and fMRI data. Arguably the most-established finding in this context is that the dynamics of perceptual multistability can be influenced by TMS applied to a locus quite anterior along the IPS [anterior parietal in **Figure 3**; its location in standard coordinates would place this locus in or near retinotopic maps IPS4–5 (Konen & Kastner 2008)]. Even though this locus does not coincide exactly with the parietal hotspot identified in our meta-analysis (**Figure 3**), it does regularly show up in the BOLD contrast between spontaneous and replayed transitions, and some TMS studies have specifically targeted this location on the basis of transition-related BOLD signals in binocular rivalry (Carmel et al. 2010, Zaretskaya et al. 2010). One study that involved offline (i.e., prior to stimulus presentation) TMS to this area observed an increased incidence of transitions (i.e., shorter percept durations) during subsequent binocular rivalry for right-hemisphere stimulation (Carmel et al. 2010). This finding was later replicated using an ambiguous SFM stimulus (Kanai et al. 2011). Although the two studies used different TMS protocols, both protocols are thought to cause reduced neural excitability in the targeted region. A study that targeted essentially the same parietal locus using an altogether different TMS protocol with online stimulation (i.e., during stimulus presentation) observed a decreased incidence of binocular rivalry transitions (Zaretskaya et al. 2010). This study stimulated the locus in both hemispheres and, although confirming an overall stronger TMS effect in the right hemisphere, demonstrated that the degree of lateralization in individual participants correlated with the degree of lateralization of the transition-related BOLD responses. Another study provided evidence that TMS of that parietal area can also affect perceptual transitions for intermittently presented ambiguous stimuli (Vernet et al. 2015). It seems reasonable to assume that differences in TMS protocol can explain the differences in effect direction reported in various studies, and, taken together, there is a compelling body of work implicating this anterior IPS region in perceptual multistability. The case is further supported by structural imaging findings showing that high gray matter density in this region correlates with longer percept durations (Kanai et al. 2011, Watanabe et al. 2014).

In several TMS studies, this anterior locus was examined in combination with a site more posterior along the IPS [posterior parietal in **Figure 3**; based on standard coordinates, this site is about 2.7 cm removed from the anterior one and would lie near retinotopic map IPS1 (Konen & Kastner 2008, Szczepanski et al. 2010)]. Using an ambiguous SFM stimulus, one study provided evidence that an offline TMS protocol that accelerates the alternation cycle when applied over the anterior locus (Kanai et al. 2011) instead decelerates the cycle when applied over this posterior locus, regardless of hemisphere (Kanai et al. 2010). Similarly, this study found that gray matter density in this posterior region was positively correlated with shorter dominance durations (see also Watanabe et al. 2014), again the opposite of what was found for the anterior region. With regard to fMRI findings, there is relatively little evidence that the posterior locus falls within the

areas that typically show enhanced transition-related BOLD responses [one region-of-interest analysis centered on the locus demonstrated such a response (Megumi et al. 2015)].

Taken together, these results provide compelling evidence that different regions along the IPS, especially in the right hemisphere, play distinct roles in perceptual multistability. Evidence for a role in multistability is not as strong for the posterior locus as it is for the anterior locus, and a recent replication study provided further support for involvement of the anterior locus but did not corroborate involvement of the posterior locus (Sandberg et al. 2016). Regardless of the status of the posterior locus, however, there is reason to believe that the effects found for the anterior coordinates are localized to that particular region along the IPS. For instance, one study found an effect on perceptual multistability when stimulating the anterior locus but not when stimulating a region only slightly more posterior (Zaretskaya et al. 2010).

The possibility that different regions along the IPS differ in their function during perceptual multistability makes it more difficult to interpret results from studies that positioned their TMS coils using less precise methods. In particular, several studies stimulated the right parietal cortex by targeting electrode P4 of the international 10–20 EEG system, the location of which varies considerably among participants (de Graaf et al. 2011, Sack et al. 2009), although it appears closer, on average, to the posterior locus than to the anterior one (de Graaf et al. 2011). This might explain why some such studies observed a reduced frequency of perceptual transitions for an ambiguous apparent motion stimulus following inhibitory TMS and an increased frequency following facilitatory TMS (Ge et al. 2008, Nojima et al. 2010; see VanRullen et al. 2008 for a potentially related finding), whereas a different study found no effect for an ambiguous SFM stimulus (de Graaf et al. 2011).

Very little TMS evidence is available for frontal regions. De Graaf et al. (2011) observed no influence of right frontal TMS on the perceptual cycle, although the same manipulation did influence participants' ability to volitionally control this cycle. A double-coil experiment, furthermore, led to the suggestion that TMS to this same frontal locus might interact with the effects of parietal TMS on multistable perception (Vernet et al. 2015). The implications of these findings in relation to functional imaging results are not entirely clear because the specific frontal area targeted in these studies does not seem to fall within the set of areas indicated by our meta-analysis (it appears to lie somewhat anterior to the FEF hotspot shown in **Figure 3**).

FUNCTIONAL ROLES OF FRONTAL AND PARIETAL SUBREGIONS

What can we conclude regarding the functional involvement of the frontal and parietal cortices in multistable perception? Can we differentiate among putative, distinct roles played by various subregions? We can say that the transition-related BOLD signal in these regions is diminished in paradigms that preserve perceptual transitions but reduce associated cognitive demands by manipulating perceptual salience or behavioral relevance. These regions' involvement, then, may be partly in evaluating and acting on a perceptual event in its wake. At the same time, it is also conceivable that involvement of a given brain region in perceptual inference itself may depend on whether the underlying sensory conflict is relevant perceptually or behaviorally.

Among the implicated frontal regions, the right IFC stands out as the strongest candidate for playing a directive role in perceptual transitions. It is the area most consistently implicated by fMRI BOLD contrasts (**Figure 3**), and analyses of chronometry and functional connectivity also support this notion. The weakest candidate, in turn, appears to be the right anterior DLPFC, given its lack of consistent activation in our meta-analysis and the observation by Frässle et al. (2014) that activation of this region was linked to manual report. By suggesting that the right IFC might be more closely associated with perception and the DLPFC with action, these results bring to

mind a posterior-to-anterior gradient in frontal cortical function that has been suggested in other contexts (Azuar et al. 2014, Badre et al. 2009). More anterior regions along this gradient would be involved in more abstract representations and in later stages of the perception–action cycle (Fuster & Bressler 2012). Supporting this view, recent work investigating the functional roles of frontal cortical subregions in perceptual decision making shows that distinct frontal regions along a posterior-to-anterior gradient support the control of progressively later stages of the perceptual decision-making process (Rahnev et al. 2016, Sterzer 2016). During a demanding perceptual decision-making task, the FEF was engaged in perceptual selection processes, whereas the DLPFC supported criterion-setting processes. Finally, a particular anterior region within the right DLPFC was involved in the metacognitive evaluation of perceptual decisions (Rahnev et al. 2016). In the context of perceptual decisions in situations of multistable perception, a similar functional subdivision of the frontal cortex may apply, with more posterior regions such as the right IFC playing a role in the process of perceptual interpretation and more anterior regions being involved in metacognitive processes, such as introspection, that are required for active report (Frässle et al. 2014). In the context of perceptual inference, one potential role of the right IFC might be to respond to prediction errors arising in the sensory cortex, a suggestion elaborated in the Discussion. One footnote to the overall relatively strong evidence regarding the right IFC comes from the study that provided the first structural imaging evidence for parietal involvement in multistable perception (see the section Brain Stimulation; Kanai et al. 2010). This same study also specifically examined a frontal cortex region extremely close to the right IFC locus of our meta-analysis (**Figure 3**), yet found no structural correlates with multistable perception in that region.

Regarding the parietal cortex, the most compelling evidence for a causal role in perceptual transitions is associated with the right anterior IPS region (discussed above). Although the transition-related BOLD signal in this region is not spared from the dependence on task relevance, as discussed above for frontal regions, this is the only specific brain region that has been implicated by both fMRI and TMS work, and, moreover, it is the sole region where TMS and structural MRI findings have been replicated multiple times.

TMS researchers have speculated about the functional nature of parietal involvement in multistable perception. Although it is reasonable to point to right parietal involvement in attention function (Carmel et al. 2010, Kanai et al. 2011, Zaretskaya et al. 2010), given plausible relations between attention and perceptual multistability (Bressler et al. 2008, Leopold & Logothetis 1999), the available evidence does not favor any specific attention-related account. For instance, an account that likens perceptual transitions to attention shifts would have to accommodate the fact that fMRI BOLD correlates of attention shifts are typically located in considerably more medial regions than either of the TMS sites discussed above (Serences 2004, Yantis et al. 2002). More generally, the functional anatomy of the parietal cortex in terms of attention does not provide clear clues as to why TMS influences on multistable perception would be so specifically localized to these particular loci along the IPS. One study attempted to address this issue by investigating the influence on attention tasks of the specific TMS manipulations previously used in studies of perceptual multistability but found no evidence for altered attention function (Schauer et al. 2016). An alternative functional account of the parietal TMS results was inspired by the hierarchical predictive coding ideas we discuss at the beginning of this review (Clark 2013, Friston 2005, Hohwy et al. 2008) and is, in that sense, more directly related to our present theme. This account holds that the anterior locus and the posterior locus play complementary roles in perception, with the anterior locus providing a top-down hypothesis as to the interpretation of sensory input and the posterior locus coding the discrepancy between this hypothesis and the present sensory

signal (Kanai et al. 2011, Megumi et al. 2015). An additional piece of the puzzle regarding parietal involvement is provided by the finding that the anterior parietal locus has strong functional connectivity with large parts of the transition-related frontoparietal network, whereas the posterior locus has strong functional connectivity with a different network that includes areas in the temporal cortex and on the medial wall (Baker et al. 2015). This latter network overlaps substantially with areas where BOLD signals are reduced, rather than enhanced, in association with perceptual alternations (Brascamp et al. 2015a), corroborating the idea that studies using parietal TMS have tapped into two genuinely complementary networks involved in resolving perceptual ambiguity.

DISCUSSION

Von Helmholtz's work is seminal in a rich tradition of thought stating that perception can be usefully understood as the process of inference based on both current sensory input and contextual information such as that provided by past experience and generic world knowledge. A principal motive for this line of thought is the notion that current sensory signals alone cannot unambiguously stipulate the real-world source of those signals. Perceptual multistability, with its plain separation between sensation and perception, was recognized by Wheatstone and developed later by von Helmholtz as a prime illustration of this notion that perception requires added ingredients besides sensory evidence. But how are these sources of contextual information integrated in the computations that generate our perceptual experiences? In this final section, we attempt to coalesce the findings reviewed above by evaluating how the empirical work relates to hypothesized mechanisms of multistable perception, focusing in particular on the ways in which top-down mechanisms, which may provide contextual information, can impact perception during perceptual multistability.

Both of the theoretical accounts described at the beginning of this review, i.e., the traditional dynamical systems account of adaptation and inhibition and the predictive coding account, posit a relative diminution of the dominant perceptual state's neural representation during the period leading up to the perceptual transition (**Figure 2**). The functional properties of the right IFC would suggest that it is exquisitely sensitive to such reduced fidelity of the current sensory signal (Haynes et al. 2005, Heekeren et al. 2004, Sunaert et al. 2000), and it is tempting to speculate that this characteristic is perhaps shared by other regions such as the anterior parietal lobe and TPJ (see Sterzer et al. 2009 for a similar suggestion). This suggests a first possible conceptualization of the nature of top-down influences during multistable perception. Transition-related activation in these regions may be related to the rising prediction error or falling fidelity of the sensory signal during a process that culminates in a switch to the previously suppressed perceptual state. Direct empirical support for this idea comes from a recent fMRI study that estimated the time course of prediction errors during multistable motion perception using a Bayesian predictive-coding model (Weilhammer et al. 2017). Concordant with the IFC's known role in sensory decision making (Baldauf & Desimone 2014, Heekeren et al. 2004) and inhibitory control (Aron et al. 2014), this region's response to the gradual change in sensory regions could be to provide feedback to these sensory regions, peaking around the time of the perceptual transitions. In the context of perceptual inference, one might think of this feedback in terms of top-down hypotheses, a reading that would certainly be consistent with one proposed role of the anterior parietal lobe during multistability (Kanai et al. 2011).

Under this first conceptualization, then, top-down signals would be most strongly associated with destabilization of sensory representations and might be expected to start rising before the actual perceptual transition. However, a second potential role that top-down signals might play,

not mutually exclusive with the first, would associate those signals more strongly with stabilization of sensory representations and with the period that follows the transition. In this view, top-down signals would play a reinforcing role in the process of settling into a new perceptual state after the temporary neural instability signified by a perceptual alternation. One could liken such a top-down role to the roles suggested in perceptual decision making, where making and committing to a perceptual decision can impact the content of the concomitant perceptual experience (Jazayeri & Movshon 2006, 2007) and the neural activity underlying it (Nienborg & Cumming 2009). Such a post hoc stabilizing role would be consistent with the observation that neural events around the time of transitions, reflected in magnetoencephalography signals, prolong subsequent perceptual phases in motion-induced blindness (Kloosterman et al. 2015). There is, furthermore, a close mutual tie between the act of reporting a perceptual decision and the perceptual decision process itself (Cisek & Pastor-Bernier 2014, Lepora & Pezzulo 2015), suggesting a natural explanation for the observed contribution of perceptual report on transition-related frontal activity in multistable perception (Frässle et al. 2014).

Regardless of the precise role of top-down signals in multistable perception, predictive coding accounts of perception have the benefit of entailing back-and-forth interactions between successive levels, in a process that repeats many times and reverberates throughout an extended hierarchy. As such, accounts that fall along these lines might naturally encompass both bottom-up and top-down factors involved in multistable perception, and they might also fit with the observation that the involvement of many regions can evidently be eliminated by stripping away various perceptual and cognitive aspects of the sensory conflict. The right IFC, for instance, may register in a bottom-up fashion prediction errors that are generated at sensory processing levels, but it may also send a prediction-based signal down to sensory processing levels, and its involvement may depend on the extent to which the competing sensory solutions correspond in fact to distinguishable perceptual states, an extent that is minimized in recent studies of binocular rivalry (Brascamp et al. 2015a, Zou et al. 2016). At the same time, even if higher-level factors can be stripped away in certain conditions, the associated brain areas might nevertheless influence the perceptual cycle in other conditions where those factors remain in play.

Although many of the ideas discussed in this section are tentative, we anticipate that crucial information regarding the specific mechanisms underlying multistable perception will become available thanks to recent methodological advances. For instance, top-down and bottom-up streams of information processing should become more clearly separable using methods such as band-limited encephalography (Bastos et al. 2015, Donner & Siegel 2011, Siegel et al. 2012), high-resolution fMRI acquisition techniques that allow the independent imaging of the different cortical layers (Fracasso et al. 2016, Kok et al. 2016), and methods for inferring effective connectivity from neuroimaging data (Friston et al. 2003). Similarly, a recent increase in sophistication in pupillometric methods (Cheadle et al. 2014, de Gee et al. 2014, Knapen et al. 2016) should help elucidate decision-related and action-related changes in cortical state (Harris & Thiele 2011; McGinley et al. 2015a,b) that might accompany perceptual transitions and that are likely reflected in pupil size fluctuations (Hupé et al. 2009, Naber et al. 2011, Sara 2009).

To conclude, it has been 150 years since von Helmholtz elaborated on Alhazen's ideas about perceptual inference and highlighted multistable perception as *prima facie* evidence for a central role of inference in perception. The findings surveyed in this review—derived from psychophysics, brain imaging, and TMS—attest to the validity of his view and the prescience of von Helmholtz's realization of the illuminating quality of perceptual multistability on the inferential nature of perception. Those of us actively involved in researching the details of those inference-like processes are indebted to his insight, and although we may disagree on the details of those processes, we are united in our respect for the unifying power of his ideas.

FUTURE ISSUES

1. Future studies will need to distinguish the specific roles that individual frontal subregions play in multistable perception. This research can be guided by the hypothesis, discussed in this review, of a functional gradient within the frontal cortex from perceptual interpretation in posterior regions to deliberative mental activity in anterior regions (see also Sterzer 2016). A related, but more specific, guiding hypothesis is that the DLPFC is not involved in the generation, but only in the report, of perceptual alternations (see also Frässle et al. 2014).
2. If it is true that the neural substrate of perceptual switching depends to a great extent on the nature of the conflict and the perceptual experience, it will be necessary to identify what determines this substrate and how this relates to the functional roles played by the neural components involved.
3. Research should continue working toward a unified picture of the effects of right IPS TMS on the rate of alternations in multistable perception. Work in this direction should focus on clarifying the dependence on stimulation protocol and on examining the extent to which the effects found for stimulation of the posterior locus can be replicated.
4. Future research should determine the extent to which candidate accounts of multistable perception can explain the pronounced individual differences in rates of perceptual fluctuations and whether those differences are associated with individual differences in other cognitive functions, such as perceptual decision making and metacognitive efficiency, subserved by the brain areas putatively involved in perceptual switching.
5. How do top-down signals arising from (the report of) a transition impact the representation of ambiguous information in the visual cortex? Recent methodological advances that allow the separation of top-down and bottom-up information flows could elucidate this issue.
6. Assuming that predictive coding is a homeostatic process, what are the time scales for inducing biases in perceptual state based on learning, reward, or context, and how are those instantiated neurally?
7. Given that many parallels exist between accounts of multistability that focus on factors such as adaptation and inhibition and accounts phrased in terms of predictive coding, future studies should establish whether the two are, in fact, distinguishable and, if so, arbitrate between the two classes of accounts.
8. More generally, the enduring popularity of the metaphor of perception as inference could be construed as evidence for its validity, but also as a sign that the idea seamlessly blends in with a wide range of scientific viewpoints and empirical findings. To express this thought in a contemporary voice, how would one go about disproving that perception entails predictive coding?

DISCLOSURE STATEMENT

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Contents

The Properties and Antecedents of Hedonic Decline <i>Jeff Galak and Joseph P. Redden</i>	1
How We Hear: The Perception and Neural Coding of Sound <i>Andrew J. Oxenham</i>	27
The Psychology of Music: Rhythm and Movement <i>Daniel J. Levitin, Jessica A. Grabn, and Justin London</i>	51
Multistable Perception and the Role of Frontoparietal Cortex in Perceptual Inference <i>Jan Brascamp, Philipp Sterzer, Randolph Blake, and Tomas Knapen</i>	77
Ensemble Perception <i>David Whitney and Allison Yamanashi Leib</i>	105
Neuro-, Cardio-, and Immunoplasticity: Effects of Early Adversity <i>Eric Pakulak, Courtney Stevens, and Helen Neville</i>	131
Prefrontal Cortex and Neurological Impairments of Active Thought <i>Tim Shallice and Lisa Cipolotti</i>	157
Infant Statistical Learning <i>Jenny R. Saffran and Natasba Z. Kirkham</i>	181
How Children Solve the Two Challenges of Cooperation <i>Felix Warneken</i>	205
Linking Language and Cognition in Infancy <i>Danielle R. Perszyk and Sandra R. Waxman</i>	231
Cognitive Foundations of Learning from Testimony <i>Paul L. Harris, Melissa A. Koenig, Kathleen H. Corriveau, and Vikram K. Jaswal</i> ...	251
Gender Stereotypes <i>Naomi Ellemers</i>	275
Attitudes and Attitude Change <i>Dolores Albarracín and Sharon Shavitt</i>	299

Persuasion, Influence, and Value: Perspectives from Communication and Social Neuroscience <i>Emily Falk and Christin Scholz</i>	329
Social Mobilization <i>Todd Rogers, Noah J. Goldstein, and Craig R. Fox</i>	357
Developmental Origins of Chronic Physical Aggression: A Bio-Psycho-Social Model for the Next Generation of Preventive Interventions <i>Richard E. Tremblay, Frank Vitaro, and Sylvana M. Côté</i>	383
Improving Student Outcomes in Higher Education: The Science of Targeted Intervention <i>Judith M. Harackiewicz and Stacy J. Priniski</i>	409
Why Social Relationships Are Important for Physical Health: A Systems Approach to Understanding and Modifying Risk and Protection <i>Julianne Holt-Lunstad</i>	437
Principles and Challenges of Applying Epigenetic Epidemiology to Psychology <i>Meaghan J. Jones, Sarah R. Moore, and Michael S. Kobor</i>	459
Psychology, Science, and Knowledge Construction: Broadening Perspectives from the Replication Crisis <i>Patrick E. Shrout and Joseph L. Rodgers</i>	487
Psychology's Renaissance <i>Leif D. Nelson, Joseph Simmons, and Uri Simonsohn</i>	511

Indexes

Cumulative Index of Contributing Authors, Volumes 59–69	535
Cumulative Index of Article Titles, Volumes 59–69	540

Errata

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TABLE OF CONTENTS FOR VOLUME 1:

Introduction, Susan A. Gelman, Sandra R. Waxman

Eleanor Maccoby: An Abridged Memoir,
Eleanor Maccoby

*Using Developmental Science to Distinguish
Adolescents and Adults Under the Law*,
Laurence Steinberg, Grace Icenogle

*Adolescent–Parent Relationships: Progress, Processes,
and Prospects*, Judith G. Smetana, Wendy M. Rote

The Life Course Consequences of Very Preterm Birth,
Dieter Wolke, Samantha Johnson, Marina Mendonça

*Early Deprivation Revisited: Contemporary Studies
of the Impact on Young Children of Institutional Care*,
Megan R. Gunnar, Brie M. Reid

The Development of Cumulative Cultural Learning,
Cristine H. Legare

*Neighborhood Effects on Children’s Development
in Experimental and Nonexperimental Research*,
Tama Leventhal, Veronique Dupéré

*Cognitive Aging and Dementia: A Life-Span
Perspective*, Elliot M. Tucker-Drob

*Brain Plasticity in Human Lifespan Development:
The Exploration–Selection–Refinement Model*,
Ulman Lindenberger, Martin Lövdén

The Pervasive Role of Pragmatics in Early Language,
Manuel Bohn, Michael C. Frank

*Early Development of Visual Attention:
Change, Stability, and Longitudinal Associations*,
Alexandra Hendry, Mark H. Johnson, Karla Holmboe

*Childhood Adversity and Neural Development:
A Systematic Review*, Katie A. McLaughlin,
David Weissman, Debbie Bitrán

*Social Relations Across the Life Span: Scientific
Advances, Emerging Issues, and Future Challenges*,
Toni C. Antonucci, Kristine J. Ajrouch, Noah J. Webster,
Laura B. Zahodne

*Safety Net Policies, Child Poverty, and Development
Across the Lifespan*, Benard P. Dreyer

The Development of Social Categorization,
Marjorie Rhodes, Andrew Baron

Developmental Effects of Parent–Child Separation,
Anne Bentley Waddoups, Hirokazu Yoshikawa,
Kendra Strouf

