Review

Sensory memory for ambiguous vision

Joel Pearson[1] **and Jan Brascamp**[2]

[1] Department of Psychology, Vanderbilt University, 111 21st Ave. S. Nashville, TN 37203, USA
[2] Functional Neurobiology and Helmholtz Institute, Utrecht University, Padualaan 8, 3584CH Utrecht, The Netherlands

In recent years the overlap between visual perception and memory has shed light on our understanding of both. When ambiguous images that normally cause perception to waver unpredictably are presented briefly with intervening blank periods, perception tends to freeze, locking into one interpretation. This indicates that there is a form of memory storage across the blank interval. This memory trace codes low-level characteristics of the stored stimulus. Although a trace is evident after a single perceptual instance, the trace builds over many separate stimulus presentations, indicating a flexible, variable-length time-course. This memory shares important characteristics with priming by non-ambiguous stimuli. Computational models now provide a framework to interpret many empirical observations.

Stabilizing unstable vision

Although most visual input produces stable vision, sometimes, when visual information is ambiguous, awareness tends to waver continuously between alternative interpretations [1,2]. For one class of ambiguous sensory stimuli, known as bistable stimuli, an observer's perception will alternate almost exclusively between only two interpretations (Figure 1a–c). During continuous viewing conditions, perceptual alternations are unavoidable, and it is impossible to predict what someone will see in the near future [3] (Figure 1d).

Surprisingly, perception of a bistable stimulus (see Glossary) can be made stable and predictable by the simple manipulation of periodically removing the stimulus from view (Figure 1e). In 1963, Orbach and colleagues [4] reported that intermittent presentation of a bistable pattern – making it appear and disappear every few seconds – reduced the overall number of perceptual alternations. More recently, a more general account by Leopold and colleagues [5] demonstrated that such presentation techniques can make perception freeze on one interpretation of a bistable stimulus (Figure 2; compare left and right panels). This perceptual stabilization contrasts dramatically with the continual perceptual changes experienced during uninterrupted viewing. This remarkable phenomenon implies a form of memory in which the visual system maintains information from past perception across blank intervals.

This is an exciting time for this relatively new phenomenon. Scientists are beginning to understand its many characteristics and components, from the type of information the brain actually stores, to where and how the brain achieves this. In this review, we first consider which aspects of perception are held in memory and which ones seem irrelevant. Second, we discuss the mechanism of the memory, its temporal dynamics and how recent modeling efforts have changed the way we think about it.

Information held in memory

What types of information are held across these blank intervals? One way to answer this question is to physically change different characteristics of the stimulus in synchrony with the on/off presentation cycle [6,7] (see Ref. [8] for commentary). For instance, if the color of the stimulus is changed from one presentation to the next (across the blank interruption), from blue to red, and this results in an observer experiencing an alternation (i.e. the stimulus interpretation changes), this indicates that the memory trace from the blue stimulus did not stabilize the red stimulus. This implies that the stimulus color is stored in the memory trace. Over multiple presentations, this scenario would result in lower perceptual stability. If, instead, stability is unaffected because the observer sees the same stimulus interpretation despite the color change, memory can be said to be blind to this feature (see Figure 3 for a summary of findings).

Structure from motion

When rotating 3D stimuli, such as a cylinder or sphere, are presented on a monitor in two dimensions, their direction

Glossary

Ambiguous stimulus: a sensory stimulus that elicits multiple distinct perceptual interpretations, which alternate in awareness while the stimulus is presented.
Binocular rivalry: a form of bistable perception in which the left and right eye each view a different image in the same region of retinotopic space. Competition between the monocular inputs causes perception to waver between the image seen by the left eye and the image seen by the right eye.
Bistable stimulus: an ambiguous stimulus that causes exactly two percepts to alternate in awareness.
Eye of origin: in binocular rivalry the eye of origin of an image refers to the eye to which the image is presented.
Flash suppression: a method for controlling which pattern is dominant during binocular rivalry. The two patterns are presented asynchronously; the pattern presented second will become dominant [53].
Memory for ambiguous perception: the phenomenon that perception of an ambiguous image leaves a trace that influences future perception of the same image.
Perceptual stabilization: arguably the most salient expression of memory for ambiguous perception, in which periodically removing an ambiguous stimulus from view causes the same percept to dominate on many presentations in a row.
Structure-from-motion: a potent cue to the 3D structure of an object is the displacement of surface locations that are seen as the object rotates in depth. This is called structure-from-motion. In the absence of other depth cues such as occlusion and perspective, structure-from-motion alone does not unambiguously indicate whether a surface point is moving toward the observer or away. This leads to salient perception of a 3D rotating object that is bistable regarding the direction of rotation of the object.

Corresponding author: Pearson, J. (joel.pearson@vanderbilt.edu).

1364-6613/$ – see front matter © 2008 Elsevier Ltd. All rights reserved. doi:10.1016/j.tics.2008.05.006 Available online 4 August 2008

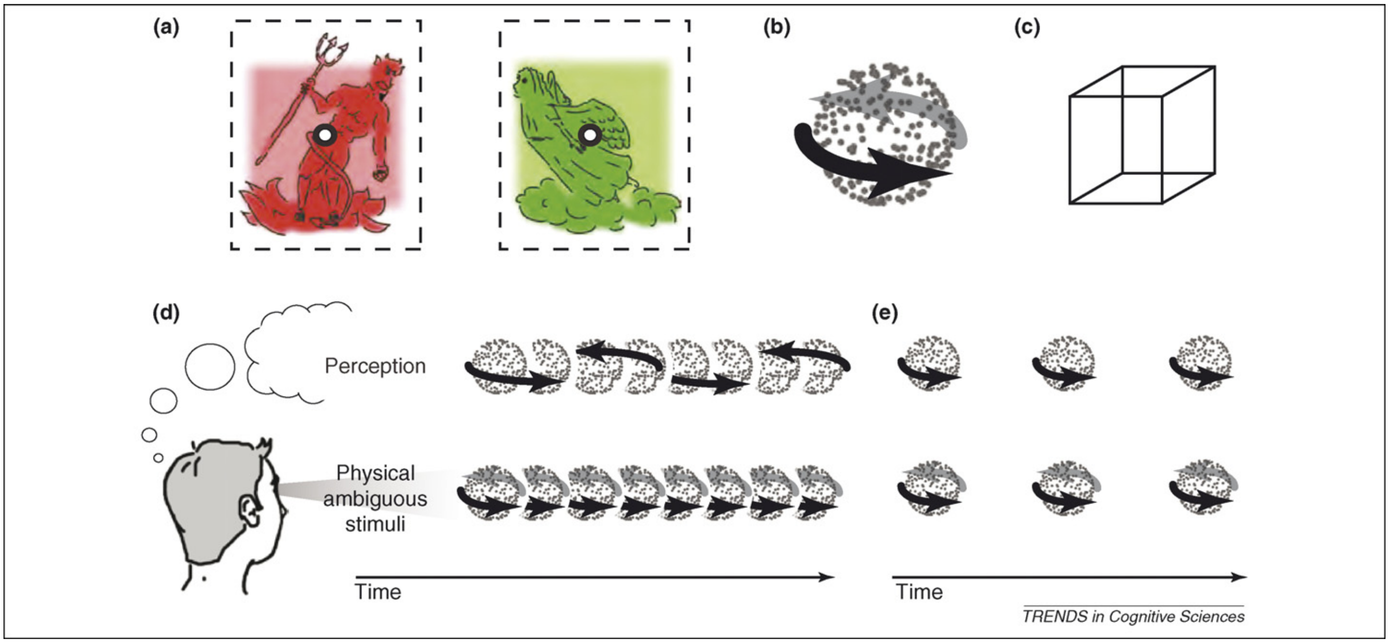


Figure 1. Ambiguous stimuli and stabilization timeline. **(a)** A binocular rivalry stimulus. Each eye is shown a different image, causing the observer to perceive both images in alternation. If you can cross-fuse these images, you can experience binocular rivalry right here on the page. **(b)** A static snap-shot of a bistable structure-from-motion stimulus. When viewed with motion, this stimulus is bistable regarding the direction of rotation of the structure, shown here as a sphere. **(c)** A wire-frame cube, known as a Necker cube. The depth relationship between the lines is ambiguous. Perception alternates between two configurations of a cube. **(d)** Continuous viewing of an ambiguous image causes unpredictable and inescapable perceptual alternations between interpretations. **(e)** Periodically removing the stimulus from view can cause one percept to dominate on each presentation. This perceptual stabilization implies some sort of automatic memory that stores perceptual information across periods of stimulus absence.

of rotation can be ambiguous. This results in perceptual alternations between the two possible directions of rotation (Figure 1b). Like many other bistable patterns, such structure-from-motion stimuli are perceptually stabilized by intermittent presentation. If the color, size or rotation speed of the stimulus is changed on each presentation, perception remains stabilized [6], indicating that these features are not contained within the memory trace. Similar findings were obtained in a related paradigm in which two different structure-from-motion stimuli were alternately presented one after the other [9]. If the two stimuli differed in color, size, rotation speed, shape or (to a lesser extent) eye of origin, alternations (although infrequent) were highly correlated between the two interleaved stimuli. A reversal of the perceived direction of motion of one stimulus was likely to be followed by a reversal in the

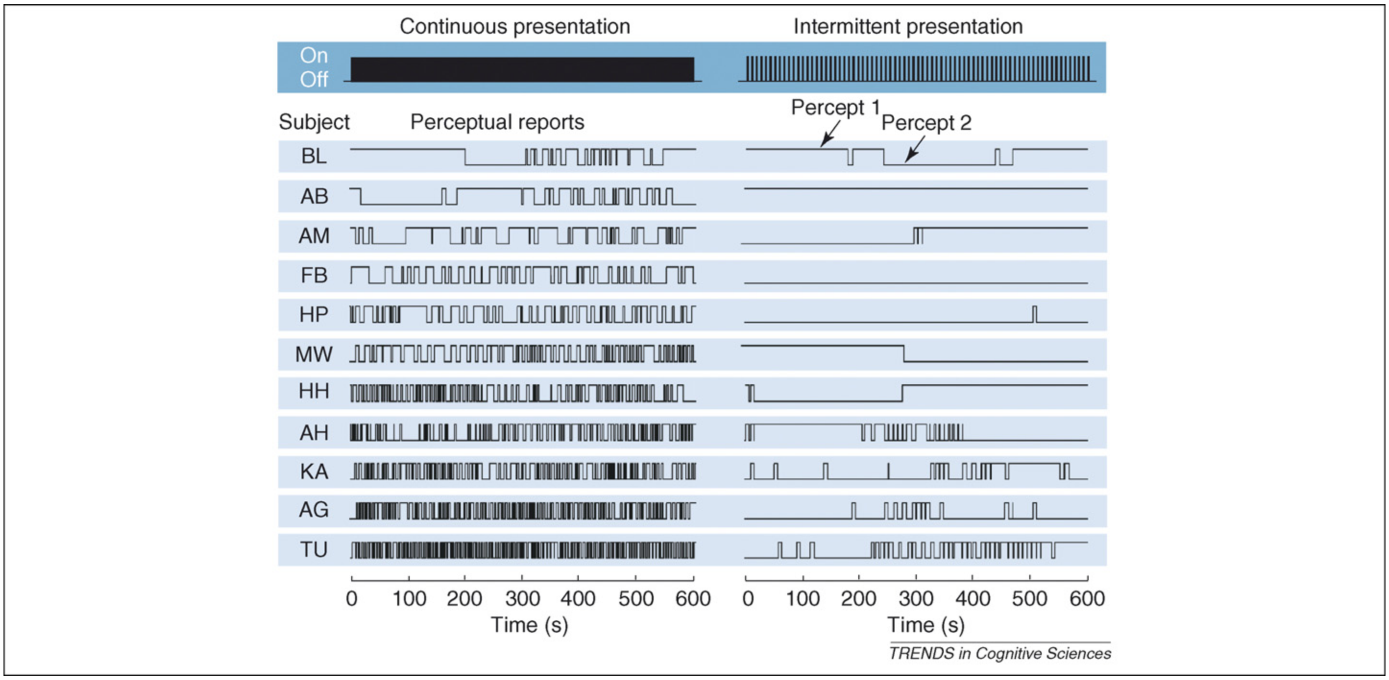
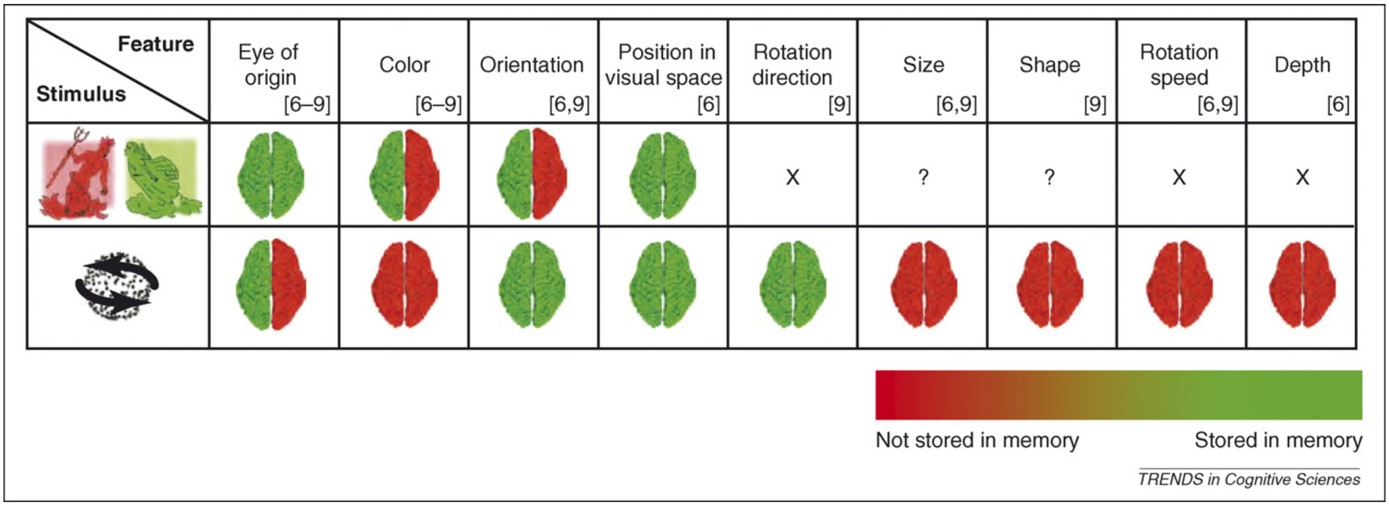


Figure 2. Perceptual stabilization. Eleven individual subjects tracked perception of a structure-from-motion stimulus presented either continuously (left) or intermittently (right). Each subject demonstrates a dramatic reduction in the number of perceptual alternations during intermittent viewing compared with continuous viewing. Adapted, with permission, from Ref. [5].



Feature Stimulus	Eye of origin [6–9]	Color [6–9]	Orientation [6,9]	Position in visual space [6]	Rotation direction [9]	Size [6,9]	Shape [9]	Rotation speed [6,9]	Depth [6]
	🟩	🟩🟥	🟩🟥	🟩	X	?	?	X	X
	🟩🟥	🟥	🟩	🟩	🟩	🟥	🟥	🟥	🟥

Figure 3. What type of information is stored in perceptual memory? This figure summarizes which attributes of a perception are stored across a blank period and which ones are seemingly forgotten. The top row shows data for binocular rivalry. The bottom row shows data for a structure-from-motion stimulus. Red brains indicate that the particular information is not stored in the memory trace; green brains denote the information is stored in memory; X indicates that a particular field is not relevant for that stimulus and question marks indicate there is not sufficient information available at this point.

perceived motion direction of the other. This indicates that, in terms of memory, two stimuli that differ along these feature dimensions are effectively treated as the same.

One factor that is stored in memory is the orientation of the axis around which a structure-from-motion stimulus revolves (e.g. horizontal or vertical). When two stimuli that differ sufficiently in their angle of rotation are presented in an interleaved cycle, they become independently stabilized [9] (Figure 4a). Here, the rotational angle of the pattern is so important to the memory that the visual system treats these two stimuli as if they were categorically different. Each pattern becomes independently stabilized, as if the other pattern was not there. This indicates the coexistence of two independent memory traces, each specific to a rotation angle.

A second factor represented in the memory trace is the visual location of the stimulus. When the retinotopic location of structure-from-motion stimulus is varied between consecutive presentations, subjects see more alternations [6]. This indicates that perceptual memory is specific to the location in retinotopic space. The spatial layout of visual information on the retina is strongly topographic in early visual cortex. Hence, the memory exhibits known characteristics of early visual areas.

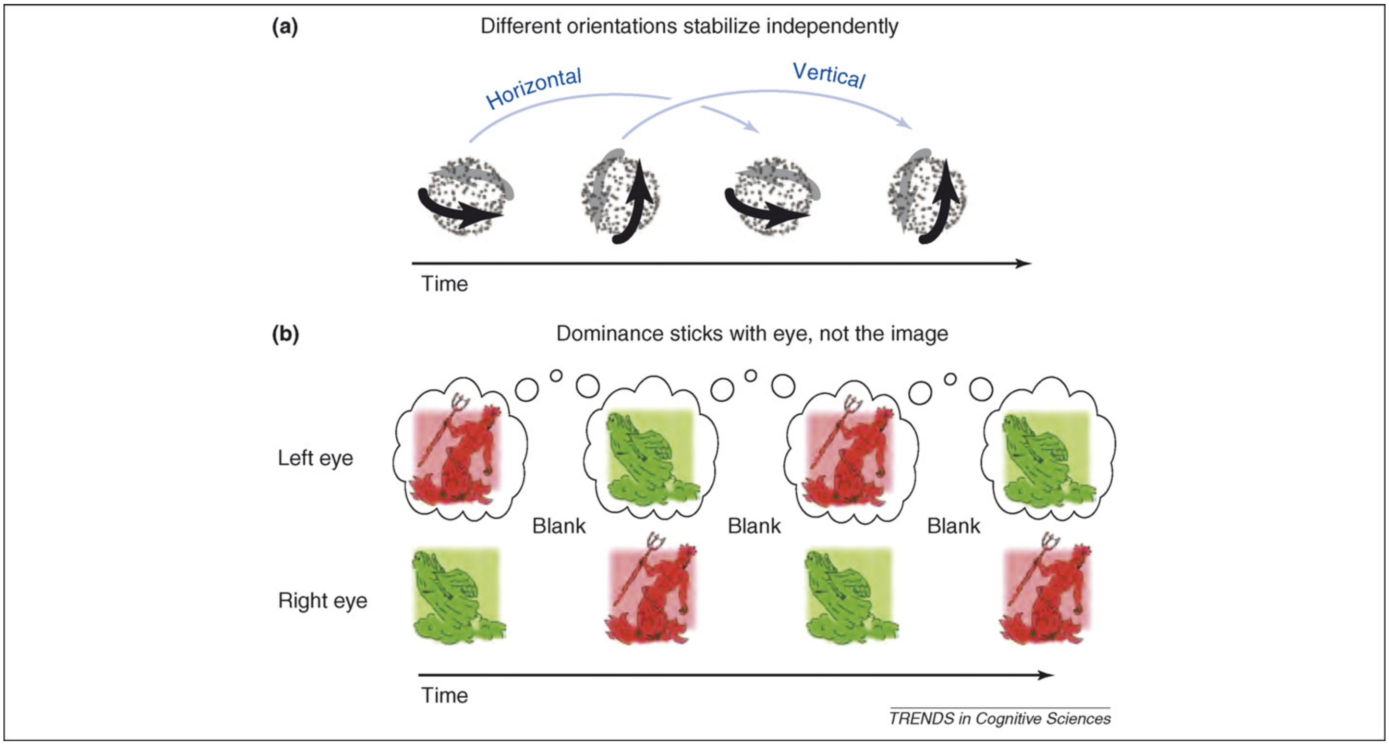


Figure 4. Different methods for investigating memory content. **(a)** When two structure-from-motion stimuli with different angles of rotation are intermittently cycled at the same location in retinotopic space in an interleaved fashion, both patterns are independently stabilized. The two memory traces can coexist for the same area of retinotopic space. Hence, the memory trace is specific to the angle of rotation [9]. **(b)** By swapping the two patterns between the eyes in synchrony with the on/off intermittent cycle of binocular rivalry, researchers have shown that it is primarily the eye of origin that is stored in memory [6,7].

In summary, for structure-from-motion stimuli, perceptual memory entails storage of the angle and direction of rotation within a limited region of the visual field, and carries little information on features such as size, shape, speed or color.

Binocular rivalry

Binocular rivalry is a form of bistability that occurs when two dissimilar stimuli are presented, one to each eye, in corresponding locations of visual space (Figure 1a). Binocular rivalry memory, like memory for structure-from-motion stimuli, is local in terms of retinotopic space [6]. Another important factor is the eye of origin (the eye that sources each pattern) of the dominant stimulus. When two competing static images are exchanged between the eyes in synchrony with the on/off intermittent presentation cycle, dominance will stick with the same eye rather than the same image [6,7] (Figure 4b). The memory retained between presentations effectively stabilizes the dominance relationship between the eyes, even when different patterns are presented. An individual experiencing binocular rivalry is unaware of which eye is sourcing the dominant pattern [10], indicating that what is stabilized can be dissociated from the conscious percept. Hence, the content of memory is not necessarily conscious perceptual information, rendering 'perceptual memory' somewhat of a misnomer. However, swapping the eye of origin across presentations is less disruptive to perceptual stability if moving 3D shapes are used as binocular rivalry images, instead of simple static patterns [11]. This indicates that the memory can be specific to the attributes in the stimulus. For example, if colored and oriented patterns are used for the rivalry stimuli, the memory not only consists of eye of origin information but also, to a lesser extent, color and orientation information [7].

Recent results have revealed that subjects exhibit a retinally specific preference for one percept over the other during binocular rivalry [12]. For example, an individual might have an intrinsic preference for a green pattern in the top-right region of visual space. This location preference could partially drive changes in perception across presentations at different locations. Hence, care is needed when interpreting memory measured across different retinotopic locations.

Perceptual bistability similar to conventional binocular rivalry can be observed when the two patterns undergoing rivalry are quickly flickered (on/off) and exchanged between the eyes approximately three times per second [13]. This form of 'stimulus rivalry' exhibits memory that is similar to classical binocular rivalry [7]. However, memory for stimulus rivalry lacks the eye of origin component prevalent in classical binocular rivalry memory [7]. Despite this difference, the memory for these two types of rivalry is effectively interchangeable [14]. Perceptual dominance in one form of rivalry will carry over to the other, stabilizing perception across the two. This is surprising because evidence indicates that these two types of rivalry are contingent on neural activity at different levels of visual processing [15].

In summary, the emerging view from these experiments is that perceptual memory elicited by a given stimulus has characteristics similar to those of the early sensory neurons that respond to the stimulus during continuous presentation. For binocular rivalry these would be neurons sensitive to information such as eye of origin, color and orientation, and specific to a region of retinotopic space. For structure-from-motion stimuli, it would be expected that neurons tuned to motion direction in addition to visual location are involved in the memory trace. We interpret this as evidence that the perceptual memory arises across the specific sensory areas that deal with the perception of a given ambiguous stimulus.

This idea is consistent with results based on event related brain potentials [16,17]. Recent functional imaging work also points to sensory areas, and also indicates the involvement of frontal areas [18].

Temporal characteristics of memory

Many studies of memory for ambiguous perception demonstrate correlations between current and past dominance. However, the exact causal relationship in this situation is unclear. Pearson and Clifford [14] used an experimental

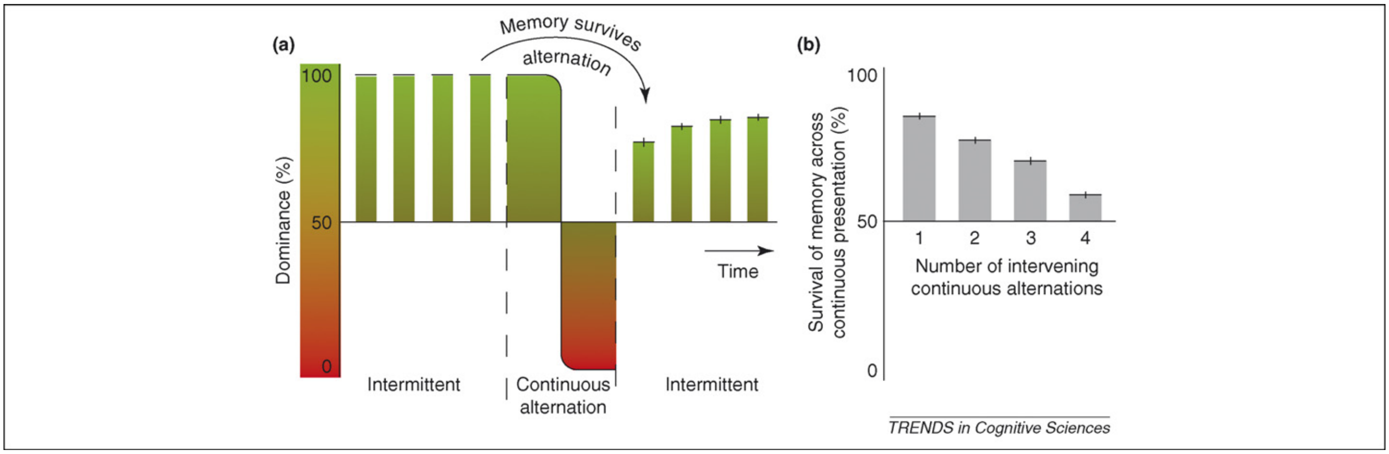


Figure 5. Perceptual memory spans back further than the most recent perception. **(a)** A period of continuous viewing was inserted halfway into an intermittent presentation sequence, prompting a perceptual alternation. Despite this alternation, perceptual stabilization was minimally affected when intermittent presentation was resumed. **(b)** In further experiments, the intervening continuous viewing period contained more than one alternation. Perceptual memory showed above-chance survival across up to four alternations. This indicates that perceptual memory is not simply memory of the latest perception, but of a more elaborate history of prior perception. Adapted, with permission, from Ref. [19].

paradigm known as flash suppression to control perceptual dominance during binocular rivalry. During flash suppression the two rivalry images are switched on asynchronously, and as the second image appears it becomes dominant. This presentation technique enables perceptual dominance to be reset to the other eye at any time throughout a cycle of stabilized rivalry presentations. When perceptual dominance was reset like this, dominance in the next normal rivalry presentation in the cycle tended to follow the percept imposed by flash suppression. This demonstrates a causal relationship between perceptual dominance before and after a blank interval, as opposed to only a correlational relationship.

Recent experiments show that perceptual memory is not limited to the effect of the single last percept but, instead, accumulates across many perceptual events [19,20]. To investigate this issue, Brascamp *et al.* [19] first stabilized perception by using an intermittent presentation cycle. Perception was then made to oscillate either by leaving the stimulus on long enough to prompt perceptual alternations or by forcing an alternation by using flash suppression. After dominance had switched to the opposite percept, intermittent presentations were resumed and perception was re-stabilized (Figure 5a). Strikingly, perception typically did not re-stabilize to the new 'reset' percept, but resumed the old stabilization sequence from before any alternations. The single last percept only had a transient influence on subsequent perception (Figure 5). The driving force for this sustained memory was the overall ratio of dominance of either percept during the prior minute of perception. Hence, memory cannot only have a transient effect across a single interval, but has the potential to grow and evolve over time, across multiple brief presentations. The dynamic nature of this memory indicates the flexibility of a variable-length time course, enabling both sustained and transient traces. The sustained components survived at least four consecutive alternations during the intervening continuous presentation (Figure 5b; right-hand column); however, the probability of stabilization surviving these alternations declined as the number of continuous alternations increased (Figure 5b). Rather than providing only a snapshot of the most recent perceptual situation before a blank, when allowed to develop, perceptual memory can reflect a balance of forces accumulated over the course of many presentations.

One implication of this flexible long-term storage is that the longevity of this memory cannot be fully estimated by comparing perception on two consecutive presentations separated by various durations. Instead, the maximum blank duration that perceptual memory can survive depends on the specific sequence of preceding perception. Another complication is that the lifetime of this memory depends on the specific conditions during memory retention. For instance, attentional manipulations can modulate the effectiveness of memory for some stimuli [21] but not others [22].

When the blank interruption during intermittent presentation is exceedingly brief, the stabilizing effect reverses. After a blank interval shorter than approximately half a second, the observer is more likely to see the interpretation that was previously suppressed than the previously dominant one; a process of perceptual destabilization [4,23]. This negative relationship still indicates an interaction across a period of stimulus absence, but this interaction does not involve a priming effect. Instead, it is reminiscent of the suppressive effect often associated with prior unambiguous stimulation on ambiguous perception (Box 1). At such brief blank intervals, the rate of switching increases to a point far above the rate during continuous viewing [4,23]. Here, instead of slowing alternations, switching the stimulus on and off has the opposite effect: it speeds up the alternation rate. Not until the blank interruptions are contracted (<100 ms) so that the presentation is almost continuous, do alternations tend to slow again, approaching the rate during continuous presentation. This range of different effects contingent on the length of the blank interruption can be understood through the interplay of adaptation and cross-inhibition, as discussed in the next section.

Box 1. Unambiguous prior stimuli

One way to think of perceptual stabilization is as a priming effect of past dominance on perception choice at the next stimulus presentation. Can normal unambiguous stimuli also prime bistable perception? Indeed, prior perception of a disambiguated stimulus can lead an ambiguous stimulus to be perceived in the same way [42,54–58]. However, the opposite, suppressive effect, is more typical [14,53,59]. Often, whether an unambiguous prior stimulus will have a positive or negative effect on subsequent bistable perception depends on its 'energy', such that sustained or high contrast prior stimuli will tend to prompt the opposite perception, whereas brief or low contrast stimuli will prime, causing percept repetition [22,42,55,57]. In the case of ambiguous prior stimuli, suppressive effects are confined to paradigms using brief blank intervals [4,23].

We suggest that the persisting neural effects evoked by a prior stimulus – be it ambiguous or unambiguous – are characterized by both positive components (priming) and negative components (suppression). In this context, perception of an ambiguous stimulus after a prior stimulus is simply a particularly sensitive way of gauging the balance between these components. In fact, binocular rivalry perception has recently been used in this way to measure the persistent effects caused by mental imagery, in the absence of incoming visual signals [22].

Modeling

Recent modeling efforts now unite many of the psychophysical findings within a plausible account of this memory for ambiguous vision [23,24]. In fact, perception during continuous and intermittent viewing can now be explained within a single framework.

Initial theories of perceptual stabilization were strongly influenced by the historical emphasis on models of continuous ambiguous perception. These models center on the concept that competing perceptual interpretations are represented in the brain by opposing neural populations. For continuous viewing, typically these models posit that perceptual alternations occur because a form of self-adaptation or neural fatigue weakens the neural representation of the dominant stimulus. When the neural representation of the dominant stimulus becomes critically weak, its neural activity is no longer sufficient to suppress the other pattern and an alternation takes place [25–27]. The evidence from neuroimaging and neurophysiology studies is ambiguous, with some studies supporting the model that neural adaptation drives perceptual changes [28–31] and other studies indicating that a distributed high level process, rather than adaptation, is responsible for driving perceptual alternations [32–34]. Inspired by these earlier models, perceptual stabilization was thought to occur because periodic stimulus removal slows the build-up of adaptation, causing adaptation to take longer to reach a critical level [4,6]. It is now clear that this reasoning is incongruent with empirical findings. A slower increase in adaptation as the cause of stabilization is hard to reconcile with the finding that, given the right timing, interruptions can also promote alternations [4,23,35]. Furthermore, adaptation is freely allowed to reach its crucial level when a period of continuous presentation is inserted halfway through a stabilized cycle of intermittent presentations; however, this does not reset the stabilization cycle [19] (Figure 5).

Classical adaptation–inhibition models, as they stand, are insufficient to explain perceptual stabilization. Mutual inhibition between two competing neural populations is a crucial element of models of continuous ambiguous perception [23,26,27,36,37]. In these models, the dominant representation strongly inhibits the suppressed representation, which reinforces the present dominance relationship. Only when adaptation of the dominant population reaches a crucial value, at which it outweighs this stabilizing force, does perception switch. After a blank interval lasting a few seconds, however, the spiking response to a stimulus (and hence mutual inhibition) has probably died out [26]. Adaptation, however, decays much more slowly. Therefore, when the stimulus reappears there is still residual adaptation but no inhibition. In other words, without the counteracting force of inhibition, there is no threshold left for adaptation to overcome and any residual adaptation will cause instant suppression. Indeed, no classic adaptation–inhibition model can explain perceptual stabilization.

One way to expand these models to account for perceptual stabilization is to add a component that is persistent (like adaptation) but, unlike classical adaptation, has a facilitating effect on future perception. Two recent studies account for stabilization using this approach. One model put forward by Noest and colleagues [23] posits that being in an adapted state has two distinct effects on a neural population. The first effect is that it causes a reduced response gain; a classic interpretation of adaptation. The second effect is different from classic accounts, and can be interpreted as a sub-threshold elevation in the baseline activation of the adapted neurons. This second, positive effect gives the more 'adapted' representation a head start when a stimulus reappears (Figure 6b; right panel). Because, in most cases, this is the recently dominant representation, this allows for the occurrence of perceptual stabilization. In addition, the model parsimoniously explains why perceptual stabilization turns into destabilization at short blank intervals [23]. A second model proposed by Wilson [24] expands an adaptation–inhibition framework with a form of long-term synaptic potentiation. Here, activity brings a neural population into a persistent state of elevated excitability (Figure 6b; left panel). It is this potentiation that provides the competitive advantage that is needed to explain perceptual stabilization. Figure 6 shows the time courses for the two hypothetical memory traces implemented by the models for a given intermittent presentation cycle. The green plots show activity and traces for the dominant interpretation, whereas the red plots show the suppressed interpretation.

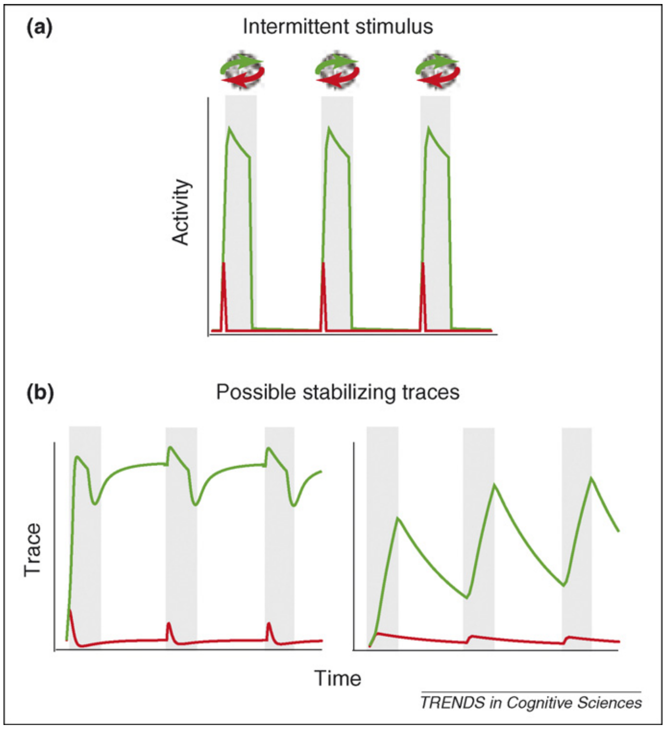


Figure 6. Model activity and traces during stabilized perception. **(a)** Activity of two competing perceptual representations during stabilized perception. During stimulus presence the representation of the dominant percept is highly active (green), whereas that of the suppressed interpretation is only weakly active (red). During the blank interval, activity for both representations falls to near zero. **(b)** Proposed memory traces that can account for stabilized perception. Left: traces of past perception proposed by Wilson [24]. A facilitatory trace of the dominant percept persists across the blank intervals. This maintains the stabilized representation in a state of heightened excitability, enabling it to gain dominance at stimulus reappearance. Right: traces of past perception proposed by Noest *et al.* [23]. A trace of the stabilized percept builds during dominance and passively decays during stimulus absence. This trace slightly elevates the baseline activation of the stabilized representation, which can enable it to gain dominance at stimulus reappearance.

The models differ in their various predictions and simulated data. The longer a stimulus interpretation has been perceived before offset, the more likely subsequent perception is to follow the same interpretation [5,19]. The model proposed by Noest and colleagues [23] predicts this empirical observation, whereas Wilson's [24] account predicts the opposite. The model by Noest and colleagues has recently been expanded by Brascamp *et al.* [19] to produce the variable-length time courses observed empirically. It is worth noting that, although these models are parsimonious implementations of our best understanding of the processes underlying this memory for ambiguous perception, they are hypotheses in progress.

The memory for ambiguous perception might be related to forms of priming [38]. Most clearly, it is similar to perceptual priming using unambiguous stimuli (Box 1). Studies have shown that low energy or weak primes can facilitate subsequent detection or discrimination [39–41], which bears some similarity to the memory trace discussed here [22,42]. We suggest these various priming phenomena, despite obvious differences, might be similar in terms of the neural

Box 2. Outstanding questions

- Can the neural trace of the memory for ambiguous vision be measured in early cortical areas such as visual area one?
- How does this memory relate to other forms of memory such as episodic or visual short-term working memory?
- Might this automatic memory have a role in perceptual learning [60,61]?
- Could this memory for ambiguous vision be symptomatic of a more general automatic memory system influencing more high level processes such as semantic or moral decisions?

events that underlie them. Other forms of priming might also be related to the memory for ambiguous vision such as the reduction in response time that occurs over repetitions of a recurring oddball target [43,44] or automatic acceleration over repetitions of a motor action [45,46].

The automatic nature of this memory differs from traditional descriptions of working memory, which involve active maintenance to prevent memory decay [47–52]. This is in clear distinction from the automatic nature of the memory for bistable vision. Currently, it is unclear how these actively maintained types of memory relate to the automatic forms of perceptual memory that are evident during ambiguous vision.

Concluding remarks

Memory for ambiguous vision is largely composed of 'early level' sensory information. Although a single instance of ambiguous vision can directly bias subsequent ambiguous perception, the memory trace does not only carry information from the single last perceptual event but can build over many perceptual events spread across time. The memory trace shares characteristics with various types of priming. Computational models currently account for a broad spectrum of empirical observations.

This is an exciting time to observe the rapidly growing body of empirical findings, which are complemented by computational frameworks forging the understanding of this memory phenomenon. Scientists now have some understanding of what information is remembered and how and where the brain might hold this information. We look forward to future growth and new directions (Box 2), as research into this phenomenon continues to excite and surprise.

Acknowledgements

We thank Tomas Knapen, Randolph Blake, Frank Tong, Bert van den Berg, André Noest, Raymond Van Ee and Jascha Swisher for helpful comments and/or discussion. We also thank JJ's for their atmosphere. J.P. holds an NHMRC (Aust.) CJ Martin Fellowship 457146. J.B. was supported by a travel grant from the IIE Fulbright program and funds from the Vanderbilt International Grant Program.

References

1 Blake, R. and Logothetis, N.K. (2002) Visual competition. *Nat. Rev. Neurosci.* 3, 13–21
2 Tong, F. *et al.* (2006) Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511
3 Fox, R. and Herman, J. (1967) Stochastic properties of binocular rivalry alternations. *Percept. Psychophys.* 2, 432–436
4 Orbach, J. *et al.* (1963) Reversibility of the Necker cube. I. an examination of the concept of "satiation of orientation". *Percept. Mot. Skills* 17, 439–458
5 Leopold, D.A. *et al.* (2002) Stable perception of visually ambiguous patterns. *Nat. Neurosci.* 5, 605–609
6 Chen, X. and He, S. (2004) Local factors determine the stabilization of monocular ambiguous and binocular rivalry stimuli. *Curr. Biol.* 14, 1013–1017
7 Pearson, J. and Clifford, C.W.G. (2004) Determinants of visual awareness following interruptions during rivalry. *J. Vis.* 4, 196–202
8 O'Shea, R.P. (2004) Psychophysics: catching the old codger's eye. *Curr. Biol.* 14, R478–R479
9 Maier, A. *et al.* (2003) Perception of temporally interleaved ambiguous patterns. *Curr. Biol.* 13, 1076–1085
10 Ono, H. and Barbeito, R. (1985) Utrocular discrimination is not sufficient for utrocular identification. *Vision Res.* 25, 289–299
11 Grossmann, J.K. and Dobbins, A.C. (2006) Competition in bistable vision is attribute-specific. *Vision Res.* 46, 285–292
12 Carter, O. and Cavanagh, P. (2007) Onset rivalry: brief presentation isolates an early independent phase of perceptual competition. *PLoS ONE* 2, e343
13 Logothetis, N.K. *et al.* (1996) What is rivalling during binocular rivalry? *Nature* 380, 621–624
14 Pearson, J. and Clifford, C.W.G. (2005) Mechanisms selectively engaged in rivalry: normal vision habituates, rivalrous vision primes. *Vision Res.* 45, 707–714
15 Pearson, J. *et al.* (2007) The effects of transcranial magnetic stimulation on visual rivalry. *J. Vis.* 7, 2.1–11
16 Kornmeier, J. and Bach, M. (2004) Early neural activity in Necker-cube reversal: evidence for low-level processing of a gestalt phenomenon. *Psychophysiology* 41, 1–8
17 Kornmeier, J. and Bach, M. (2005) The Necker cube – an ambiguous figure disambiguated in early visual processing. *Vision Res.* 45, 955–960
18 Sterzer, P. and Rees, G. (2008) A neural basis for percept stabilization in binocular rivalry. *J. Cogn. Neurosci.* 20, 389–399
19 Brascamp, J.W. *et al.* (2008) Multi-timescale perceptual history resolves visual ambiguity. *PLoS ONE* 3, e1497
20 Maloney, L.T. *et al.* (2005) Past trials influence perception of ambiguous motion quartets through pattern completion. *Proc. Natl. Acad. Sci. U. S. A.* 102, 3164–3169
21 Kanai, R. and Verstraten, F.A. (2006) Attentional modulation of perceptual stabilization. *Proc. Biol. Sci.* 273, 1217–1222
22 Pearson, J. *et al.* (2008) The functional impact of mental imagery on conscious perception. *Curr. Biol.* 18, 982–986
23 Noest, A.J. *et al.* (2007) Percept-choice sequences driven by interrupted ambiguous stimuli: a low-level neural model. *J. Vis.* 7, 1–14
24 Wilson, H.R. (2007) Minimal physiological conditions for binocular rivalry and rivalry memory. *Vision Res.* 47, 2741–2750
25 Blake, R. *et al.* (2003) Visual motion retards alternations between conflicting perceptual interpretations. *Neuron* 39, 869–878
26 Wilson, H.R. (2003) Computational evidence for a rivalry hierarchy in vision. *Proc. Natl. Acad. Sci. U. S. A.* 100, 14499–14503
27 Freeman, A.W. (2005) Multistage model for binocular rivalry. *J. Neurophysiol.* 94, 4412–4420
28 Tong, F. and Engel, S.A. (2001) Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* 411, 195–199
29 Tong, F. *et al.* (1998) Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759
30 Leopold, D.A. and Logothetis, N.K. (1996) Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379, 549–553
31 Sheinberg, D.L. and Logothetis, N.K. (1997) The role of temporal cortical areas in perceptual organization. *Proc. Natl. Acad. Sci. U. S. A.* 94, 3408–3413
32 Lumer, E.D. *et al.* (1998) Neural correlates of perceptual rivalry in the human brain. *Science* 280, 1930–1934
33 Lumer, E.D. and Rees, G. (1999) Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1669–1673
34 Sterzer, P. *et al.* (2002) Neural correlates of spontaneous direction reversals in ambiguous apparent visual motion. *Neuroimage* 15, 908–916
35 Orbach, J. *et al.* (1966) Reversibility of the Necker cube VII. Reversal rate as a function of figure-on and figure-off durations. *Percept. Mot. Skills* 22, 615–618

36 Laing, C.R. and Chow, C.C. (2002) A spiking neuron model for binocular rivalry. *J. Comput. Neurosci.* 12, 39–53

37 Mueller, T.J. (1990) A physiological model of binocular rivalry. *Vis. Neurosci.* 4, 63–73

38 Schacter, D.L. *et al.* (2004) Specificity of priming: a cognitive neuroscience perspective. *Nat. Rev. Neurosci.* 5, 853–862

39 Campana, G. *et al.* (2002) Priming of motion direction and area V5/MT: a test of perceptual memory. *Cereb. Cortex* 12, 663–669

40 Tanaka, Y. and Sagi, D. (1998) A perceptual memory for low-contrast visual signals. *Proc. Natl. Acad. Sci. U. S. A.* 95, 12729–12733

41 Bar, M. and Biederman, I. (1999) Localizing the cortical region mediating visual awareness of object identity. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1790–1793

42 Brascamp, J.W. *et al.* (2007) Flash suppression and flash facilitation in binocular rivalry. *J. Vis.* 7, 1–12

43 Kristjansson, A. (2006) Rapid learning in attention shifts: a review. *Vis. Cogn.* 13, 324–362

44 Maljkovic, V. and Nakayama, K. (1994) Priming of pop-out: I. Role of features. *Mem. Cognit.* 22, 657–672

45 Dorris, M.C. *et al.* (2000) Immediate neural plasticity shapes motor performance. *J. Neurosci.* 20 (RC52), 1–5

46 Soetens, E. *et al.* (2004) Sequence learning and sequential effects. *Psychol. Res.* 69, 124–137

47 Averbach, E. and Sperling, G. (1961) Short term storage of information in vision. In *Information Theory* (Cherry, C., ed.), pp. 196–211, Butterworth

48 Coltheart, M. (1983) Iconic memory. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 302, 283–294

49 Magnussen, S. and Greenlee, M.W. (1999) The psychophysics of perceptual memory. *Psychol. Res.* 62, 81–92

50 Sperling, G. (1960) The information available in brief visual presentations. *Psychological Monographs. General and Applied* 74, 1–29

51 Pasternak, T. and Greenlee, M.W. (2005) Working memory in primate sensory systems. *Nat. Rev. Neurosci.* 6, 97–107

52 Baddeley, A. (2003) Working memory: looking back and looking forward. *Nat. Rev. Neurosci.* 4, 829–839

53 Wolfe, J.M. (1984) Reversing ocular dominance and suppression in a single flash. *Vision Res.* 24, 471–478

54 Kanai, R. *et al.* (2007) Disruption of implicit perceptual memory by intervening neutral stimuli. *Vision Res.* 47, 2675–2683

55 Kanai, R. and Verstraten, F.A. (2005) Perceptual manifestations of fast neural plasticity: motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Res.* 45, 3109–3116

56 Long, G.M. and Moran, C.J. (2007) How to keep a reversible figure from reversing: teasing out top-down and bottom-up processes. *Perception* 36, 431–445

57 Long, G.M. *et al.* (1992) Prime time: fatigue and set effects in the perception of reversible figures. *Percept. Psychophys.* 52, 609–616

58 Wilton, R.N. (1985) The recency effect in the perception of ambiguous figures. *Perception* 14, 53–61

59 Nawrot, M. and Blake, R. (1989) Neural integration of information specifying structure from stereopsis and motion. *Science* 244, 716–718

60 Haijiang, Q. *et al.* (2006) Demonstration of cue recruitment: change in visual appearance by means of Pavlovian conditioning. *Proc. Natl. Acad. Sci. U. S. A.* 103, 483–488

61 Suzuki, S. and Grabowecky, M. (2007) Long-term speeding in perceptual switches mediated by attention-dependent plasticity in cortical visual processing. *Neuron* 56, 741–753