

Stable perception of visually ambiguous patterns

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During the viewing of certain patterns, widely known as ambiguous or puzzle figures, perception lapses into a sequence of spontaneous alternations, switching every few seconds between two or more visual interpretations of the stimulus. Although their nature and origin remain topics of debate, these stochastic switches are generally thought to be the automatic and inevitable consequence of viewing a pattern without a unique solution. We report here that in humans such perceptual alternations can be slowed, and even brought to a standstill, if the visual stimulus is periodically removed from view. We also show, with a visual illusion, that this stabilizing effect hinges on perceptual disappearance rather than on actual removal of the stimulus. These findings indicate that uninterrupted subjective perception of an ambiguous pattern is required for the initiation of the brain-state changes underlying multistable vision.

Visual perception involves coordination between sensory sampling of the world and active interpretation of the sensory data. Human perception of objects and scenes is normally stable and robust, but it falters when one is presented with patterns that are inherently ambiguous or contradictory. Under such conditions, vision lapses into a chain of continually alternating percepts, whereby a viable visual interpretation dominates for a few seconds and is then replaced by a rival interpretation. This multistable vision, or ‘multistability’, is thought to result from destabilization of fundamental visual mechanisms, and has offered valuable insights into how sensory patterns are actively organized and interpreted in the brain^{1,2}. Despite a great deal of recent research and interest in multistable perception, however, its neurophysiological underpinnings remain poorly understood. Physiological studies have suggested that disambiguation of ambiguous patterns draws on activity within the visual cortex^{3–10}, but how this activity ultimately contributes to perceptual solution is not yet known. Even less clear is the nature of the perceptual alternation process itself. Traditional views hold that it is an automatic consequence of incompatible, antagonistic stimulus representations in the sensory visual cortex^{11,12}. Recent evidence challenges this notion, suggesting instead that perceptual alternations are initiated outside the primarily sensory areas^{13,14} (for a review, see ref. 15).

In the present study, we report that the spontaneous changes of multistable perception can be greatly slowed, and even brought to a standstill, when the inducing patterns are viewed intermittently rather than continuously. Specifically, when we introduced blank periods of several seconds into an extended period of continuous viewing, we consistently slowed the rate of alternation by two orders of magnitude. Individual periods of perceptual dominance often exceeded 10 minutes. The stabilization effect was present for a variety of bistable patterns, and could not be attributed to a permanent perceptual bias. In addition, we used a visual illusion called motion-induced blindness¹⁶ to show that the stabilization effect depended on intermittent subjective dis-

appearance of the pattern, not on intermittent disappearance of the sensory representation itself.

RESULTS

The initial aim of this study was to examine the influence of recent visual history on the perceptual organization of an ambiguous pattern. To address this, we repeatedly presented a rotating sphere (RS) stimulus (Fig. 1a), whose three-dimensional structure is ambiguous¹⁷, in a train of 3-s presentations separated by 5-s periods during which the screen was blank. Whenever the stimulus was present, subjects reported whether it appeared to be rotating upward or downward around the horizontal axis. For intermittent viewing, perception tended to become ‘stuck’ in a particular configuration, often for several minutes at a time (Fig. 2). As compared with the continuous viewing condition, phases of perceptual dominance were markedly lengthened, and some subjects saw no reversals in rotation for the duration of the 10-min session. Stabilization for the RS was present in 22 of 23 subjects tested in different experiments throughout the study, with no consistent difference between horizontal and vertical rotation. This effect was not the result of a permanent perceptual bias or reset mechanism following each new stimulus presentation, as there was often sequential stabilization of both possible percepts (subjects BL, AM, MW, HH & AH, Fig. 2). In general, subjects with shorter mean dominance phases during continuous presentation exhibited less stabilization during the intermittent condition. As each presentation time was fixed at 3 s for all subjects, we attribute this trend to an increased probability for ‘fast-switchers’ to experience perceptual reversal during a single stimulus presentation.

Stabilization increased when the stimulus was absent for longer periods of time (Fig. 3a), indicating that a perceptual configuration, once established, could survive even relatively long epochs in which the stimulus was gone. There was no apparent decline in the survival of a percept for blank times as long as 40 s

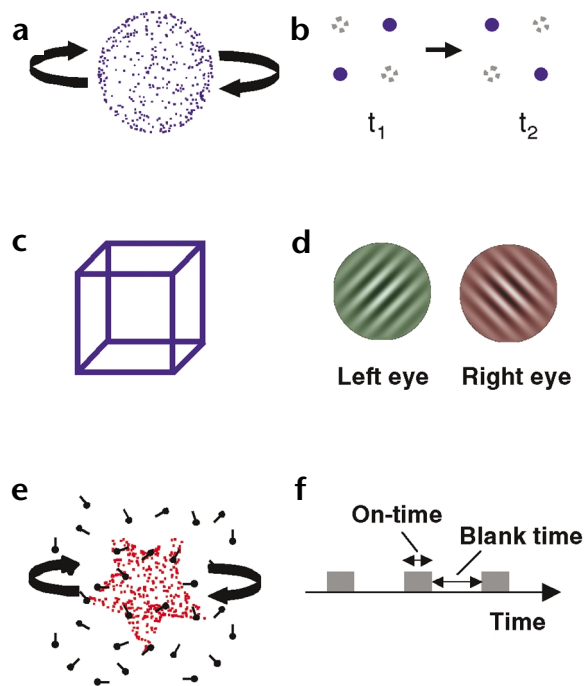


Fig. 1. Stimuli used in the study. (a) Rotating sphere (RS), which turned about either the vertical or horizontal axis; (b) quartet dots (QD); (c) Necker cube (NC); (d) binocular rivalry (BR); and (e) rotating star (RSt) amid randomly moving dots used to provoke the motion-induced blindness illusion. (f) Stimuli were presented either continuously or intermittently, with variable on-times and blank-screen durations.

(Fig. 3b). Notably, when alternations did occur, the probability of a configuration persisting until the subsequent presentation was highly dependent on how long it was seen before the stimulus was removed. Only when a perceptual configuration was seen consistently (without reversals) for 2 s or longer before stimulus disappearance was there a high probability that it would persist to the next stimulus presentation (Fig. 3c).

Given the reliable persistence of a perceptual configuration across blank periods, could the increased stabilization with longer blank times be accounted for simply by the decreased overall time of exposure to the stimulus? This cannot be the case, because the actual reduction in total alternations far exceeded that expected from stimulus presentation time alone (Fig. 3d). This also was true for the blink condition, where subjects mimicked the disappearance and reappearance of the stimulus by periodically shutting and opening their eyes when they heard appropriately timed tones. For blinking, even higher stabilization was observed. Finally, alternation rates were measured for a 1-minute sliding window shifted by 1-s increments, pooled for all subjects and compiled into a histogram for each condition (with blanks, Fig. 3e; with blinks, Fig. 3f). Note that for both conditions, very low reversal rates dominated the inter-

mittent/blinks presentation, whereas a mix of higher rates was seen during continuous presentation.

To examine whether this stabilization effect holds for multi-stable stimuli other than the RS, we repeated the experiment with three other common, but inherently different, bistable patterns (Fig. 1b–d): the Necker cube¹⁸ (NC, ambiguous static depth), quartet dots¹⁹ (QD, ambiguous motion correspondence) and binocular rivalry²⁰ (BR, introcular conflict). For each stimulus, we first adjusted the time the stimulus was present (on-time) to be markedly shorter than the mean dominance phase during continuous viewing. Subjects again viewed each pattern either continuously or intermittently, reporting which of the two perceptual configurations they saw whenever the stimulus was present. Results for these three additional stimuli were similar to those obtained with the RS (Fig. 4).

Finally, we asked whether physical removal of the stimulus was necessary to achieve stabilization, or whether its mere subjective disappearance would give similar results. To test this, we exploited the recently described visual illusion of motion-induced blindness (MIB)¹⁶ to provoke frequent illusory fading of an ambiguous rotating star (RSt) pattern (Fig. 1e). The RSt was similar in many respects to the RS: during continuous viewing, it produced perceptual reversals in the direction of rotation. Instead of comparing continuous with intermittent presentation as before, we overlaid the RSt with a field of randomly moving black dots, which caused the star to periodically fade from perception (several times per minute; Fig. 5). As with the RS, subjects were required to track the rotational direction of the moving star whenever it was visible. These epochs of illusory fading had the same stabilizing effect on the perceived direction of rotation as did the physical blanking described above for the RS. This result indicates that the subjective disappearance of the pattern, rather than the actual sensory representation, ultimately underlies this stabilization phenomenon.

Fig. 2. Effects of intermittent presentation on perception of a RS rotating around the horizontal axis (11 subjects). Alternation in the perceived motion of the front surface is shown here as fluctuation between the upper (gray) and lower (black) levels, corresponding to upward and downward rotation, respectively. Each row compares the condition when the stimulus was continuously present (left) to that when it was only intermittently present (right). Intermittent viewing consisted of 3-s on-periods interleaved with 5-s blank periods, illustrated at the bottom. For each subject, ordered from top to bottom according to their inherent switch rate during continuous viewing, the total number of perceptual reversals during each stimulus condition is shown at the right.

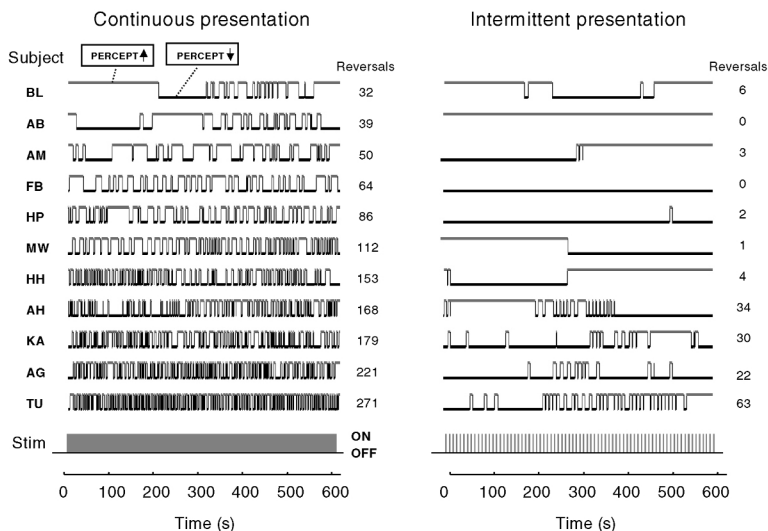
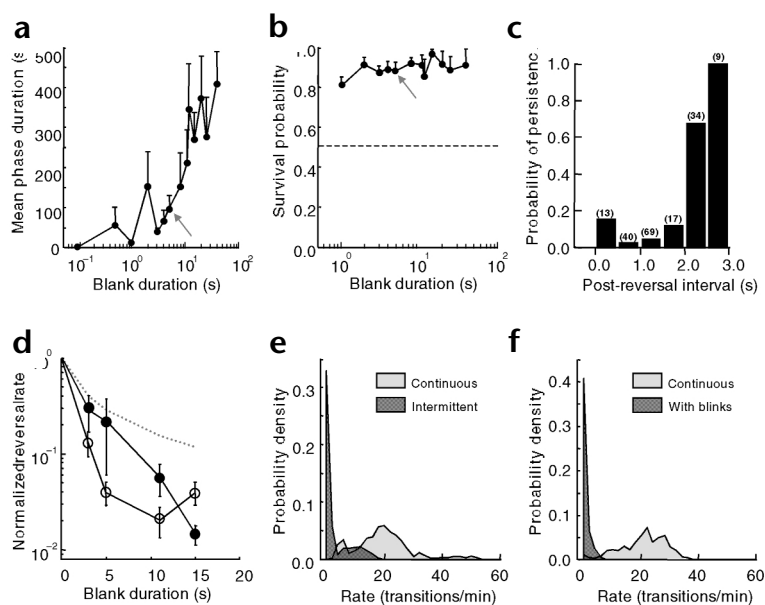


Fig. 3. Factors contributing to stabilization of the RS. **(a)** Mean phase duration (\pm s.e.m.) for intermittent presentation as a function of blank duration (six subjects, on-time 5 s). **(b)** Probability that a given perceptual state survived variable-length blanking period (same data as in **a**). Arrows indicate the blank durations for the experiment shown in **Fig. 2**. **(c)** Probability that a spontaneous perceptual reversal persists to the next stimulus presentation, as a function of post-reversal interval (time between the perceptual change and stimulus blanking). The number of instances contributing to each bin is shown above the corresponding bars (same data as in **a**). **(d)** Reversal rate for intermittent condition, normalized to the reversal rate under continuous viewing, shown for periodic removal of the stimulus (\bullet , five subjects, on-time 2 s) and timed eye closure (\circ , six subjects, eyes open 2 s). The dotted line represents the rate decrease expected if the diminished overall presentation time were the only factor. **(e)** Distribution of reversal rates for continuous versus intermittent (on-time 2 s, blank 5 s) viewing of RS (five subjects), calculated using a sliding window (see Results). Probability density plotted for continuous (light gray) and intermittent (dark gray) conditions. **(f)** Same as **(e)**, but with eye blinking instead of stimulus blanking (six subjects, pooled).



DISCUSSION

The inevitability of perceptual alternations during ambiguous vision has often been taken as evidence for a stimulus-induced but autonomously maintained reaction of the sensory processing apparatus to multistable patterns, prompting models whose basis was limited to the visual system^{11,12,21}. More recently, the switching mechanism has been postulated to lie outside of exclusively visual areas. Several lines of evidence have suggested that frontoparietal areas associated with selective visual attention are centrally involved in the initiation of perceptual alternations^{13,15}. Other evidence has suggested that alternation in hemispheric dominance, controlled by a free-running oscillator circuit in the brainstem, might underlie visual bistability^{14,22}.

Although the present results cannot pinpoint specific structures responsible for perceptual reversal, they do offer new insights into the process itself. First, the stabilization effect described here is evidence against the notion that perceptual

reversal is governed by an autonomous oscillator that operates independently of the visual stimulus¹⁴. If that were the case, a simple stimulus manipulation probably would not bring perceptual alternation to a standstill. Second, our results indicate that continuous, prolonged viewing of an ambiguous stimulus is a requirement for the initiation of the fluctuations underlying multistable perception. Moreover, the MIB illusion experiment showed that the continuous presence of the sensory stimulus does not automatically lead to perceptual instability as predicted by models of alteration based on reciprocal sensory connectivity and adaption. Instead, the periodic subjective fading of the ambiguous stimulus had approximately the same stabilizing effect as its physical removal. Perceptual switching thus appears to be governed by an active mechanism that continuously monitors the conscious perceptual representation of the stimulus itself. Perceptual changes may involve the reorganization of neural networks related to sensory processing, but they do not seem to be triggered by competition in such networks, nor do they reflect the workings of a separate, endogenous bistable circuit whose impact is merely probed by an ambiguous pattern. The fact that the greatest stabilization was obtained when subjects made the stimulus disappear by purposefully closing their eyes adds further support to the notion that active, endogenous mechanisms ultimately govern the occurrence of a perceptual reversal.

Finally, ambiguous perception has often been described as ‘memoryless’ because of the lack of

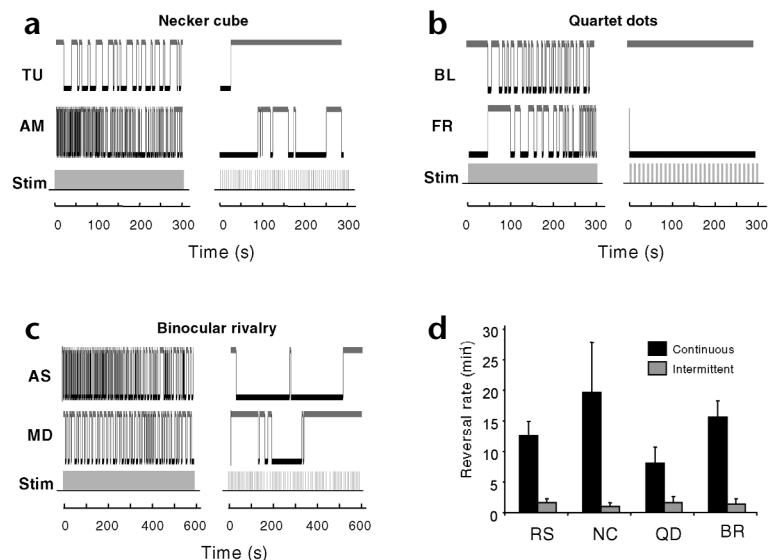


Fig. 4. Stabilization of different bistable patterns. **(a–c)** Effects of continuous (left) versus intermittent (right) presentation on the perception of NC, QD and BR stimuli (two subjects shown for each stimulus). **(d)** Total number of reversals for continuous versus intermittent viewing (means \pm s.e.m. shown). Blank durations were 5 s in all cases, and on-times were RS, 3 s (eight subjects); NC, 1 s (seven subjects); QD, 5 s (eight subjects); BR, 1.2 s (eight subjects).



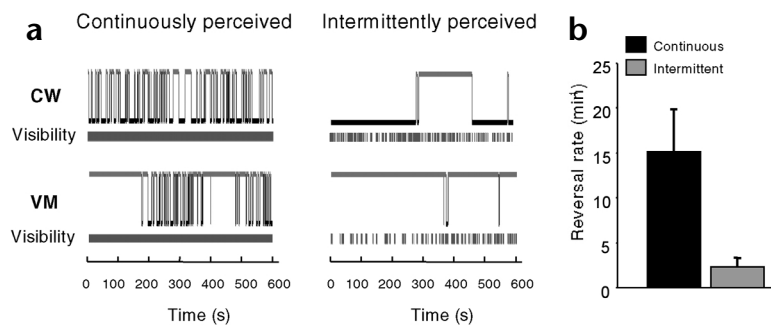


Fig. 5. Effect of subjective disappearance on perceptual reversal of the RSt. **(a)** Comparison of continuous visibility (left) versus intermittent visibility (right). Intermittent visibility was achieved by motion-induced blindness (see Methods). In both cases, the physical stimulus was continuously present. Data is shown for two subjects (CW and VM). The pattern of subjective appearance and disappearance is shown at the bottom for each subject, with gray periods representing times when the stimulus was visible. **(b)** Mean reversal rate (\pm s.e.m.) with and without epochs of perceptual disappearance (five subjects).

statistical correlation between successive reversal intervals^{23,24}. Nonetheless, we found that once the ambiguous stimulus was removed, recent perceptual history was the dominant factor in determining how that stimulus was interpreted on subsequent viewings. Thus, with each presentation, perceptual organization seems to be guided by some sort of implicit perceptual memory that does not decline over several seconds. This 'memory', which may be important during normal vision, was abolished by the continuous presentation of an ambiguous stimulus. Whereas a number of previous studies have demonstrated that external stimuli can act to deterministically bias the perception of an ambiguous pattern^{25–28}, the stabilization observed here depended entirely on the persistence of an internally generated perceptual state. Further experiments may reveal whether the same frontoparietal cortical areas that have been implicated in perceptual alternation during bistable pattern viewing^{13,29} also contribute to perceptual stabilization during intermittent viewing.

METHODS

Subjects. Thirty-nine subjects (19 female, 20 male) between the ages of 15 and 36 years (median 25) participated in the study. The experiments were done in accordance with guidelines of the local authorities (Regierungspraesidium), and all subjects gave informed written consent. Each subject had normal or corrected-to-normal vision, and most had prior experience as a psychophysical subject. Apart from two authors (subjects MW and AM), each subject was completely naive to the hypotheses and goals of the experiment, and was paid for participation. An interview after each session revealed that most subjects (>80%) were unaware that the perceptual changes they experienced were entirely subjective.

Visual stimuli. Stimuli were generated on a computer (Intergraph Zx10 PC, Huntsville, Alabama; Intense3D Graphics, Sunnyvale, California) and presented in color on two 21-inch monitors, presented separately to each eye by a mirror stereoscope. The spatial resolution of each monitor was 1,280 × 800 pixels, with an eye–screen distance of 123 cm and a refresh rate of 90 Hz. Unless otherwise mentioned, all stimuli were drawn on the center of a gray screen (5.50 cd/m²) with no fixation spot. Four white, radially protruding bars (0.14° × 3.6°), starting 2.8° from the center of the screen and extending outward, were used to ensure proper binocular vergence for all conditions.

The RS, QD and NC stimuli were blue (CIE $x = 0.250$, $y = 0.208$, 7.30 cd/m²) and were presented monocularly to the left eye while the right eye viewed a blank screen. Subjects verified that under this condition the stimuli did not subjectively fade (indicating that there was no binocular rivalry). The RS stimulus consisted of an orthographic projection of 450 blue dots (0.044° in diameter) uniformly covering a virtual sphere with a diameter of 1.72° in diameter. The sphere rotated rigidly with a period of 4.0 s, giving the appearance of three-dimensional structure. Because no size or perspective cues differentiated the front from rear surfaces, the direction of rotation was ambiguous. The NC, containing ambiguous information about static depth, was com-

posed of blue lines (0.12° in thickness) and covered an area of 4.2° × 4.2°. The QD consisted of solid blue circles (0.36° in diameter) appearing in pairs on opposite corners of an imaginary square (2.7° × 2.7°) centered on the middle of the screen. At each moment, only two circles were displayed. The stimulus alternated between the two possible configurations every 311 ms, generating the perception of apparent motion between either vertically or horizontally corresponding points. The BR stimulus consisted of two dichoptically presented Gabor patches (radius, 2.25°; spatial frequency, 2.7 cycles/°), with the left eye viewing a 45° leftward-tilted greenish patch and the right eye viewing a 45° rightward-tilted pinkish patch. The RSt was similar to the RS in that it was ambiguous in its three-dimensional structure from motion. It was 1.15° in extent, composed of dots (0.044° in diameter) that were red (CIE $x = 0.547$, $y = 0.319$, 7.61 cd/m²) and rotated once every 1.3 s. In the MIB condition¹⁶, the RSt was presented amid a large field of small black dots moving in random directions (dot diameter, 0.072; density, 9.9 dots/°; speed, 5.4°/s; lifetime, 330 ± 30 ms). While the RSt was presented monocularly to the left eye, the dots were shown binocularly in correspondence. Pilot experiments showed that binocular presentation of the dots nearly doubled the disappearance time of the star, an effect that may be facilitated, in part, by binocular rivalry. The eccentricity of presentation ranged from 0.0–1.6° and was determined initially for each subject based on the position providing the highest frequency of stimulus disappearance.

Experimental task. Participants rested their chins on a padded bar and were instructed to inspect the stimulus without special regard to fixation, except for the MIB experiment, where they were instructed to maintain fixation on a small cross. For each bistable stimulus, buttons were assigned beforehand to each of the two potential percepts. Subjects were required to press the button corresponding to the perceived configuration of each pattern when it appeared, and to release the button when it disappeared. In the case of BR, where percepts could be mixed, they were instructed to respond according to the dominant pattern, even if its dominance was incomplete. All relevant events, including stimulus presentations and subject responses, were recorded on a computer for analysis.

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Competing interests statement

The authors declare that they have no competing financial interests.

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