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Perception of Temporally Interleaved Ambiguous Patterns

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Summary

Background: Continuous viewing of ambiguous patterns is characterized by wavering perception that alternates between two or more equally valid visual solutions. However, when such patterns are viewed intermittently, either by repetitive presentation or by periodic closing of the eyes, perception can become locked or "frozen" in one configuration for several minutes at a time. One aspect of this stabilization is the possible existence of a perceptual memory that persists during periods in which the ambiguous stimulus is absent. Here, we use a novel paradigm of temporally interleaved ambiguous stimuli to explore the nature of this memory, with particular regard to its potential impact on perceptual organization.

Results: We found that the persistence of a perceptual configuration was robust to interposed visual patterns, and, further, that at least three ambiguous patterns, when interleaved in time, could undergo parallel, stable time courses. Then, using an interleaved presentation paradigm, we established that the occasional reversal in one pattern could be coupled with that of its interleaved counterpart, and that this coupling was a function of the structural similarity between the patterns.

Conclusions: We postulate that the stabilization observed with repetitive presentation of ambiguous patterns can be at least partially accounted for by processes that retain a recent perceptual interpretation, and we speculate that such memory may be important in natural vision. We further propose that the interleaved paradigm introduced here may be of great value to gauge aspects of stimulus similarity that appeal to particular mechanisms of perceptual organization.

Introduction

Ambiguous or reversible figures are illustrations that spontaneously vary in their appearance over time (e.g., [1], Figure 1). Although the brain mechanisms underlying this multistable perception have long been a central theme in vision research, they remain poorly understood and continue to be a topic of intensive research and debate [1–7]. For example, the characteristic reversals of such figures have been thought to be stochastic and autonomous, reflecting instances of reorganization of the perceptual system. Yet, we have previously demonstrated that intermittent, rather than continuous, presentation of ambiguous stimuli disrupts the normal course of perceptual alternation. In fact, it sharply reduces the frequency of reversals and can essentially freeze the appearance of the stimulus into one configuration for up to several minutes [8].

In that study, the observed perceptual stabilization was not contingent upon the actual removal of the stimulus; its mere perceptual disappearance in illusory displays had equally powerful effects on the reversal rate of ambiguous patterns. In light of these results, the following hypothesis is tempting: the neural expression of a state of perceptual organization may have an inherent storage capacity that promotes the reestablishment of the same state during the subsequent dynamic processing of visual information. In other words, any perceptual state may, at least to some extent, also act as a kind of memory system, the read-in of which is not exclusively sensory and whose properties may differ from those described for the various well-known visual information stores.

The experiments presented here offer a means to explore mnemonic aspects of this stabilization phenomenon following an operational approach. We first examine whether stabilization is susceptible to interference from visual stimuli presented during the gap periods. We then probe the nature of this interference (e.g., precategorical, object based) by using different types of stimuli, including other ambiguous patterns. The latter experiment aims also to examine whether two reversible figures can undergo independent, stabilized time courses in parallel. Finally, using multiple interleaved ambiguous patterns, we asked whether a perceptual reversal occurring in one has a direct impact on the interpretation of another. The results are discussed in the context of visual memory and how it may bear on the perception of ambiguous patterns.

Results

Experiment 1: Interference from Unambiguous Patterns

The visual stimulus of this experiment consisted of 2-s presentations of an ambiguous rotating sphere (RS) interleaved with 2-s presentations of one of several other "interfering" patterns. A short (1 s) blank period was introduced between successive stimuli (Figure 2A). One of the conditions was repeated for a second group of subjects consisting of the same stimuli shown in alteration, but without any blanking periods in between, to evaluate whether the introduction of a blank screen in itself would be critical for the effect. Assuming some analogy between the observed perceptual persistence of ambiguous patterns and other forms of visual memory, the question addressed here is whether the interfering patterns will disrupt the perceptual stabilization.

The results are presented in Figure 2, displaying the survival probability (SP) for cases in which different visual patterns are inserted into the gaps. The SP re-

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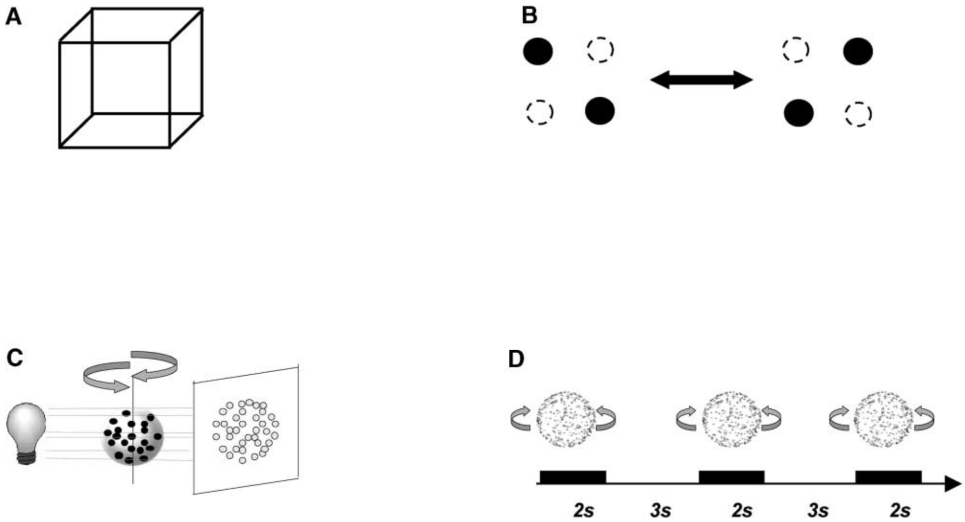

Figure 1. Multistable Stimuli Used in the Present Study

(A) The Necker cube (NC), a well-known structure to induce frequent reversals of subjective geometric depth.

(B) The quartet dots (QD), an apparent multistable motion phenomenon in the frontal plane.

(C) The rotating sphere (RS), an ambiguous structure-from-motion stimulus consisting of the orthographic projection of a randomly speckled rotating object, provokes subjective changes in the direction of rotation upon reversal of illusionary depth.

(D) Repetitive presentation used to promote stable perception of a single configuration.

mained very high under all conditions, with values similar to those obtained in the experiments in which no stimulus was inserted in the gap periods [8]. Stimulus attributes such as featural composition (dots, squares), static or dynamic state, and categorical nature (right versus left) were all equally ineffective in changing stabilization and are thus presumably irrelevant to the maintenance of the most recent perceptual configuration. No systematic difference could be observed between the experiments that comprised blanks and the control where the unrelated (i.e., checkerboard) pattern spanned the entire period without ambiguous stimulation.

Experiment 2: Interference from Ambiguous Patterns

Unambiguous patterns do not interfere with the stabilization process. Does this also hold when the patterns presented in the gap period are themselves ambiguous? And, if there is no destructive interaction, might then two or more ambiguous patterns simultaneously undergo stabilization, with perceptual organization in each case guided not by the very last stimulus presentation, but rather by the last *like* stimulus presentation? To examine this question, we designed a stimulus paradigm in which we temporally interleaved two or three different bistable patterns (Figures 3A and 3B).

We started with patterns having entirely different reversing attributes, such as depth or motion correspondence. Although it is conceivable that the event of a perceptual reversal is not restricted to specific stimulus attributes, we assumed that such patterns would have a lower chance of interaction. Subjects responded once again by means of a two-choice button box; however, in this case, they responded for each of the ambiguous patterns independently as it appeared. The subjects had previously learned an arbitrary mapping between each of the two configurations for each stimulus and the right and left buttons. The presentation and blanking times were chosen carefully for each of the stimuli to ensure proper stabilization for a wide range of subjects (see below).

Representative examples of the data obtained during such an experiment with two and three stimuli are shown in Figure 4. As in the previous experiment, the strong reduction of reversals of one pattern was found to be unaffected by the other, now ambiguous, stimulus. That is, the perception of each reversible pattern remained locked for up to several minutes at a time. If stabilization indeed relies on perceptual stores, these stores may coexist independently and may be accessed selectively by the subsequent sensory representation. Although not studied exhaustively, the capacity of the system based on the present experiment was found to be sufficient for supporting at least three stabilized percepts in parallel (see Figures 4 and 5).

Experiment 3: Coupling of Reversals

In the previous experiments, occasional reversals occurred during the interleaved stimulus presentation (see Figure 5). This experiment examined whether any conditions exist (e.g., pattern similarity) for which the reversals of the interleaved patterns are temporally coupled; that is, they occur together within a small time window.

Important for the evaluation of such coupling is ensuring that stabilized patterns undergo an *occasional* reversal. Above, we demonstrated that interleaved ambiguous patterns could be reliably stabilized. We then optimized these stimuli not for maximum stability, but rather in such a way to promote the occasional reversal. We did this mainly by manipulating the duration of each presentation, or the ON time. We have previously shown that this is the most critical parameter for stabilization, and that when the value exceeds the mean reversal time

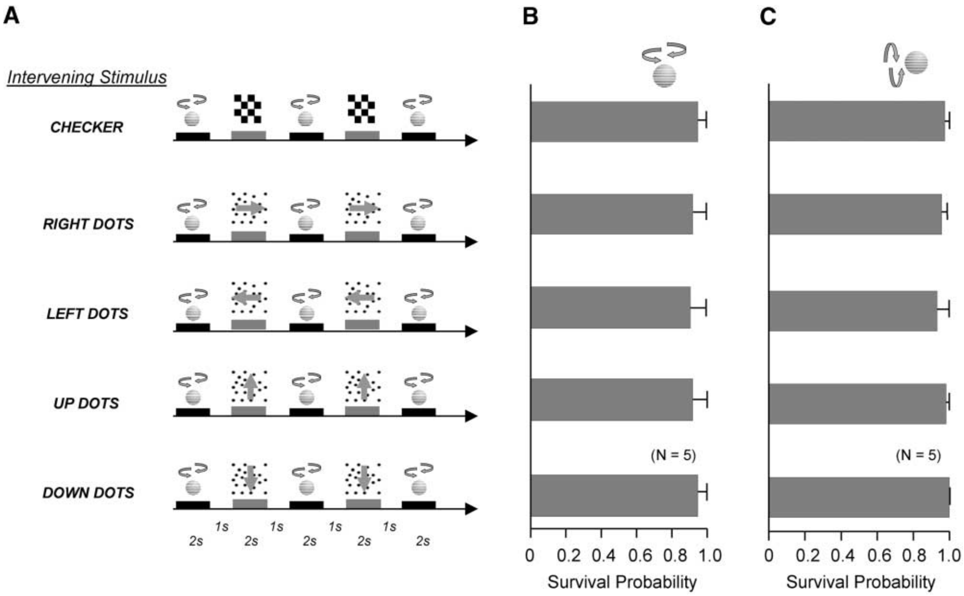

Figure 2. Interleaved Presentation of Unrelated Stimuli

(A) Stimulus presentation. Subjects were shown the ambiguous RS stimulus for 2 s, followed by a 1-s blank and a 2-s presentation of either a static checkerboard pattern or random dots moving coherently in one of the cardinal directions. After another blank interval (1 s), the RS reappeared, starting a new cycle of ambiguous and unrelated stimulus presentation.

(B) The "survival probability" (SP) of a perceptual state in the horizontally rotating RS; SP is shown across all periods of unrelated stimulus presentations. This indirect measure of memory strength corresponds to the percentage of identical percepts before and after the presentation of the unrelated visual patterns. The means and standard errors for five subjects are shown.

(C) Survival probability for vertically rotating RS.

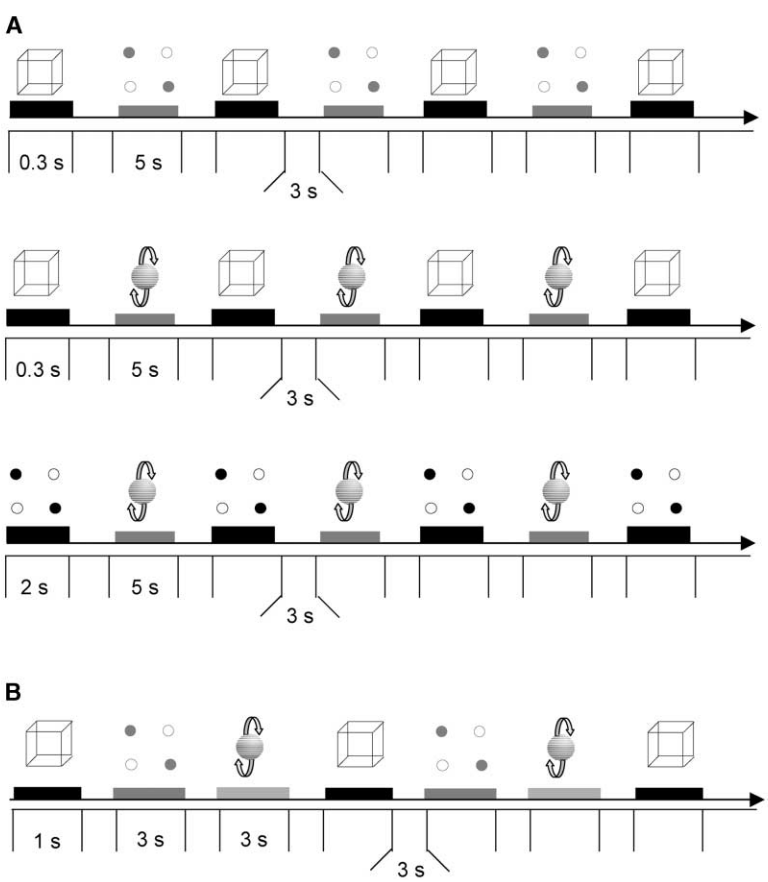

Figure 3. Interleaved Presentation of Different Ambiguous Patterns

(A and B) Subjects were presented either (A) two or (B) three ambiguous stimuli in an interleaved manner. Note that much shorter presentation times were used for the NC than for the other stimuli to obtain a similar reduction in reversal rate.

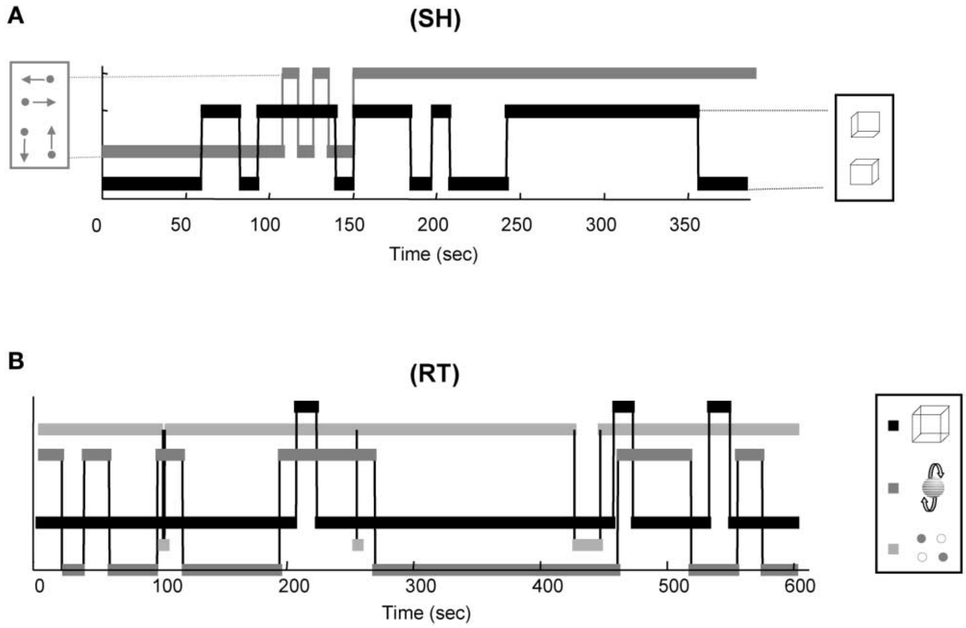

Figure 4. Representative Time Courses during Interleaved Perception of Several Unrelated Ambiguous Stimuli of One Subject

(A and B) Subjects made their perceptual report only upon stimulus visibility. Button presses to each of the stimuli were interpolated to display (color-coded) the changing perceptual states for each of the stimuli. For both (A) two and (B) three ambiguous stimuli, the interleaved presentation resulted in long (minute-lasting) phases of perceptual dominance. More importantly, infrequent reversals were largely uncorrelated between the stimuli, which ultimately resulted in parallel and independent time courses of perceptual alternation for the same position in the visual field.

of a stimulus for a particular subject, the stabilization effect is diminished [8]. When the ON times were significantly shorter than the subjects' inherent mean reversal time (which can vary greatly among subjects [9, 10]), we often had the problem that there were almost no reversals during the entire 10-min testing period. Here, we empirically adjusted this parameter to achieve between 3 and 15 reversals for each stimulus within the 10-min testing period. The frequency of reversals following such adjustments is typified by the raw data in Figure 4 and allowed us to compare the timing of occasional reversals between the two patterns.

The co-occurrence of reversals was quantified by means of the coreversal index (CRI, see the Experimental Procedures). A high value of CRI might suggest that either the perceptual reversal event in the brain is general and is applied to many stimuli regardless of how dissimilar or that the two interleaved patterns are, at least with respect to some attributes, sufficiently similar for a configurational change in one to be automatically "inherited" by the other. A low CRI would evidently indicate that the two, stable, interleaved patterns were independent in their perceptual reversals.

Inspection of Figure 4 already suggests that the reversals of dissimilar stimuli (see example of stimuli in Figure 3) are independent. The CRI values for these patterns are shown in Figure 6, which represents the mean of five subjects. They demonstrate low coincidence in the timing of perceptual reversals between the stimuli and suggest that the alternation process operates independently for each stimulus.

The effects of similarity were examined by using the stimuli displayed in Figure 7A. One stimulus was always the RS used in previous experiments, while the other was another RS, differing in its color (blue versus red), eye of stimulation (left versus right), rotational speed (0.2 cycles/s versus 0.25 cycles/s), diameter (1.72° versus 2.58°), or axis of rotation (horizontal versus vertical). Subjects responded according to their perceived direction of motion for each sphere as long as it was present.

Figure 7B shows single experiments from one observer, and Figure 7C depicts the mean CRI from nine subjects. The high CRI values in this figure show that for most transformations, perceptual transitions in the two patterns were tightly coupled. The transfer between the two perceptual configurations was not always immediate (black bars), but it sometimes appeared only after two or three presentations (gray bars). This observation can be accounted for by the period of instability that often accompanies a perceptual reversal, which also prevents the CRI from ever reaching 100%, even in the control case (where identical stimuli are interleaved). Often, this instability is resolved only after several presentations of the pattern, at which point it stably adopts the new configuration [8].

Experiment 4: Perceptual Transfer As a Measure of Stimulus Similarity

The broad range of CRI values obtained for different stimuli raises an interesting question. Can the coupling of reversals provide new insights into the mechanisms of perception by revealing classes of configurations that are treated as "similar" by the mechanisms underlying perceptual organization?

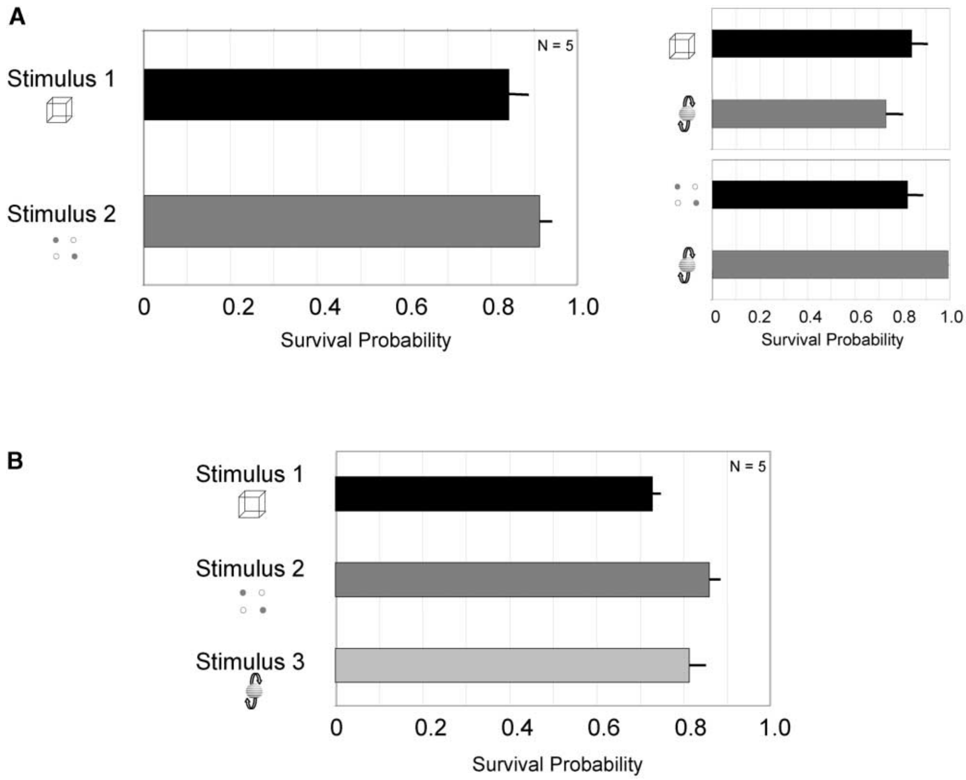

Figure 5. The Survival Probability for Each of the Stimuli during Interleaved Perception of Dissimilar Ambiguous Patterns

The means and standard errors for five subjects are shown.

(A) When two dissimilar ambiguous patterns are interleaved, the SP is about 90%, indicating an effect of stabilized perceptual organization across the periods during which another ambiguous pattern is presented.

(B) In the case of an interleaved presentation of three ambiguous stimuli, the SP is a little bit declined, but it is still far above chance, suggesting that perceptual stabilization holds for at least up to three alternating multistable visual patterns.

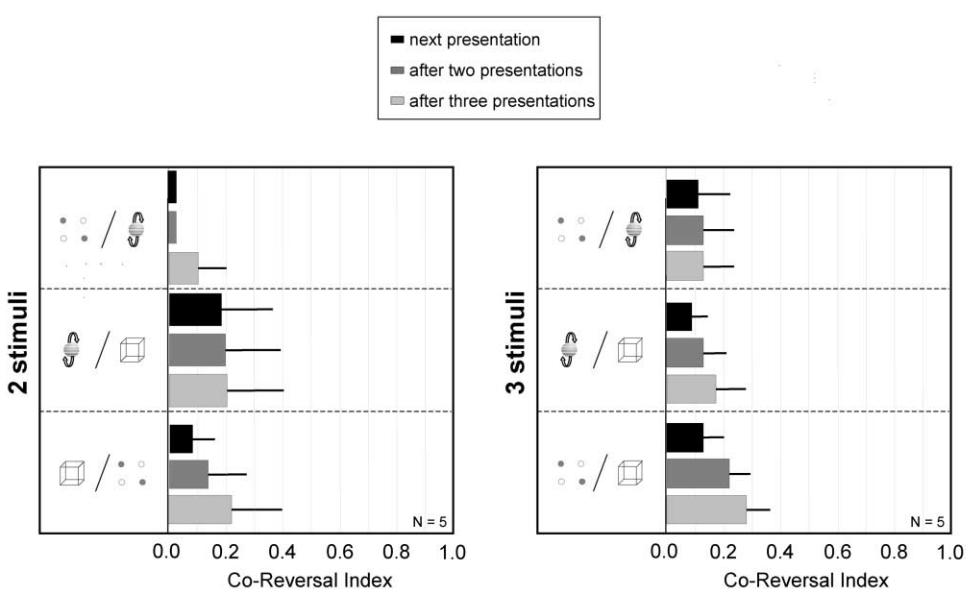

Figure 6. Index of Coreversals As a Measure of Correlation of Perceptual Reversal between the Interleaved Stimuli

For both two and three alternating stimuli, the means and standard errors of CRI is shown for five subjects.

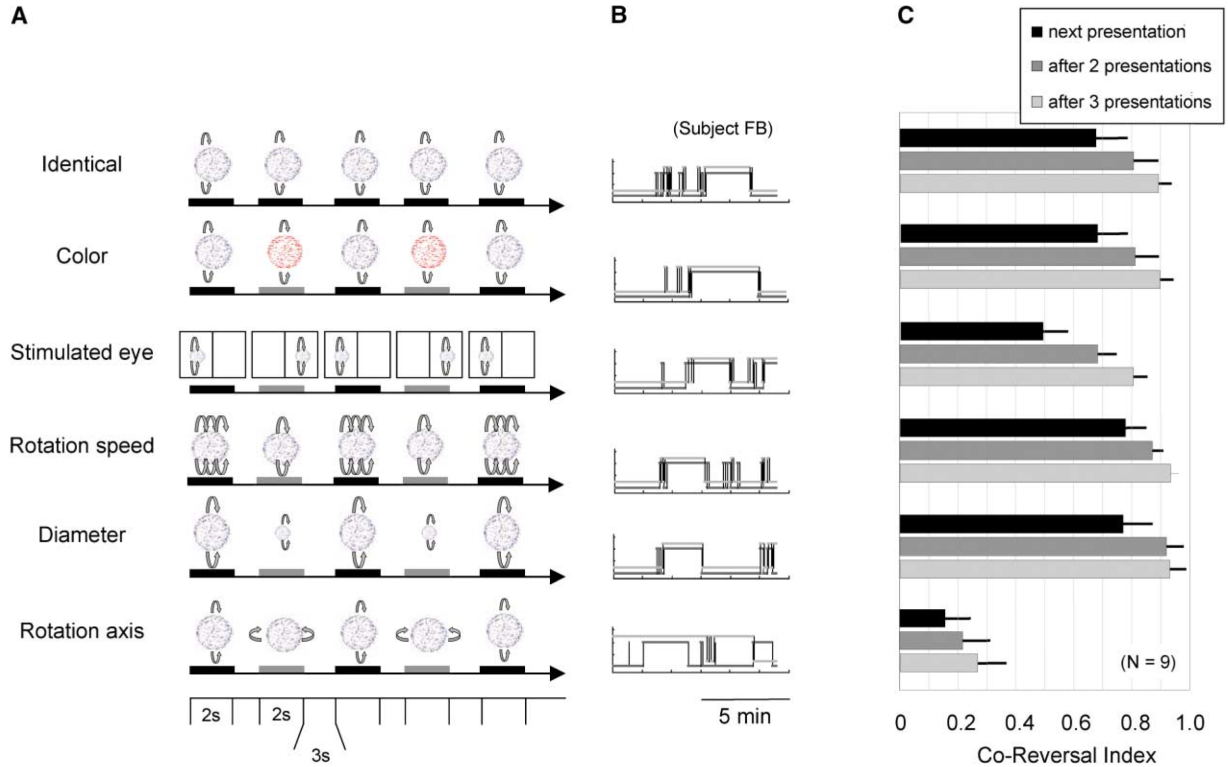

Figure 7. Interleaved Presentation of Related Ambiguous Patterns that Share Large Structural Similarities

(A) The intermittent presentation of the RS was alternated with derivatives of it that solely differed either in color, the stimulated eye, the rotational speed, their overall size, or their rotational angle.

(B) Single subject raw data showing the degree of perceptual coupling for the different combinations shown in (A).

(C) Quantitative calculation of the coreversal index (CRI), together with the standard errors for nine subjects for the different pairs of stimuli. High values of CRI indicate that a reversal of one of the interleaved stimuli was followed, on average, by a reversal in its counterpart.

In the previous experiment, the transfer of a perceptual configuration was robust to differences in most simple stimulus attributes (e.g., color, speed, size) that made the interleaved patterns highly discriminable. On the other hand, the low CRI obtained for perpendicularly rotating RS patterns suggests that at least some forms of object constancy may be irrelevant for the selection of a perceptual solution when viewing ambiguous patterns.

To investigate this point further, we systematically varied the difference in the rotation axis of interleaved RS patterns, as we were curious when the coupling between reversals in the interleaved patterns might disappear. The resulting CRI values are shown in Figure 8A as a function of the angle between the rotation axes. Note that the fraction of coincident reversals declines as a function of this value, beginning near 1.0 when both spheres rotate about the vertical and reaching a very low value when the rotation angles are perpendicular. However, there was a rather high intersubject variability regarding the transition points for this experiment, and the gradual decline shown in the mean was sometimes much sharper for individual subjects.

Finally, we asked what would happen if the RS pattern were interleaved not with another RS pattern, but with one of an entirely different shape. To test this, we interleaved the RS with another bistable, rotating pattern (a pyramid) that was similar in all respects, except in its three-dimensional shape (Figure 8B). The coreversal index for the interleaved patterns, as well as the two controls, are shown in Figure 8C and suggest that for those visual mechanisms determining the depth from motion, the two patterns are considered to be largely equivalent. This is despite substantial differences in the two patterns on several levels, including the cognitive level, where the two shapes clearly represent different objects. These results, taken together, suggest that the degree of perceptual transfer between two interleaved ambiguous patterns can be determined by unintuitive factors that are unrelated either to the discriminability or the distinctiveness of the interleaved patterns. A better understanding of the factors that determine this transfer may provide a deeper understanding of the requirements and causes of perceptual reversal and yield insights into the role of visual history in perceptual organization during natural vision.

Discussion

We showed previously that repetitive presentation of ambiguous figures reduces their spontaneous alternation, promoting the retention of a given perceptual state across periods of stimulus absence [8]. The present study is an attempt to better understand the mechanisms underlying this retention.

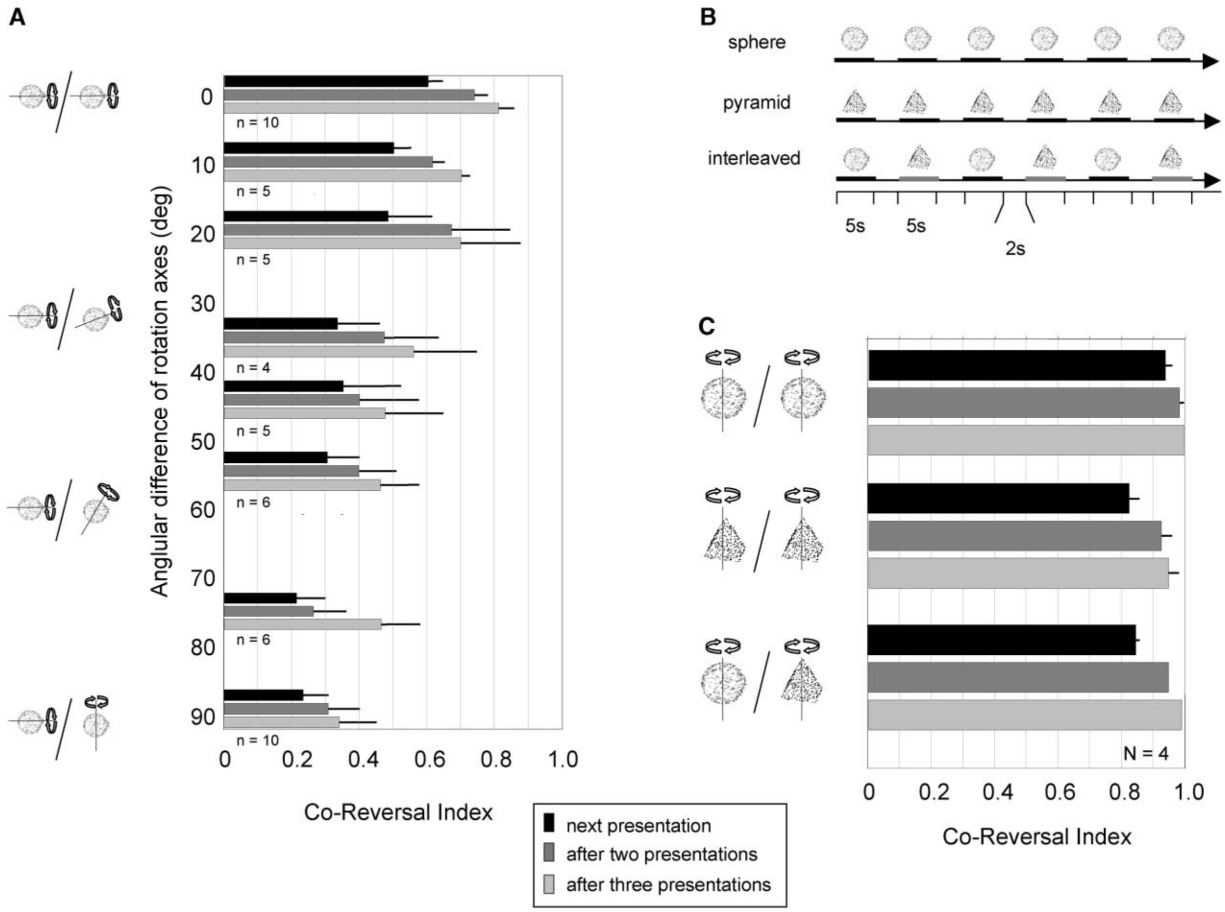

Figure 8. Coreversal Index As a Function of Rotation Angle and Shape Similarity

(A) Increasing disparity in the angle between the two interleaved RS patterns diminished the degree to which reversals would occur together.

(B) Stimuli for the shape similarity experiment, where the RS from before was interleaved with a rotating pyramid object.

(C) Coreversal index for alternation of all combinations of the sphere and pyramid demonstrate high values of perceptual transfer.

Persisting States of Perceptual Organization

Given the potential role of memory in the stabilization we observe, it is worth comparing the retention of a perceptual state across a blank period to other forms of visual memory. Memory systems are traditionally defined on the basis of their properties, including duration, content, capacity, and decay process (for example, see [11, 12]). We therefore set out to investigate some properties of the periods during which the ambiguous patterns were absent (gaps), assuming that the readout of any potential memory process involved in the stabilization process directly affects its efficiency. Moreover, rather than examining the properties of a possible storage mechanism in terms of a subject's correct performance, we evaluated the effective retention by gauging the incidence of reversals following periods of stimulus absence.

The duration of the storage for a perceptual configuration was on the same order of magnitude as other forms of perceptual storage [13–16], but it was out of the range of the iconic visual memory thought to reside in the sensory apparatus [13, 17, 18]. This finding might exclude the primary sensory areas in the brain as candidates for the locus of a persisting perceptual state. Also, the robustness of this perceptual memory to interference from intervening stimuli is similar to visual (but, interestingly, not auditory) short-term memory [19]. Finally, invariance to a host of basic image transformations (e.g., size and color) appears to suggest similarity to visual object priming [20]. The latter has often been linked to other paradigms involving reversible figures, particularly in studies in which the presentation of an ambiguous pattern follows that of an unambiguous one [7, 21–23]. Such exposure is known to have a strong impact on the perception of ambiguous patterns [21–37], although attempts to map these effects onto a particular memory system are marred by the existence of both positive and negative effects, often referred to as *facilitation* and *satiation*, respectively.

All in all, the retention of a perceptual state in our paradigm appears to bear some similarities to other forms of visual memory. Yet, unlike many other examples, its content is neither sensory nor categorical in nature, but instead it merely reflects the state of perceptual organization at any given time. Moreover, the fact that the subjects were never asked to remember anything, but instead to only report their immediate percept, suggests that this type of retention has an implicit nature. The latter has some interesting implications for the role of memory in perceptual organization during natural vision.

Perceptual Coupling

The present experiments revealed that pairs of stimuli show a great range of coupling strengths (quantified by the CRI). For stimuli that differed greatly in their structure, the reversal of one pattern bore no particular temporal relationship to reversals in another. This was true even when stimuli conveyed the same general information about the structure of an object, such as its depth (e.g., NC versus RS) or direction of motion (QD versus RS). In contrast, when two interleaved stimuli were very similar, their perceptual reversals were often tightly coupled. For the RS, this coupling was robust to the simple transformations of size and color mentioned above, as well as to speed of rotation, elongation, and eye of presentation. Taken together, these findings suggest that the retrieval mechanisms of the memory system involved operates on the basis of similarity in the global representation of the tested objects rather than on the parameters of basic perceptual qualities such as depth and motion.

Previous experiments investigating perceptual coupling have generally relied upon simultaneous presentation of multiple reversible figures. These studies have generally found a strong interaction between ambiguous patterns that are presented simultaneously [1, 38–47]. While such coupling is usually well above that expected by chance in these experiments, it is most often imperfect, with even identical stimuli in close proximity sometimes adopting opposite configurations [41, 48], particularly with long observation times [49]. In addition, recent results suggest that there may be a fundamental difference between the coupling of two ambiguous patterns and that of an ambiguous to an unambiguous pattern [50, 51]. This interesting observation suggests that it is not only the perceived configuration of a pattern that is important for biasing perception, but that the level of ambiguity in the stimulus leading to that perception is also important.

The large range in CRIs found here raises the possibility that the interleaved paradigm might be used to assess the similarity of visual stimuli, from the point of view of mechanisms of perceptual organization. Object similarity is typically assessed on the basis of a subject's explicit similarity (or dissimilarity) judgments between stimuli; after object similarity is assessed, relative psychological distances for several stimuli can be computed [52–54]. Here, the "similarity" of a pattern taps into largely automatic processes, hidden from conscious access, and may provide insight into the brain's analysis of visual structure that is inaccessible through the typical categorization tasks (see Experiment 4 and Figure 8).

Conclusions

We have previously addressed how a repetitive presentation sequence might specifically interfere with the mechanisms of perceptual alternation [8], whether these are mediated within the sensory domain (e.g., [1]), by a high-level exploratory network (see [5]), or by an autonomous oscillator (i.e., [55]). The present study offers interesting insights into the retention mechanism characterizing this phenomenon. The interleaved paradigm further offers a new means to evaluate the perceptual similarity of reversible patterns without the need for a subject to make explicit comparisons. Nonetheless, further research is required to identify the primary cause of perceptual alternation, as well as the reason for its reduction when ambiguous patterns are viewed only intermittently.

Experimental Procedures

Participants

Forty subjects (21 females) between the ages of 15 and 40 (median age of 24) participated in the study (15 of them participated in experiment 1 [Figure 2], 6 participated in experiment 2 [Figures 3–6], 9 participated in experiment 3 [Figure 7], and 15 participated in experiment 4 [Figure 8]). Data from two subjects were not included in the analysis of coreversals because the stabilization effect was too strong and they never experienced a reversal. Each subject had normal or corrected-to-normal vision, and most had previous experience as psychophysical subjects. Each subject was completely naïve to the hypotheses and goals of the experiment and was paid for his/her participation The experiments were done in accordance with guidelines of the local authorities (Regierungspraesidium), and all subjects gave informed written consent.

Visual Stimuli

The main stimuli used in this study are shown in Figure 1. Each was an ambiguous, bistable pattern involving either changes in perceived depth (the Necker cube [56], NC and the rotating sphere [57], RS) or apparent motion correspondence (Quartet Dots [39, 58], QD). The main RS stimulus consisted of an orthographic projection of 450 blue dots (0.044° diameter) uniformly covering a virtual sphere with a diameter of 2.7°. Its rotation was rigid with a period of 4.0 s, giving the appearance of three-dimensional structure. The NC, containing ambiguous information about static depth, was composed of blue lines (0.12° thickness) and covered an area that was $4.2 \times 4.2°$. The QD consisted of solid blue circles (0.36° diameter) appearing in pairs on opposite corners of an imaginary square ($2.7 \times 2.7°$) centered on the middle of the screen. At each moment, only two circles were displayed. The stimulus alternated every 311 ms between the two possible configurations, generating the perception of apparent motion between either vertically or horizontally corresponding points. Unless otherwise mentioned, the stimuli were blue (CIE $x = 0.250$, $y = 0.208$, 7.30 cd/m^2) on a gray screen (5.50 cd/m^2) and were presented monocularly to the left eye by means of a mirror stereoscope. Four white radially protruding bars ($0.14 \times 3.6°$, beginning 2.8° from the center) were always shown to both eyes to ensure proper binocular convergence. In no case did this presentation condition lead to binocular rivalry (i.e., the monocular stimulus never subjectively disappeared). There was no fixation spot. All stimuli were generated with custom-made software by using OpenGL on a personal computer (Intergraph Zx10, Intense3D Graphics) running MS Windows 2000. They were drawn on two synchronized 21-inch monitors, with spatial resolution of 1280×800, an eye-screen distance of 123 cm, and a refresh rate of 90 Hz.

Procedure

Each subject rested her/his chin on a padded bar and was instructed to inspect the stimulus in the center of the screen passively without special regard to eye movements. For each multistable stimulus, buttons were assigned beforehand to each of the two possible percepts, and pressing of the buttons was practiced during a trial of continuous stimulus presentation of variable length. Subjects were required to press the button corresponding to the perceived configuration of each pattern when it appeared and to release it when it disappeared. All relevant events, including stimulus presentations and subject responses were recorded on a second computer running under a real-time operating system (QNX Software Systems, Kanata) and were stored for offline analysis. A session typically lasted 60–90 min and was followed by a short interview.

Analysis

The data were analyzed by using custom software based on MATLAB (MathWorks). Two quantities, the *survival probability* (SP) and the *coreversal index* (CRI), were used to gauge the retention of a particular reported configuration between subsequent gaps and the interaction between interleaved ambiguous patterns, respectively. The SP was computed as the fraction of "same" to total number of reports and gave a direct measure of persistence across the blank period. The CRI, in contrast, regarded the coincidence of perceptual reversals between different interleaved ambiguous patterns. It was computed as the number of occasions for which the two patterns changed their appearance "together" (i.e., a change in one was directly followed by a change in the other) divided by the total number of reversals for both stimuli. A high CRI (near 1.0) therefore indicated that two interleaved patterns were tightly coupled in the timing of their perceptual reversals. In practice, a value of 1.0 was never achieved because even when the two interleaved stimuli were identical, periods of instability would result in a decline of this measure. Such instability during transitions is common during this paradigm, as we have previously reported [8]. To account for this effect, we calculated the CR index as a cumulative measure for the first, second, and third presentations following an event of perceptual change. In the computation of CRI, trials in which the perception of both ambiguous stimuli was completely stable (i.e., no reversals at all) were discarded.

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