

Perceptual alternation induced by visual transients

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Abstract. When our visual system is confronted with ambiguous stimuli, the perceptual interpretation spontaneously alternates between the competing incompatible interpretations. The timing of such perceptual alternations is highly stochastic and the underlying neural mechanisms are poorly understood. We show that perceptual alternations can be triggered by a transient stimulus presented nearby. The induction was tested for four types of bistable stimuli: structure-from-motion, binocular rivalry, Necker cube, and ambiguous apparent motion. While underlying mechanisms may vary among them, a transient flash induced time-locked perceptual alternations in all cases. The effect showed a dependence on the adaptation to the dominant percept prior to the presentation of a flash. These perceptual alternations show many similarities to perceptual disappearances induced by transient stimuli (Kanai and Kamitani, 2003 *Journal of Cognitive Neuroscience* **15** 664–672; Moradi and Shimojo, 2004 *Vision Research* **44** 449–460). Mechanisms linking these two transient-induced phenomena are discussed.

1 Introduction

When we are presented with a stimulus that has multiple perceptual interpretations, we experience a sequence of spontaneous perceptual alternations between the possible interpretations. Such multistable stimuli have been used to dissociate perceptual from stimulus-driven mechanisms to study visual awareness. The timing of the alternations is highly variable, and the underlying mechanisms as well as the neural substrates are poorly understood. Understanding the mechanisms underlying the perceptual alternations is important not only for understanding bistable perception per se, but also for understanding the dynamics of normal vision (Blake and Logothetis 2002).

The perceptual alternations can be explained, to some extent, in terms of passive decays of perceptual signals (or adaptation). Although adaptation indeed increases the probability of alternations, it does not seem to directly cause them (Köhler and Wallach 1944; Hock et al 1997). That is, an additional factor seems necessary for an alternation to actually occur. Contributions of more active, top–down processes have been suggested to mediate alternations. Imaging studies have shown the involvement of parietal and frontal cortical areas (Kleinschmidt et al 1998; Lumer et al 1998). Also, bottom–up signals following small eye movements have been suggested to be responsible for perceptual alternations (Levelt 1966, 1967; Murata et al 2003; but see Blake et al 1971; Wade 1973). Since eye movements result in a transient signal due to new retinal input, the visual transient may contribute to, or is even responsible for, the induction of perceptual alternation. Surprisingly, to the best of our knowledge, this possibility has not been investigated systematically.

In this study, we show that a visual transient can trigger a perceptual alternation. The induced alternations were time-locked to the transient, and therefore the timing is highly predictable. We show that presenting a flash behind a bistable figure results in a sudden transition of the current perception into the competing interpretation.

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This effect, termed induced perceptual alternation (IPA), is demonstrated with a variety of ambiguous stimuli including structure-from-motion, binocular rivalry, Necker cube, and ambiguous apparent motion.

The IPA manifests characteristics similar to another transient-induced phenomenon where visual transients induce perceptual disappearance of objects (Kanai and Kamitani 2003; Moradi and Shimojo 2004). In both cases, transient stimuli cause a drastic change of the percept to a constant visual stimulus. We attempt to offer a schematic model that explains how visual transients produce a drastic perceptual change both in perceptual rivalry and disappearance.

2 Experiment 1. Basic effect

In our first experiment, we show that perceptual reversals can be induced by transients in a variety of bistable stimuli; structure-from-motion, binocular rivalry, Necker cube, and bistable apparent motion.

2.1 Methods

2.1.1 Observers and apparatus. Four naive observers and one of the authors (RK) participated. All observers had normal or corrected-to-normal vision. The stimuli were generated on a Macintosh computer with Matlab PsychToolbox (Brainard 1997; Pelli 1997) and presented on a 22-inch CRT monitor (LaCie Blue Electron). The refresh rate of the display was 85 Hz; and the resolution, 1280×1024 . The viewing distance was 57 cm.

2.1.2 Stimuli. We displayed four types of bistable stimuli. These stimuli were structure-from-motion (SFM), binocular rivalry (BR), Necker cube (NC), and bistable apparent motion (AM). The details of the stimulus parameters are described below. A fixation cross was placed in the geometric center of each stimulus. At random intervals, every 2–4 s, the background was flashed for 47 ms without occluding the bistable stimuli. The flash was white (56 cd m^{-2}).

SFM (figure 1a). The SFM consisted of 400 blue dots with a lifetime of 1 s presented against a black background. The shape of the structure was a cylinder rotating around the vertical axis centered at the fixation cross (red). The size of the cylinder was 3.9 deg in height and 3.12 deg in diameter. The rotation speed was $0.2 \text{ revolution s}^{-1}$. For this stimulus, the transient was a flash (47 ms) that had a rectangular shape covering the background of the stimulus area of SFM.

BR (figure 1b). Two orthogonal square-wave gratings, red–black versus green–black (45° and 135°) were presented in a circular area (diameter 7.8 deg). The gratings were presented dichoptically with the use of red and green color filters. The gratings had a spatial frequency of $0.8 \text{ cycle deg}^{-1}$ and the duty cycle was 20%. To support binocular fusion, a white ring (0.4 deg in width) was surrounding the stimulus. The combinations of color (red and green), eye (left and right), and orientation (45° and 135°) were randomly chosen for each trial. Transient flashes were presented by briefly changing the black part of the gratings (ie the background) into white for 47 ms.

NC (figure 1c). The skeletal drawing of a cube was presented in blue against a black background. The length of each edge was 1.95 deg when viewed from a perpendicular angle. The flash (47 ms) was a solid white disk with a diameter of 7.81 deg centering at the fixation.

AM (figure 1d). AM was created by presenting a pair of blue disks alternately against a black background. The diameter of each disk was 0.98 deg. In one frame, the disks were presented in the upper-right and lower-left quadrants, and in the other frame, in the upper-left and lower-right quadrants. These two frames were alternated every 200 ms, and there was no blank interval between the frames. The four disk positions were 1.17 deg away from the fixation point along both the horizontal and vertical axes. The flash was a white disk (4.69 deg in diameter) centering at the fixation cross.

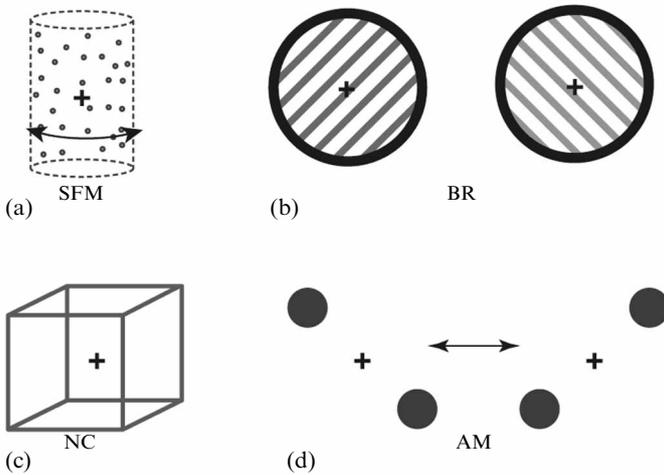


Figure 1. The four types of bistable stimuli used in experiment 1. (a) Structure-from-motion (SFM). Dots can be perceived as a rotating cylinder and the perceived direction of rotation alternates spontaneously. (b) Binocular rivalry (BR). Two square gratings (orthogonal to each other) are viewed dichoptically. Percept alternates between the two gratings (eyes). (c) Necker cube (NC). One surface of the cube appears in front and then the same surface is perceived in the rear. (d) Apparent motion (AM). Two frames are alternately shown. In one frame, two disks are at the upper-left and lower-right positions, and in the other frame, they are at the upper-right and lower-left positions. The correspondence between these disks across the two frames is ambiguous. Therefore, this stimulus is typically perceived as two disks moving along either horizontal or vertical axis, and these two percepts alternate.

2.1.3 Procedure. Before starting the experiment, naive observers were familiarized with bistable stimuli and perceptual reversals. It is known that it can be difficult for naive observers to experience the first alternation (see Girgus et al 1977; Rock and Mitchener 1992). In a trial, the observers viewed a bistable stimulus continuously for 30 s, and responded by a key press when they experienced a perceptual reversal at any time during a trial. A flash (lasting 47 ms) was presented randomly between 2 and 4 s after the previous flash (uniform sampling). The flashes were always presented behind the ambiguous stimulus, without occluding any part of them.

As a control, we conducted the same experiment without the flashes to obtain the spontaneous reversal rates. Thus, there were eight conditions (the flash and control conditions for each of the four stimulus types). For each condition, the observer performed ten trials in a single session (the total viewing duration was 300 s). The order of the conditions was randomized for each observer.

2.2 Results and discussion

Figure 2 shows the frequency of alternation with respect to the flash onset. Alternations were observed often around 500–1000 ms after the flash, indicating that sudden perceptual changes occurred just after the flash. The dashed lines show the frequency of alternation in the control experiment where the same stimuli were viewed but without the flash. Overall, the frequency of the alternation is significantly higher than the spontaneous alternation rates (*t*-test: SFM, $p < 0.05$; BR, $p < 0.01$; NC, $p < 0.01$; AM, $p < 0.05$).

The median of the time to alternation after the flash was presented was 706 ms, 612 ms, 1024 ms, and 824 ms for SFM, BR, NC, and AM, respectively. These values are larger than reaction times for simple detection tasks (< 500 ms). This suggests that observers responded to the percept that occurred after the flash, and did not simply react to the sudden flash. Figure 2b shows the mean alternation rates for each stimulus type. In all stimulus types, the rates were higher in the flash condition than in the control conditions (SFM, $p < 0.01$; BR, $p < 0.05$; NC, $p < 0.01$; AM, $p < 0.01$).

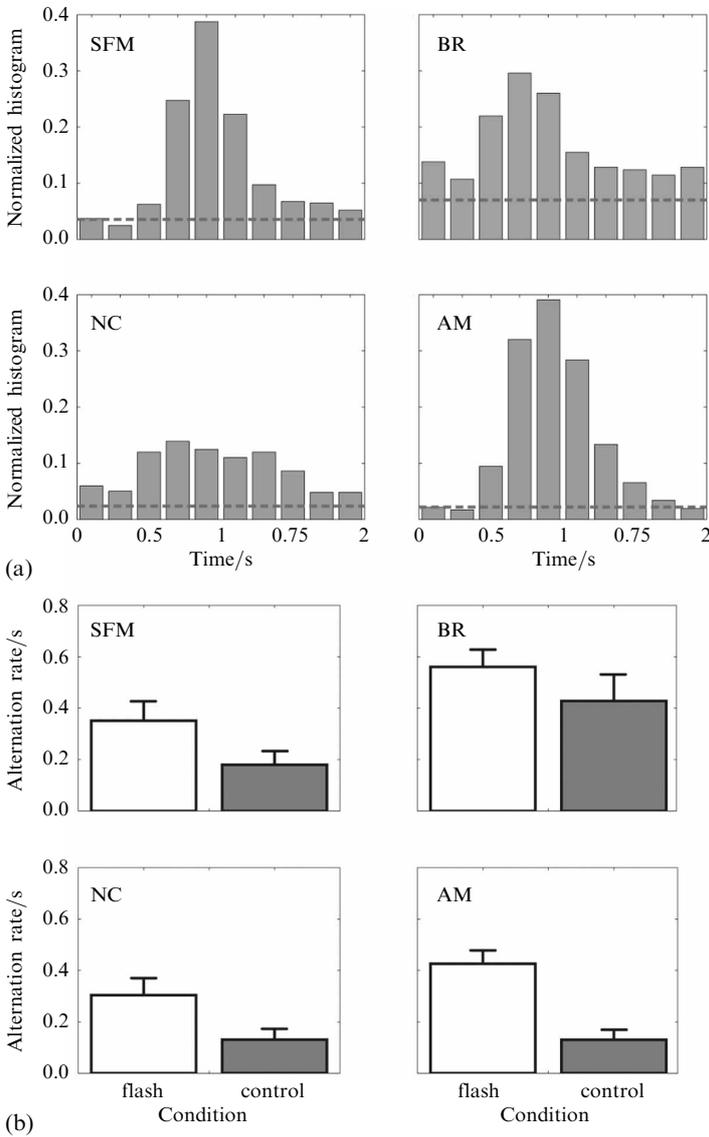


Figure 2. The results of experiment 1. (a) The frequency of perceptual reversals is shown with respect to flash (time zero). All perceptual alternations after a flash are included (not just the first one). The frequency is shown in a normalized scale. That is, the bar height corresponds to the probability that a reversal occurs within a certain bin (200 ms) after a flash, ie the number of alternations (within the bin) divided by the total number of flash events. For comparison, dashed lines are drawn to indicate the frequency of reversals in the unit bin width (200 ms) when the alternations rates were estimated without presenting the flash (control). The histograms for the four types of bistable stimuli show that observers' responses to reversals frequently occurred at 0.5–1.0 s after a flash. This pattern was evident in all four stimuli. The data are from four observers. (b) Alternation rate for each condition. The rate was higher in the condition with flash (white bars) than in the control condition (gray bars).

The IPA seems more remarkable in the conditions with SFM and AM compared to BR and NC (figure 2a). Why the flash was more effective at inducing alternations in these two types of stimuli is unclear. A difference between SFM/AM and BR/NC is that the former stimuli are dynamic, ie continuously moving, whereas the latter stimuli are constant. Thus, IPA may possibly have a stronger effect with dynamic stimuli.

3 Experiment 2A. Spatial specificity

In experiment 1, we showed that a flash indeed induces alternations of the perceptual interpretation of ambiguous stimuli. However, the flash was always presented at the same location as the ambiguous stimuli. In the next experiment, we address the question whether the IPA is spatially limited to the location of the flash or is caused by transient stimuli of all kinds.

We compared two conditions while presenting bistable stimuli in the periphery: (i) flash was presented at the same location as a bistable stimulus, and (ii) flash was presented on the other side of the visual field (at the same eccentricity).

3.1 Methods

3.1.1 Observers and apparatus. Five new naive observers participated in the experiment with SFM and four naive observers in the experiment with NC. Control data were obtained from three observers who participated in both experiments. Stimuli were presented on a CRT monitor with a resolution of 1152×864 , and a refresh rate of 85 Hz, and were viewed binocularly from a distance of 57 cm.

3.1.2 Stimuli. We chose to use two types of bistable stimuli, SFM and NC, as examples of dynamic and static ambiguous stimuli, respectively. We describe details of the parameters of these stimuli below.

SFM. An imaginary cylinder consisted of 200 white dots (3.5 min of arc diameter) against a black background. The cylinder subtended $4.4 \text{ deg} \times 4.4 \text{ deg}$, and was presented at an eccentricity of 2.93 deg from the nearest edge to fixation in the left visual field (LVF). The cylinder rotated around a horizontal axis at $0.9 \text{ revolution s}^{-1}$.

NC. A Necker cube ($4.4 \text{ deg} \times 4.4 \text{ deg}$) was displayed in LVF. The edge nearest to the center of the screen was 2.93 deg to the left. The NC was presented on a gray background. Steady fixation while viewing a stationary object in the periphery results in the disappearance of the object due to adaptation (Troxler 1804), especially when transient stimuli are presented nearby (Kanai and Kamitani 2003; Moradi and Shimojo 2004). To avoid retinal adaptation and perceptual disappearance during observation, observers were made to track a small dot (7 min of arc from the center) slowly rotating around a fixation cross (at $0.32 \text{ revolution s}^{-1}$).

The bistable stimuli were presented in the LVF. At a random timing between 3 and 5 s (uniform sampling), a white flash of the same size was briefly presented for 35 ms. There were two conditions as regards the position of the flash. In the ipsilateral condition, the flash was presented at the same location (ie LVF) as the bistable stimuli. In the contralateral condition (control), the flash was presented at the opposite location, in the right visual field (RVF). Other factors—such as eccentricity, duration of the flash, etc—were similar.

3.1.3 Procedure. Observers pressed a key to report the percept at the beginning of each session and when a percept switched to another one. In a session, a bistable stimulus was shown continuously for 150 s. Three observers participated in 4 sessions (2 ipsilateral sessions and 2 contralateral sessions). Two observers participated only in the ipsilateral condition. The order of experiments was counterbalanced within and between the observers.

3.2 Results and discussion

The frequency of perceptual alternations is plotted as a function of the time elapsed after the flash was presented (figure 3). It can be seen from the histograms that, in the ipsilateral condition, the alternations occurred following the flash. This resulted in a high frequency of reversals around 500 to 1000 ms, both in the SFM (figure 3a) and in the NC (figure 3c) condition. This was followed by a reduction of the frequency around 1.5 s. In contrast, these peaks were not evident in the contralateral condition

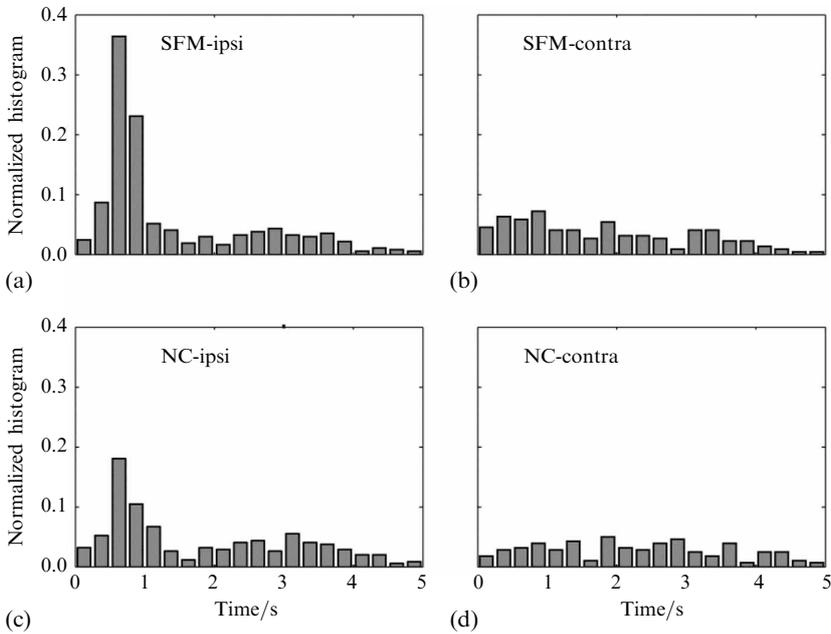


Figure 3. The results of experiment 2A. The frequency of perceptual reversals is shown with respect to flash (time zero). The frequency is shown in a normalized scale, that is as the probability that a reversal occurs within a certain bin (250 ms) after a flash. (a) The results for the condition where SFM and flash were presented in the same visual field (LVF). Alternations occurred frequently just after the flash (<1000 ms). (b) The results for the condition where SFM and flash were presented in different visual fields. The peak after the flash is not as evident as in the ipsilateral condition. (c) The result of NC-ipsilateral condition. (d) The result of NC-contralateral condition.

where the flash was presented in the opposite visual field (figures 3b and 3d). The mean time of alternations with respect to the flash was significantly smaller in the ipsilateral condition (Kruskal–Wallis ANOVA, $p < 0.001$ for both SFM and NC). Also, the probability of reversals—as measured by the number of alternations per flash—was significantly larger in the ipsilateral condition than in the contralateral condition (SFM: 1.133 versus 0.736, $\chi^2 = 17.28$, $p < 0.001$; NC: 0.925 versus 0.739, $\chi^2 = 7.21$, $p < 0.01$).

The results indicate that the IPA retains a certain level of spatial specificity. That is, perceptual alternation is not triggered just by any transient event visible to the observers. The interaction between the flash and bistable stimuli is limited. This spatial specificity is informative with regard to the level where the flash interacts with the representations for bistable stimuli. It shows that the interaction is presumably occurring in relatively early visual areas where visual inputs are retinotopically organized.

The fact that the flash presented on the opposite side does not induce perceptual alternation also suggests that the IPA is not caused by a secondary effect. For example, the perceptual alternations could be produced by a secondary effect of the peripheral flash like eye movements or eye blinks (but see Tse et al 2002). If the flash were to induce eye movements or blinks, perceptual alternations would be expected to occur also in the contralateral condition. However, this was not the case. Thus, the IPA appears to be mediated via local interactions between a transient stimulus and the representations for bistable stimuli.

4 Experiment 2B. Spatial specificity

As mentioned earlier, the spatial specificity gives us a hint where the flash interacts with the representations for bistable stimuli. While the previous experiment shows that alternations are not induced by transient events of any kind, it was not sufficient to tell how large the effective range is. Therefore, we devised a similar, but more thorough experiment. Instead of comparing the two locations of the flash across visual hemifields, we now used 25 locations surrounding a bistable stimulus in the same hemifield as the target bistable stimulus.

4.1 Methods

4.1.1 Observers and apparatus. Six new naive observers participated in this experiment. Stimuli were presented on a CRT monitor with a resolution of 1280×1024 , and a refresh rate of 75 Hz, and were viewed binocularly from a distance of 57 cm.

4.1.2 Stimuli. For this experiment, we used a cylinder-shaped SFM consisting of 200 blue dots (2.4 min of arc) against a black background. The cylinder subtended $3.2 \text{ deg} \times 3.2 \text{ deg}$, and was presented at an eccentricity of 6.4 deg from the nearest edge to fixation in the left visual field (LVF). The cylinder rotated around a horizontal axis at $1.0 \text{ revolution s}^{-1}$.

The stimulus configuration is shown in figure 4a. The display was segmented into 25 regions in a grid fashion. Bistable stimuli were always shown at the central square, and a white square was flashed (67 ms) in one of the 25 regions.

4.1.3 Procedure. In a trial, the observers viewed a bistable stimulus for 1 s, and then the flash appeared at one of the 25 regions. The size of the flash was $3.2 \text{ deg} \times 3.2 \text{ deg}$. The bistable stimulus was continuously viewed for another 1 s, and then removed from the display. The observers reported whether alternation occurred during the trial by pressing a key. 20 samples were made for each flash location. Thus one block consisted of 500 (25 positions \times 20) trials.

4.2 Results and discussion

The results are shown in figure 4b. The probability of perceptual alternation per trial is displayed in a gray-scale. As can be seen from the figure, the highest rate of alternations was observed at the position of SFM. The strength of the effect gradually decreased as the distance between the SFM and the flash increased (Spearman $R = -0.786$, $p < 0.001$).

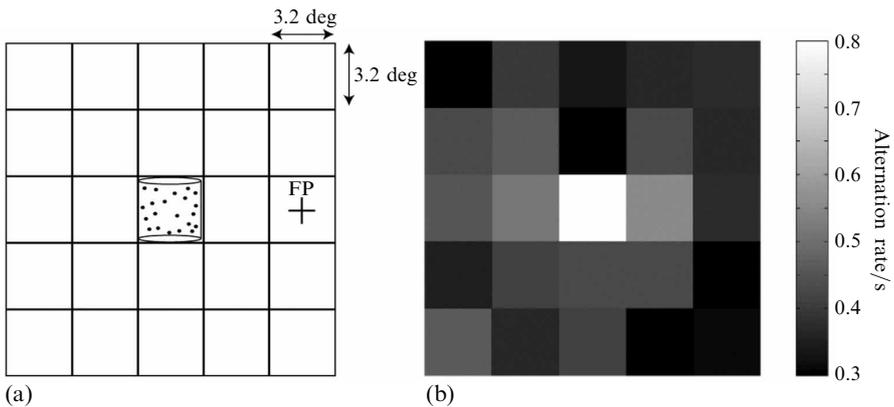


Figure 4. The design and results of experiment 2B. (a) The lines are drawn for illustration purposes, and are not shown during the experiment. An SFM is shown at the center of the grid pattern which is 6.4 deg left of the fixation. A square flash was shown at one of the 25 locations. (b) The probability that a flash at a given position induces an alternation of the rotation direction is shown in a gray-scale. White indicates high probability of perceptual alternation, while black indicates low probability.

So we can draw two conclusions from these data. First, the IPA is spatially confined to the location of the flash. Second, the specificity is not so strict; in other words, spatial overlap between the flash and a bistable stimulus is not a requirement. Thus, the flash has an effect over a spatial range which is slightly larger than the flash itself.

5 Experiment 3. Location specificity versus perceptual grouping

Experiments 2A and 2B demonstrate that a flash near the location of a bistable stimulus induces perceptual alternation, whereas a flash distant from the bistable stimulus does not.

Is the effective area of the transient limited solely by the spatial separation? Here, we are interested in characterizing the nature of this spatial specificity. In particular, the question we address in this experiment is whether the spatial specificity is defined in an object-based manner, or is based solely on spatial separation.

We examined whether a flash presented on a distant, but perceptually grouped object can induce an alternation. We presented two SFM cylinders in the LVF, rotating around a vertical axis. In this configuration, both cylinders are perceptually grouped together and often perceived to rotate in the same direction (Gillam 1972; Eby et al 1989; Grossmann and Dobbins 2003). Observers were asked to report reversals for just one of the cylinders (target), while a flash was presented either at the target or non-target locations. If perceptual alternation operates in an object-based fashion, then presenting a flash at either location should induce alternations.

In these tasks, attention is conceivably directed only to the target. This attentional bias may disrupt the perceptual grouping of the two cylinders. Therefore, these tasks could possibly undermine the grouping effect. Therefore, using the same configuration, we also performed an experiment where observers were asked to report whether both cylinders are moving in the same direction or in the opposite directions. This task requires the observers to attend to both cylinders.

These experiments were meant to tell us whether the effective range of a transient is affected by perceptual grouping, or simply determined by the spatial distance.

5.1 Methods

Eleven naive observers participated in the experiment. Two SFM stimuli (cylinders) were presented ± 0.6 deg apart from the horizontal meridian (figures 5a–5b and 5g–5h). Thus, the distance between the cylinders (edge to edge) was 1.2 deg. At a random timing between 3 and 5 s (uniform sampling), a white flash of the same size was presented at the same location as one of the stimuli. The apparatus and stimuli parameters were identical to those in experiment 2.

Five conditions were tested in separate blocks. In conditions 1–3, the two cylinders were rotating around the vertical axis, and observers were asked to report the reversals of the top cylinder (condition 1, $n = 10$), or bottom cylinder (condition 2, $n = 11$), or whether both cylinders were rotating in the same direction (condition 3, $n = 10$). In conditions 4 and 5, the two cylinders had orthogonal axes. Unlike coaxial configuration, spontaneous perceptual alternations are not linked for orthogonal SFM cylinders. Observers were asked to report the reversals of the top cylinder (condition 4, $n = 7$), or bottom cylinder (condition 5, $n = 9$). The target cylinder was always rotating around the vertical axis.

The SFM stimuli were presented continuously in each block for 200 s. The order of the experiments was randomized for each observer. In all the conditions, the flash occurred at the target location or the non-target location randomly.

5.2 Results and discussion

The results for each stimulus condition are shown in figures 5a–5b and 5g–5h, and the number of induced reversals (ie reversals occurring within 0.5–1 s after the flash) for

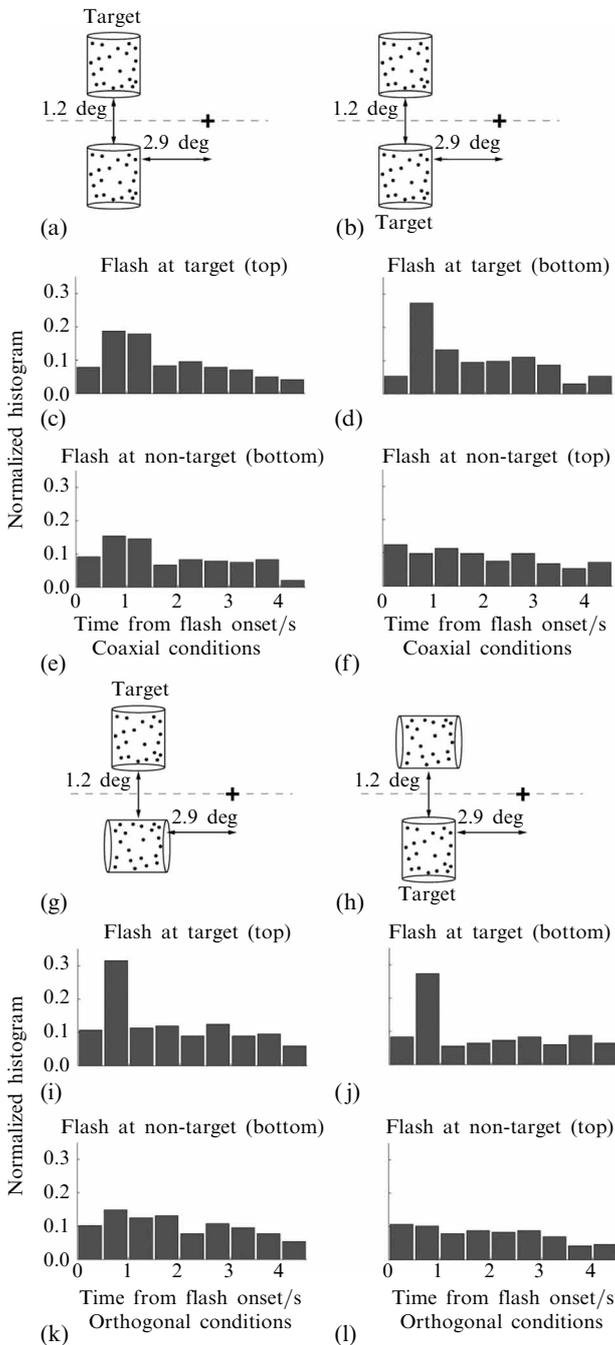


Figure 5. The results of experiment 3. (a) Schematic diagram of the stimulus used in condition 1. Two SFM cylinders, rotating around the vertical axis, were presented in the LVF 0.6 deg off the horizontal meridian. The observers reported the reversals of the top cylinder (target). (b) The stimulus used in condition 2. The configuration is the same as in condition 1, but the target was the bottom cylinder. (g, h) The stimuli used in conditions 4 and 5, respectively. The non-target cylinder was rotating around the horizontal axis. (c, d) and (i, j) The alternation frequency of the condition shown in (a, b) and (g, h) in which the flash was presented at the target cylinder. The histogram shows the alternation frequency as a function of the time elapsed after a flash. The bin width is 0.5 s. The histogram is normalized by the total number of flashes. (e, f) and (k, l) The results of the same conditions (a, b) and (g, h) in which the flash was presented at the non-target cylinder (bottom).

Table 1. Frequency of reversals.

| Condition | Frequency of reversals at target location/% | Frequency of reversals at non-target location/% | Significance |
|-------------------------------------|---|---|--------------|
| Coaxial cylinders | | | |
| target at the top (conditions 1a) | 18.8 ± 2.5 | 15.4 ± 2.3 | $p = 0.4$ |
| target at the bottom (condition 2a) | 27.3 ± 2.7 | 9.8 ± 1.8 | *** |
| Orthogonal cylinders | | | |
| target at the top (conditions 1b) | 31.5 ± 3.6 | 14.9 ± 2.7 | *** |
| target at the bottom (condition 2b) | 27.3 ± 3.0 | 10.2 ± 2.1 | *** |

*** Same location versus different location: $p < 0.001$.

each condition is summarized in table 1. As in the previous experiments, perceptual alternations were successfully induced when the flash was presented at the location of the target (figures 5c–5d and 5i–5j).

Our interest here is whether an alternation is induced when the flash is presented on a spatially separate, but perceptually grouped stimulus. The results were ambiguous as regards this question. In fact, we found an asymmetrical effect between the upper and lower visual fields for coaxial SFM. When the target was the cylinder in the upper visual quadrant (condition 1, figure 5e), there was an effect of perceptual grouping. That is, the flash on the lower cylinder produced a time-locked perceptual alternation of the top cylinder. Indeed, the IPA occurred about equally frequently independently of the flash position (condition 1: same versus different, $p = 0.92$). On the other hand, when the target was the lower cylinder (condition 2, figure 5f), the flash on the upper cylinder did not produce the IPA of the lower cylinder (condition 2: same versus other, $p < 0.001$, χ^2 test). This shows that the IPA is spatially very specific with regard to the target position when the target is in the lower visual field.

Why is there such an asymmetry between the upper and lower visual quadrants? Perceptual grouping between the top and bottom cylinders seems to be an important factor, because IPA was confined to the target location for orthogonal configuration of SFM stimuli, regardless of the target being in the upper or lower visual quadrant (figures 5k and 5l). Another possible factor is attentional resolution, which is also known to manifest an upper–lower asymmetry (He et al 1996). Since attentional resolution is higher in the lower visual field, attention to the bottom cylinder may more effectively individuate the target stimulus from the other cylinder. If so, the perceptual grouping of the two cylinders would be weaker when the lower cylinder is attended.

When the observers were required to attend to both cylinders (condition 3), the flash disrupted the synchronous rotations of the two cylinders (figure 6a), which often took 0–1 s to recover (figure 6b). We did not find a noticeable difference in the effect depending on the flash position (top or bottom) as in the other conditions where the observers were monitoring the rotation direction of either cylinder. Three observers reported that the flash induced counterrotation quite frequently. This implies that, for these observers, the flash had often a local effect. However, other observers experienced the counterrotation rarely, as if the rotations of both cylinders were always linked. Probably, the difference across observers is due to their tendency to attend either locally or globally without intending to do so. These observations, together with the asymmetry between the upper and lower visual fields, suggest that a flash can have an effect both locally and globally, depending on the observer's attentional state.

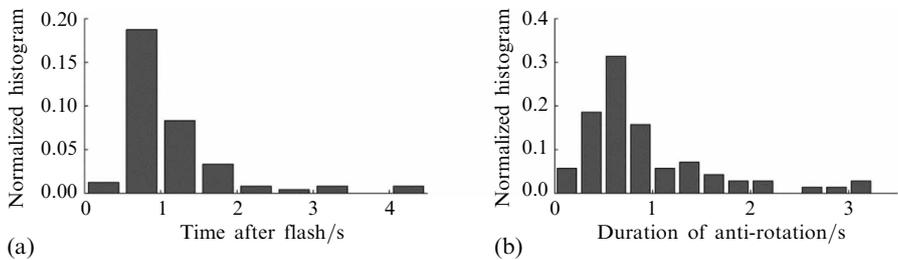


Figure 6. The results of experiment 3 (condition 3). (a) The occurrences of anti-rotation as a function of the time elapsed after a flash. The histogram is normalized by the total number of flashes. (b) The durations of anti-rotation. The histogram is normalized by the total number of the occurrences of anti-rotation.

Taken together, the IPA manifests both a spatial specificity and an effect of perceptual grouping depending on the position of the target. Currently, we cannot specify what other factors determine on which principle the IPA operates. However, as discussed above, one of the likely candidates is attention. When a local aspect of a stimulus is attended, it will be relatively isolated from the rest. In such a situation, the IPA is limited to this area, ie a flash outside the attended part does not induce an alternation. On the other hand, when attention is directed to an object as a whole (two cylinders as one grouped object), a transient stimulus presented within this object seems to have a global impact on the entire object, including the portions that are not directly stimulated by the transient.

6 Experiment 4A. Effects of adaptation

In the previous experiments, we presented a flash repeatedly and showed that the flash is responsible for the increase in the frequency of perceptual reversals. In bistable perception, adaptation to the dominant percept is widely considered as one of the key factors causing perceptual alternations (Köhler and Wallach 1944; Cornwell 1976; Babich and Standing 1981; Merk and Schnakenberg 2002; Blake et al 2003). How is the effect of a flash related to the adaptation process in bistable percepts? The purpose of the next experiment was to examine the possible interactions between a transient stimulus and adaptation. Prior to a flash, we presented bistable stimuli for a variable duration of time, and examined the dependence of IPA on the duration of adaptation.

If the flash directly causes an alternation independently of sensory adaptation to a dominant percept, the alternation frequency will not depend on the adaptation duration. Conversely, if adaptation does have an effect on the IPA, the frequency of IPA will depend on the adaptation duration.

6.1 Methods

6.1.1 Observers and apparatus. Six observers including the author (RK) participated in this experiment. One observer was excluded from the analysis because he had difficulty in perceiving perceptual alternations in SFM, even when he continuously viewed the stimulus for several minutes. The stimuli were presented on a 22-inch CRT monitor (LaCie Blue Electron). The refresh rate of the display was 60 Hz, and the resolution 1280×1024 . Viewing distance was 57 cm.

6.1.2 Stimuli. In this experiment, we used SFM and NC. One trial consisted of three phases: adaptation phase, flash phase, and post-flash phase (figure 7a). In all phases, a bistable stimulus was continuously shown on a black background. The duration of adaptation phase was varied between 250 ms, 500 ms, 1000 ms, 2000 ms, and 3000 ms. In the flash phase, the stimulus background turned into white for 82 ms. Subsequently, the same stimulus was observed for another 500 ms so that observers could make a judgment whether there was a perceptual reversal or not.

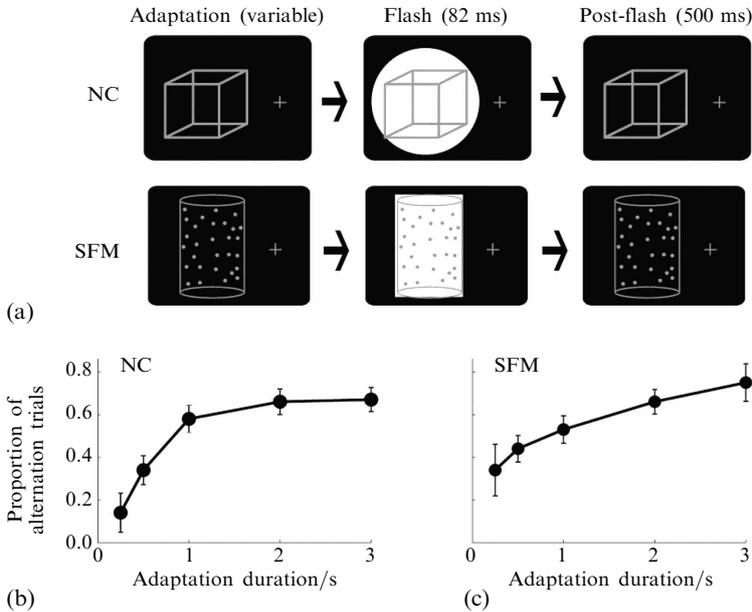


Figure 7. The design and results of the adaptation experiment (experiment 4A). (a) The stimuli used in experiment 4A. Ambiguous figures (NC and SFM) were presented next to the fixation cross throughout a trial. After a variable duration of adaptation, a flash was presented in the background. This was followed by 500 ms of observation. Observers reported alternations triggered by the flash. The trials where alternation was observed before the flash were discarded and repeated later in the session. (b) The results of NC condition in experiment 4A. Proportion of trials in which observers perceived an alternation as a function of the adaptation duration. (c) The results of SFM condition in experiment 4A.

The exact parameters used in this experiment are described below. The center of the stimuli was located 5.9 deg to the left of the fixation cross.

SFM. The cylinder of the SFM stimulus had a radius of 1.9 deg and a height of 4.5 deg. It consisted of 800 blue dots with a lifetime of 583 ms (35 frames) and rotated at a speed of 0.5 revolution s^{-1} .

NC. The Necker cube was drawn in blue subtending approximately 2.5 deg when viewed from the perpendicular angle.

6.1.3 Procedure. At the end of each trial, observers reported whether perceptual reversals occurred just after the flash. The observers also reported whether the spontaneous alternation occurred before the flash. In order to avoid the contamination of spontaneous alternations, those trials were not counted and were repeated later. Observers were instructed to attend to the initial percept once the trial was started. This manipulation of attention is known to keep spontaneous alternations lower (Pelton and Solley 1968), thus preventing frequent early alternations before the flash. Observers performed 20 trials for each condition.

6.2 Results and discussion

The results for the SFM and NC stimuli are displayed in figures 7b and 7c. The proportion of trials in which the flash triggered a perceptual alternation is shown as a function of adaptation duration. The results show that the flash was more effective at inducing an alternation when one interpretation had been perceived for a longer time, which results in deeper adaptation. The alternations increased monotonically as the adaptation duration increased (Spearman's rank order correlation: $R = 0.79$, $p < 0.001$ for NC; $R = 0.65$, $p < 0.001$ for SFM). The results indicate that some adaptation is required for an alternation to occur and a flash by itself is not necessarily sufficient.

7 Experiment 4B. Effects of adaptation

In the previous experiments, the trials in which an alternation was observed before the presentation of a flash were discarded. While an increase in alternation rate is consistent with our interpretation that adaptation is required for the IPA, this is not conclusive. For example, spontaneous alternation should also occur more frequently as the viewing duration increases as in experiment 4A. The purpose of this experiment was to compare the rate of the alternation induced by transients with the spontaneous alternation rate.

7.1 Methods

7.1.1 Observers and apparatus. Three new observers and one of the authors (RK) participated in this experiment. The apparatus was the same as in experiment 4A.

7.1.2 Stimuli and procedure. In this experiment, we used the same stimuli as in experiment 4 (ie SFM and NC). However, we used a different set of adaptation durations (1, 2, 3, and 4 s). Post-flash observation duration was again 500 ms.

At the end of each trial, observers reported whether perceptual reversals occurred at any time during the trial regardless of whether the alternation coincided with the timing of the flash. Thus, the results include both the IPA and spontaneous alternations. Also, observers were instructed to attend to the initial percept as in experiment 4A. We included a control condition to measure the spontaneous alternation rates as a function of viewing duration. The order of the main condition and the control condition was counterbalanced across observers. In both conditions, observers performed 40 trials per viewing duration.

7.2 Results and discussion

The results for the SFM and NC stimuli are displayed in figures 8a and 8b. As expected, the proportion of alternation trials increased as the viewing duration became longer both in the flash condition (Spearman's rank order correlation: $R = 0.826$, $p < 0.001$ for NC; and $R = 0.877$, $p < 0.001$ for SFM) and in the control condition (Spearman's rank order correlation: $R = 0.682$, $p < 0.01$ for NC; and $R = 0.690$, $p < 0.01$ for SFM). The results indicate that alternation was facilitated in the flash condition over the control condition. (Two-tailed paired t -test for each adaptation duration. Both in SFM and NC, $p < 0.05$ for 1 s, and $p < 0.01$ for other durations. The p -values are Bonferroni corrected for multiple comparisons.)

If the flash produces an alternation with a certain probability regardless of the depth of adaptation, the proportion of alternation trials should increase simply because of the increase in the spontaneous alternations. Thus, in order to gain insight into the role of adaptation in the IPA, we need to look at the differences in the increase rate for the IPA and spontaneous alternations. If the IPA interacts with the adaptation level, the alternation in the flash condition should increase at a faster rate than the spontaneous rate alone. On the other hand, if the IPA is a constant effect independent of adaptation, the increase rate in the flash condition should equal that in the control condition unless there is a ceiling effect due to saturation. Therefore, we compared the increase rate between the flash condition and the control condition. The increase rate for each time epoch was calculated by subtracting the proportion of alternation trials at time T s from that at time $(T + 1)$ s.

The analysis shows that the increase rate is not identical for the two conditions. In the NC experiment, the increase rate was higher for the flash condition than for the control condition when the adaptation duration increased from 2 s to 3 s (figure 8c, paired t -test, $p < 0.05$). In the SFM experiment, it was higher when the adaptation duration increased from 1 s to 2 s (figure 8d, paired t -test, $p < 0.05$). These results support the conclusion that the size of the effect of the IPA depends on the adaptation depth preceding the presentation of the flash.

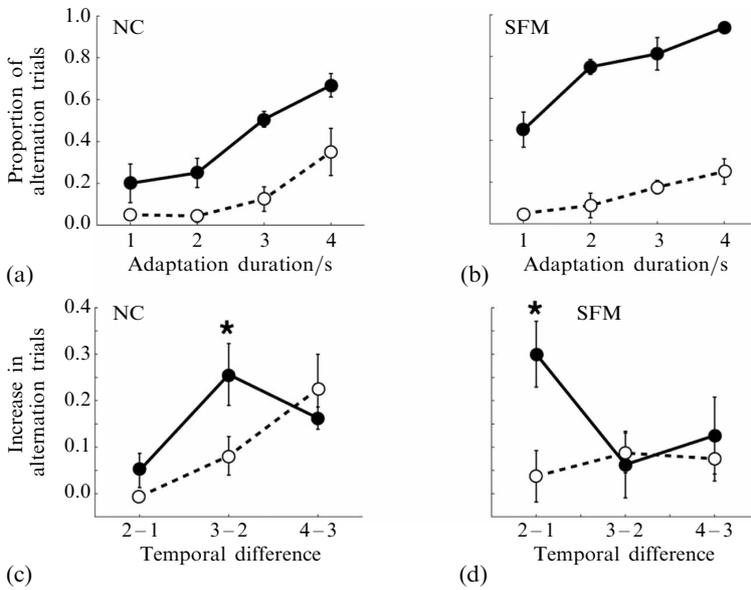


Figure 8. The results of experiment 4B. (a) The results of NC condition. The filled circles show the proportion of trials in which alternation was observed for the flash condition. The open circles show the results of the control condition. Error bars indicate 1 SEM. (b) The results of SFM condition. (c) The increase rate for the NC condition (shown in figure 8a). The filled circles and open circles indicate the flash condition and the control condition, respectively. (d) The increase rate for the SFM condition (shown in figure 8b). Error bars indicate 1 SEM. The star symbol denotes a significant difference based on a paired *t*-test ($p < 0.05$).

8 General discussion

We have shown that perceptual reversals during the observation of ambiguous stimuli can be induced by a transient stimulus. This induced perceptual alternation (IPA) provides us with a means to investigate the dynamics underlying the perceptual alternation.

Our experiments revealed the basic characteristics of the IPA. First, the reversals are time-locked to the flash. Second, the effect is largely confined to the location of the flash. That is, the flash needs to be presented near the target stimulus. Third, adaptation to the dominant perceptual interpretation is necessary, and the strength of the effect depends on the depth of adaptation.

These characteristics are shared by another transient-induced phenomenon, where a transient stimulus triggers fading of an object presented in the periphery (Kanai and Kamitani 2003; Moradi and Shimojo 2004; see also Breitmeyer and Rudd 1981; Wilke et al 2003). The fading effect shows the time-locked characteristics. It is confined to a limited spatial region near the transient stimulus. Also, pre-adaptation, although brief, is necessary for fading to be reliably triggered. In addition to the similarities in these basic characteristics, what is common between the perceptual alternations and disappearances is that conscious perception for a physically constant stimulus is drastically changed by transient stimuli. In fact, results of other studies also suggest that there is a common mechanism underlying both perceptual disappearance and bistable percepts (Bonneh et al 2001; Carter and Pettigrew 2003). Given these similarities between perceptual alternations and fading, we need to understand the function of a visual transient both in the perceptual fading and the IPA in a unified scheme. Here we address this issue in two parts: first, what kind of dynamics can result in such a behavior, and, second, what is the possible underlying neural mechanism for such dynamics.

8.1 Neural model and simulation

We propose a schematic model of the effects of transient input that incorporates both the alternation and fading effects. Perceptual bistability is often considered analogous to the alternation between states or attractors in bistable or multistable neural networks or dynamical systems (Poston and Stewart 1978; Kawamoto and Anderson 1985). Stability can be analyzed in such models by constructing a so-called energy function (or Lyapunov function) such that in the absence of noise the energy always decreases until the system reaches a fixed state or a stable attractor. The stable states of such models are determined by local minima of the energy function. In figure 9, two mutually exclusive percepts for a bistable stimulus are illustrated as two locally stable minima in the energy function (left and right).

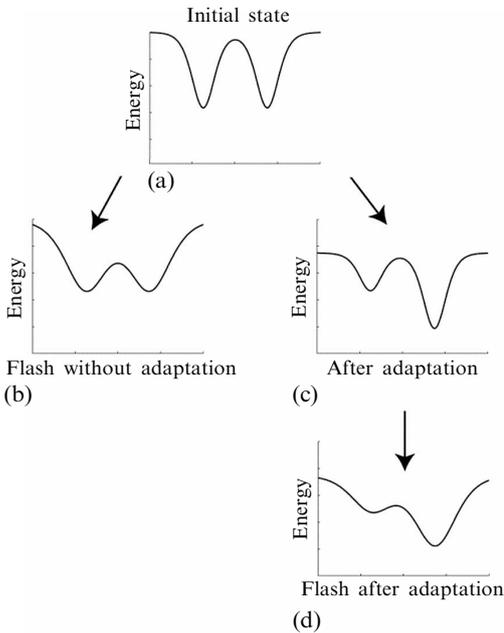


Figure 9. A schematic model of the flash-induced alternation. Two mutually exclusive percepts are illustrated as the two energy wells (left and right). (a) Upon stimulus onset, energy wells for both percepts are deep. (b) When a flash is presented without a substantial adaptation, the smoothing effect (see text) is not sufficient to produce an energy well low enough for perceptual alternation to occur. (c) After adaptation, the energy well for the dominant percept becomes shallow (here the left well). (d) When a flash is presented after adaptation, the smoothing effect of the flash produces an energy well sufficiently low for the perceptual state to transit to the other interpretation.

Experimental evidence suggests that prior adaptation can increase the reversal rate from the adapted percept to the unadapted percept (Long et al 1992). This finding is consistent with a scheme in which adaptation changes the energy landscape of the system by increasing the energy of the adapted state (figure 9c). Conceivably, a transient stimulus at the same location should induce a reversal either by changing the state of the network, or by modifying the energy landscape.

It has been suggested that a salient transient signal triggers a rapid change in the gain of the input (Moradi and Shimojo 2004). This type of response is necessary for efficient coding of information in a changing environment. In the absence of the transient signal, the gain gradually returns to the level before the flash. However, the change in the input gain following a flash results in smoothing of the energy landscape (figure 9b). Consequently, our model predicts that the spontaneous reversal rate increases following the flash. However, if a flash follows sufficient adaptation, the combined effect of adaptation and reduction of the gain makes the previous local minima unstable and as a result, induces a perceptual alternation (figure 9d).⁽¹⁾

⁽¹⁾ The observer who did not perceive any perceptual alternation in the SFM condition in experiment 4A reported that flash makes the SFM flat temporarily, and the cylinder shape restores after some duration. This observation is consistent with our interpretation that a flash makes the energy landscape smooth. In this observer, energy minimum for one interpretation was predominant, and the smoothing effect could only make the minimum briefly unstable, and was not sufficient to induce an alternation.

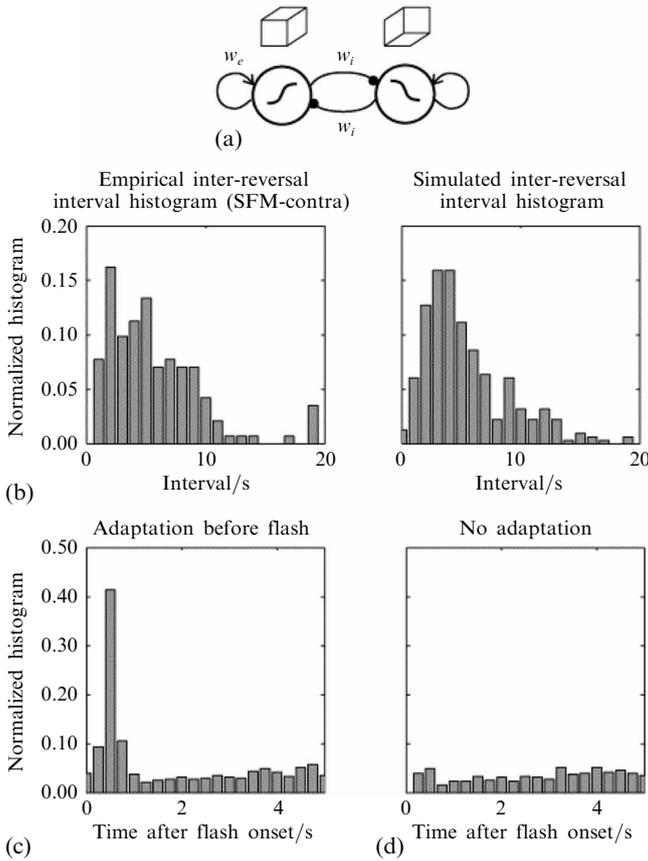


Figure 10. (a) Bistability model: two opponent neurons inhibit each other. (b) Histogram of the intervals between perceptual reversals for experimental data (experiment 2A, SFM-contra) versus simulation. (c) Simulated effect of the flash. Flash onset was 5 s after onset of each simulated trial. (d) Flash by itself does not result in any effect in the model. Flash occurs at the onset of simulated trial, thus the neurons are not adapted at the time of the flash. Figures are based on 500 simulated trials with a time-step of 10 ms.

Figure 10 demonstrates a minimal implementation of the aforementioned schematic account. We modeled the bistability in our network using opponent neurons (that selectively respond to opposite directions) with symmetric inhibitory connections (figure 10a). When there is no noise in the network, the state always converges to one of the two stable minima (percepts) and the outcome is determined by the initial condition. In the presence of stochasticity, however, the system occasionally alternates between the two percepts. The rate for switching from one state to another depends on the difference between their energies and noise level, as well as the height of the energy separating the minima.

The output of each Ising neuron at each time-step is modeled as follows (Hinton and Sejnowski 1986):

$$\text{Output} = \begin{cases} 1, & \text{with probability } \frac{1}{1 + \exp[-2(ax - b)]} \\ -1, & \text{otherwise,} \end{cases}$$

where x is the total input given $w_e = -w_i = 1$, $a = 2.5$ is the slope, and b reflects the change in threshold following adaptation:

$$\tau \frac{db}{dt} = \begin{cases} 2 - b & \text{if output} = 1 \\ -b & \text{otherwise.} \end{cases} \quad \tau = 1 \text{ s}$$

Figure 10b compares the distribution of intervals between perceptual reversals in experiment 3 (SFM-contra, actual data) and simulation data. This rudimentary model seems, at least qualitatively, to capture the stochastic nature of spontaneous perceptual alternations.

The effect of the transient was modeled by a transient decrease in the slope as follows:

$$a(t) = a - k\{\exp[-(t - t_0)/\tau_2] - \exp[-(t - t_0)/\tau_1]\}, \quad t > t_0$$

where $\tau_1 = 150$ ms, $\tau_2 = 300$ ms, $k = 3$, and t_0 reflects the onset of the transient plus 150 ms visual processing delay. Figure 9c demonstrates that such reduction in the slope can induce reversals comparable to the empirical data in figure 3a (reaction time is not included in the simulation). We also verified that, if the transient slope change occurs before enough adaptation, it fails to induce any alternation (figure 10d).

Thus, our model can explain the time-locked nature, and the requirement of adaptation in IPA. In this model, the effect of a transient is a brief loss of neural sensitivity. Previously, we have shown that modeling the effect of a transient in a similar fashion can explain the perceptual disappearance induced by visual transients (see Moradi and Shimojo 2004). Thus, our simple model covers both the perceptual alternation and disappearance phenomena.

8.2 Underlying neural mechanism

Experiments 4A and 4B suggest that IPA results from a combination of two components: adaptation to a dominant percept, and the effect of a transient. What are the neural foundations underlying these components? The adaptation process is specific for the stimulus and is likely to occur in early visual areas where visual inputs are still retinotopically organized. For example, it is known that adaptation to a Necker cube is specific to the location at which the stimulus is presented. Alternation rates of Necker cube usually increase during continuous viewing. However, the accelerated alternation rate due to adaptation restores to the original level when the cube is moved elsewhere in the visual field (Babich and Standing 1981). Recently, Blake et al (2003) have shown that bistable stimuli (BR and SFM) that are moving continuously in the visual field manifest slower alternation rates. This indicates also the involvement of location-specific (retinotopic) adaptation.

On the other hand, the neural circuitry responsible for the effect of a flash is somewhat elusive. The increase in gain and the smoothing of the energy landscape in our proposed model can be achieved biophysically via nonspecific shunting inhibition (Torre and Poggio 1978). Whether this is mediated through local interactions or attentional mechanisms via top-down feedback remains unclear. Nonetheless, we are tempted to attribute this effect of visual transients to attentional mechanisms mediated by the parietal attention system. First, attentional shift is suggested to induce perceptual alternations in ambiguous figures (Tsal and Kolbet 1985; Georgiades and Harris 1997). Also the alternation slows down when observers are engaged in a secondary task (Reisberg 1983). While we emphasized that the effective range of transients is spatially confined, this does not necessarily mean that the interactions should occur within the retinotopically organized visual areas. In particular, in the parietal cortex, many cells have spatially confined receptive fields and they are involved in attentional control (eg Colby and Goldberg 1999). The involvement of the parietal system in both the perceptual disappearance and perceptual alternation has been suggested before. Bonnef et al (2001) compared motion-induced blindness to the extinction of salient stimuli experienced by patients with parietal lesions. Parietal patients often fail to perceive a salient object presented contralateral to the damaged cortical hemisphere (Rees et al 2000; Driver and Vuilleumier 2001). Moreover, their perceptual disappearance is facilitated (Mennemeier et al 1994; Wolpert et al 1998).

The past studies on bistable perception concern internally induced alternations, i.e. spontaneous alternations during the view of a constant stimulus, or voluntary (top-down) control of dominant percept (Pelton and Solley 1968; Reisberg 1983; Lumer et al 1998; see Leopold and Logothetis 1999). In these cases, it has been suggested that endogenous shifts of attention play a causal role in perceptual alternations. On the other hand, our method of presenting a transient stimulus is closely related to exogenously triggered attention (Posner and Cohen 1984; Hikosaka et al 1993; Theeuwes et al 1998). In this view, the IPA may be regarded as the exogenous counterpart of attentional shifts in bistable perception. And the parietal area involved in orienting spatial attention (LIP in particular; see Colby and Goldberg 1999) is a likely candidate for producing perceptual alternations in response to transient inputs.

Our experiment 2B showed that the spatial specificity of IPA is not strictly confined to the location of the target stimulus. This mild form of spatial specificity is also observed in perceptual disappearance induced by transient stimuli (Kanai and Kamitani 2003; Wilke et al 2003; Moradi and Shimojo 2004). This extended spatial specificity is in contrast to sensory adaptation, which typically requires strict stimulus overlap.

The finding that a flash sometimes influences the percept in an object-based manner (see experiment 3) also seems to suggest the involvement of a slightly higher mechanism rather than non-selective effects in the lower sensory areas. In experiment 3, a flash presented on a coaxial SFM cylinder sometimes induced an alternation in the other cylinder, which was presumably perceptually grouped. This implies that the effect of a flash transferred to a distant, but grouped object. Previously, a similar effect has been reported in perceptual disappearance (Kanai and Kamitani 2003). When a long bar is presented in a periphery, presenting a flash at one end of the bar was sometimes sufficient to induce a fading of the entire bar. This also suggests an object-based effect of visual transients.

These comparisons suggest that there is a connection between perceptual fading and frontoparietal functions. Moreover, recent evidence indicates the involvement of top-down feedback in the perception of bistable stimuli. For example, the right frontoparietal cortex is involved in the disambiguation of bistable stimuli such as the Necker cube (Bisiach et al 1999; Inui et al 2000; Sengpiel 2000). Also, frontoparietal areas associated with selective visual attention are considered to be involved in initiating perceptual alternation (Kleinschmidt et al 1998; Lumer et al 1998; Leopold and Logothetis 1999; Miller et al 2000; Pettigrew 2001; Sterzer et al 2002). So the current evidence shows that frontoparietal areas play a critical role both in perceptual fading and in alternation. This makes it tempting to suggest that these alternation-related areas may be the source of the inhibition by a flash, and causing IPA.

8.3 *Concluding remarks*

In the field of the perception of bistable stimuli there has been an extensive debate as regards the mechanisms underlying perceptual alternations. The first explanation involves adaptation of the currently dominant stimulus interpretation (Köhler 1940; Long and Toppino 1994; Blake et al 2003). Proponents of the second explanation assume that attention-related processes actively trigger perceptual alternations (Kleinschmidt et al 1998; Lumer et al 1998; Leopold and Logothetis 1999). However, these explanations are not necessarily mutually exclusive and bistable perception seems to be mediated at a multitude of processing levels in the visual system (Blake and Logothetis 2002). Our model combines adaptation at lower sensory level and transient gain change via feedback. Finally, it is the first model that provides an account for both perceptual alternations and disappearances in a single scheme.

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References

- Babich S, Standing L, 1981 "Satiation effects with reversible figures" *Perceptual and Motor Skills* **52** 203–210
- Bisiach E, Ricci R, Lai E, De Tanti A, Inzaghi M G, 1999 "Unilateral neglect and disambiguation of the Necker cube" *Brain* **122** 131–140
- Blake R, Fox R, McIntyre C, 1971 "Stochastic properties of stabilized image binocular rivalry alternations" *Journal of Experimental Psychology* **88** 327–332
- Blake R, Logothetis N K, 2002 "Visual competition" *Nature Reviews Neuroscience* **3** 1–11
- Blake R, Sobel K V, Gilroy L A, 2003 "Visual motion retards alternations between conflicting perceptual interpretations" *Neuron* **39** 869–878
- Bonneh Y, Cooperman A, Sagi D, 2001 "Motion induced blindness in normal observers" *Nature* **411** 798–801
- Brainard D H, 1997 "The Psychophysics Toolbox" *Spatial Vision* **10** 433–436
- Breitmeyer B, Rudd M E, 1981 "A single-transient masking paradigm" *Perception & Psychophysics* **30** 604–606
- Carter O L, Pettigrew J D, 2003 "A common oscillator for perceptual rivalries?" *Perception* **32** 295–305
- Colby C L, Goldberg M E, 1999 "Space and attention in parietal cortex" *Annual Review of Neuroscience* **22** 319–349
- Cornwell H G, 1976 "Necker cube reversal: Sensory or psychological satiation?" *Perceptual and Motor Skills* **43** 3–10
- Driver J, Vuilleumier P, 2001 "Perceptual awareness and its loss in unilateral neglect and extinction" *Cognition* **79** 39–88
- Eby D W, Loomis J M, Solomon E M, 1989 "Perceptual linkage of multiple objects rotating in depth" *Perception* **18** 427–444
- Georgiades M S, Harris J P, 1997 "Biasing effects in ambiguous figures: Removal or fixation of critical features can affect perception" *Visual Cognition* **4** 383–408
- Gillam B, 1972 "Perceived common rotary motion of ambiguous stimuli as a criterion of perceptual grouping" *Perception & Psychophysics* **11** 99–101
- Girgus J J, Rock I, Egatz R, 1977 "The effect of knowledge of reversibility on the reversibility of ambiguous figures" *Perception & Psychophysics* **22** 550–556
- Grossmann J K, Dobbins A C, 2003 "Differential ambiguity reduces grouping of metastable objects" *Vision Research* **43** 359–369
- He S, Cavanagh P, Intriligator J, 1996 "Attentional resolution and the locus of visual awareness" *Nature* **383** 334–337
- Hikosaka O, Miyauchi S, Shimojo S, 1993 "Voluntary and stimulus-induced attention detected as motion sensation" *Perception* **22** 517–526
- Hinton G E, Sejnowski T J, 1986 "Learning and relearning in Boltzmann machines", in *Parallel Distributed Processing: Explorations in the Microstructure of Cognition* volume 1: *Foundations* Eds D E Rumelhart, J L McClelland (Cambridge, MA: MIT Press) pp 282–317
- Hock H S, Schoner G, Voss A, 1997 "The influence of adaptation and stochastic fluctuations on spontaneous perceptual changes for bistable stimuli" *Perception & Psychophysics* **59** 509–522
- Inui T, Tanaka S, Okada T, Nishizawa S, Katayama M, Konishi J, 2000 "Neural substrates for depth perception of the Necker cube; a functional magnetic resonance imaging study in human subjects" *Neuroscience Letters* **282** 145–148
- Kanai R, Kamitani Y, 2003 "Time-locked perceptual fading induced by visual transients" *Journal of Cognitive Neuroscience* **15** 664–672
- Kawamoto A H, Anderson J A, 1985 "A neural network model of multistable perception" *Acta Psychologica* **59** 35–65
- Kleinschmidt A, Büchel C, Zeki S, Frackowiak S J, 1998 "Human brain activity during spontaneously reversing perception of ambiguous figures" *Proceedings of the Royal Society of London B: Biological Sciences* **265** 2427–2433
- Köhler W, 1940 *Dynamics in Psychology* (New York: Liveright)
- Köhler W, Wallach H, 1944 "Figural after-effects: An investigation of visual processes" *Proceedings of the American Philosophical Society* **88** 269–357

- Leopold D A, Logothetis N K, 1999 "Multistable phenomena: changing views in perception" *Trends in Cognitive Sciences* **3** 254–264
- Levelt W J M, 1966 "The alternation process in binocular rivalry" *British Journal of Psychology* **57** 225–238
- Levelt W J M, 1967 "Note on the distribution of dominance times in binocular rivalry" *British Journal of Psychology* **58** 143–145
- Long G M, Toppino T C, Mondin G W, 1992 "Prime time: fatigue and set effects in the perception of reversible figures" *Perception & Psychophysics* **52** 609–616
- Lumer E D, Friston K J, Rees G, 1998 "Neural correlates of perceptual rivalry in the human brain" *Science* **280** 1930–1934
- Mennemeier M S, Chatterjee A, Watson R T, Wertman E, Carter L P, Heilman K M, 1994 "Contributions of the parietal and frontal lobes to sustained attention and habituation" *Neuropsychologia* **6** 703–716
- Merk I, Schnakenberg J, 2002 "A stochastic model of multistable visual perception" *Biological Cybernetics* **86** 111–116
- Miller S M, Liu G B, Ngo T T, Hooper G, Riek S, Carson R G, Pettigrew J D, 2000 "Inter-hemispheric switching mediates perceptual rivalry" *Current Biology* **10** 383–392
- Moradi F, Shimojo S, 2004 "Suppressive effect of sustained low-contrast adaptation followed by transient high-contrast on peripheral target detection" *Vision Research* **44** 449–460
- Murata T, Matsui N, Miyauchi S, Kakita Y, Yanagida T, 2003 "Discrete stochastic process underlying perceptual rivalry" *NeuroReport* **14** 1347–1352
- Pelli D G, 1997 "The VideoToolbox software for visual psychophysics: Transforming numbers into movies" *Spatial Vision* **10** 437–442
- Pelton L H, Solley C M, 1968 "Acceleration of reversals of a Necker cube" *American Journal of Psychology* **81** 585–588
- Pettigrew J D, 2001 "Searching for the switch: Neural bases for perceptual rivalry alternations" *Brain and Mind* **2** 85–118
- Posner M I, Cohen Y, 1984 "Components of visual orienting", in *Attention and Performance* volume x, Eds H Bouma, D Bouwhuis (Mahwah, NJ: Lawrence Erlbaum Associates) pp 531–536
- Poston T, Stewart I, 1978 "Nonlinear modeling of multistable perception" *Behavioral Sciences* **23** 318–334
- Rees G, Wojciulik E, Clarke K, Husain M, Frith C, Driver J, 2000 "Unconscious activation of visual cortex in the damaged right hemisphere of a parietal patient with extinction" *Brain* **123** 1624–1633
- Reisberg D, 1983 "General mental resources and perceptual judgment" *Journal of Experimental Psychology: Human Perception and Performance* **9** 966–979
- Rock I, Mitchener K, 1992 "Further evidence of failure of reversal of ambiguous figures by uninformed subjects" *Perception* **21** 39–45
- Sengpiel F, 2000 "An alternative view of perceptual rivalry" *Current Biology* **10** R482–R485
- Sterzer P, Russ M O, Preibisch K, Kleinschmidt A, 2002 "Neural correlates of spontaneous direction reversals in ambiguous apparent visual motion" *Neuroimage* **15** 908–916
- Theeuwes J, Kramer A, Hahn S, Irwin D E, 1998 "Our eyes do not always go where we want them to go: capture of the eyes by new objects" *Psychological Science* **9** 379–385
- Torre V, Poggio T, 1978 "Synaptic mechanism possibly underlying directional selectivity to motion" *Proceedings of the Royal Society of London B: Biological Sciences* **202** 409–416
- Troxler D, 1804 "Über das Verschwinden gegebener Gegenstände innerhalb unseres Gesichtskreises", in *Ophthalmologische Bibliothek* Eds K Himly, J A Schmidt, volume 2 (Jena: Frommann) pp 1–119
- Tsal Y, Kolbet L, 1985 "Disambiguating ambiguous figures by selective attention" *Quarterly Journal of Experimental Psychology* **37** 352–373
- Tse P U, Sheinberg D L, Logothetis N K, 2002 "Fixational eye movements are not affected by abrupt onsets that capture attention" *Vision Research* **42** 1663–1669
- Wade N J, 1973 "Binocular rivalry and binocular fusion of afterimages" *Vision Research* **13** 999–1000
- Wilke M, Logothetis N K, Leopold D A, 2003 "Generalized flash suppression of salient visual targets" *Neuron* **39** 1043–1052
- Wilson H R, Blake R, Lee S H, 2001 "Dynamics of traveling waves in visual perception" *Nature* **412** 907–910
- Wolpert D M, Goodbody S J, Husain M, 1998 "Maintaining internal representations: the role of the human superior parietal lobe" *Nature Neuroscience* **1** 529–533

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