Disruption of implicit perceptual memory by intervening neutral stimuli

Ryota Kanai [a,b,*], Tomas H.J. Knapen [c], Raymond van Ee [c], Frans A.J. Verstraten [a]

[a] *Universiteit Utrecht, Helmholtz Institute, Department of Experimental Psychology, Heidelberglaan 2, NL 3584 CS Utrecht, The Netherlands*
[b] *California Institute of Technology, Division of Biology, M-C 114-96, Pasadena, CA 91125, USA*
[c] *Universiteit Utrecht, Helmholtz Institute, Department of Physics, Princetonplein 5, NL 3584 CC Utrecht, The Netherlands*

Abstract

After viewing directional motion, one is likely to perceive a subsequently presented directionally ambiguous motion as being in the same direction as the prior motion. The perceptual bias towards the most recent percept gradually develops as the interval between the prior stimulus and a subsequent test becomes longer. This form of positive bias, or priming, is created in an automatic fashion. It remain unclear how such perceptual bias could be eliminated by a stimulus manipulation. Here we examine whether presentation of a stimulus, which was neutral as to the competing perceptual interpretations, during the interval between prior and test stimuli, disrupts the development of the priming effect. In experiments with ambiguous motion, we used stationary gratings as the neutral stimuli, and in an experiment with binocular rivalry between orthogonal gratings, we used a plaid pattern consisting of the two rival gratings. In both cases, presenting the neutral stimuli reduced the perceptual bias. These findings show that the visual system dynamically calibrates its internal bias using a recent percept and that this internal bias can be nullified by presenting neutral stimuli.
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1. Introduction

A brief exposure to a stimulus often has a perceptual effect on a subsequently presented stimulus. This can be a facilitatory or a suppressive effect depending on the stimulus condition (Brascamp, Knapen, Kanai, van Ee, & van den Berg, in press; Kanai & Verstraten, 2005; Pearson & Clifford, 2005). Facilitation and suppression triggered by a preceding stimulus are generally called *priming* and *aftereffect*, respectively.

Previously we have shown that brief adaptation (e.g. 320 ms) to unambiguous visual motion results in both a *rapid motion aftereffect* (rMAE) and a priming effect, which we termed *perceptual sensitization* (Kanai & Verstraten, 2005). Typically, the rMAE dominates just after the offset

of the adaptation stimulus and it lasts for a few seconds. As the adaptation–test interval becomes longer, the perceptual bias shifts from negative (aftereffect) to positive (priming) effects. Even when the adaptation stimulus itself is ambiguous, the sensitization still occurs. Thus, it is the subjective percept as opposed to the motion signal as such that produces the positive bias on a subsequent ambiguous motion.

The perceptual sensitization, which develops over the course of a few seconds, is closely related to the stabilization phenomenon in bistable stimuli (Leopold, Wilke, Maier, & Logothetis, 2002; Noest, van Ee, Nijs, & van Wezel, 2007; Orbach, Ehrlich, & Heath, 1963). Usually, when observing a bistable stimulus, the percept spontaneously alternates between possible interpretations every few seconds. However, if the stimulus is presented intermittently with blank intervals of 3–5 s, the percept is locked to one percept and this can last for several minutes (Brascamp et al., submitted for publication; Chen & He, 2004; Leopold et al., 2002; Maier, Wilke, Logothetis, & Leopold, 2003). The time course of the perceptual sensitization is

consistent with the fact that the presence of a blank period between successive stimulus presentations is required to obtain stabilization. This is because in an intermittent display of an ambiguous stimulus, each presentation serves as an ambiguous adaptation and repeatedly produces the sensitization for the next presentation.

Stabilization in an intermittent presentation is a robust phenomenon and thus difficult to disrupt. For example, when multiple ambiguous stimuli are interleaved, the presence of other types of stimuli between successive presentations of one type of ambiguous stimulus hardly affects the strength of stabilization (Maier et al., 2003). When different kinds of bistable stimuli are interleaved one after another, the percept for each stimulus is stabilized independent of each other. This finding indicates that presenting an unrelated stimulus during the intervals does not disrupt the stabilization.

Uncovering conditions in which stabilization can be reduced or even abolished is informative for advancing our understanding of the underlying mechanisms. We have previously shown that distraction of attention during and even after the encoding of the prime diminishes the strength of stabilization (Kanai & Verstraten, 2006). In the present paper, we report a new method to disrupt stabilization (or equivalently sensitization) in a stimulus-driven fashion. In our experiments, we insert a stimulus neutral to possible interpretations of a bistable stimulus during the blank interval. When the neutral stimuli are presented continuously throughout the adapt–test interval, stabilization is reduced. In the case of ambiguous apparent motion, stationary stimuli were found to be effective at attenuating stabilization. In the case of binocular rivalry in which two orthogonal gratings are shown dichoptically, a plaid pattern composed of the two competing gratings effectively disrupted stabilization. These findings imply that the implicit perceptual bias produced by past percepts can be equalized by stimuli neutral to the rivaling patterns.

2. Experiment 1: Stopping the motion

We measured the effect of adaptation to a brief motion stimulus (320 ms). The adaptation stimuli were either directional (unambiguous) or ambiguous. After a variable time interval, a test stimulus (ambiguous motion) was presented, and observers reported whether the adaptation stimulus and the test stimulus moved in the same direction or opposite direction. During the adaptation–test intervals, either a blank display or a stationary stimulus (the final frame of the adaptation stimulus) was shown.

2.1. Methods

2.1.1. Observers

Ten observers participated in this experiment. One of them was the author (R.K.), but the others were naïve as to the purpose of the experiment. All observers had normal or corrected-to-normal visual acuity.

2.1.2. Apparatus

Stimuli were generated on a Macintosh computer running Matlab PsychToolbox (Brainard, 1997; Pelli, 1997) and presented on a 22-in. CRT monitor. The refresh rate of the display was 75 Hz and the resolution 1280×1024 pixels. Stimuli were viewed from a distance of 57 cm. We used a linearized color lookup table for gamma correction.

2.1.3. Stimuli

We presented either a directional motion stimulus or ambiguous apparent motion for a brief adaptation period and subsequently measured the bias on the percept for the test stimulus (Fig. 1). Both the adapting stimulus and the test stimulus had a constant duration (320 ms), but the interval between the offset of the adapting stimulus and the onset of the test (ISI) was varied between 480, 1000, 2000, 3000, 4000 and 5000 ms.

The stimuli consisted of a series of sine-wave luminance gratings with a contrast of 1 (Michelson contrast) and a spatial frequency of 1 cpd. The gratings were spatially enveloped by a 2-D Gaussian with a sigma of 4 degrees. The central part of the stimulus was replaced by a disk (2 degrees in radius) with the background luminance (46 cd/m^2). A fixation point (a white dot) was drawn at the center (see Fig. 1).

Motion stimuli were created by shifting the phase of the sine-wave grating. For the directional motion, the phase was shifted by 90 degrees every 40 ms. This resulted in either leftward or rightward horizontal movement depending on the direction of the phase shift. The direction was randomized across trials. The duration of the adapting stimulus was 320 ms (eight steps). For the ambiguous apparent motion (test stimulus), the phase shift was 180 degrees every 80 ms. The total stimulus duration was 320 ms (four steps). The speed of motion was 6.25 degrees/s for both types of stimuli.

2.1.4. Procedure

The observer's task was to judge whether the test stimulus moved in the same direction or in the opposite direction as compared to the adapting stimulus. On half of the trials, the last frame of the adapting stimulus remained on the display during the interval, and started moving as a test stimulus. On the other half, the interval was a blank display with just the fixation point.

There were 24 conditions in total; 2 (adapting stimulus types [directional or ambiguous]) × 2 (interval types [blank or stationary]) × 6 (ISIs). Each observer performed 40 trials per condition. The order of the conditions was randomized across trials.

2.2. Results and discussion

The results are shown in Fig. 2. The percentage of trials in which observers reported that the adaptation stimulus
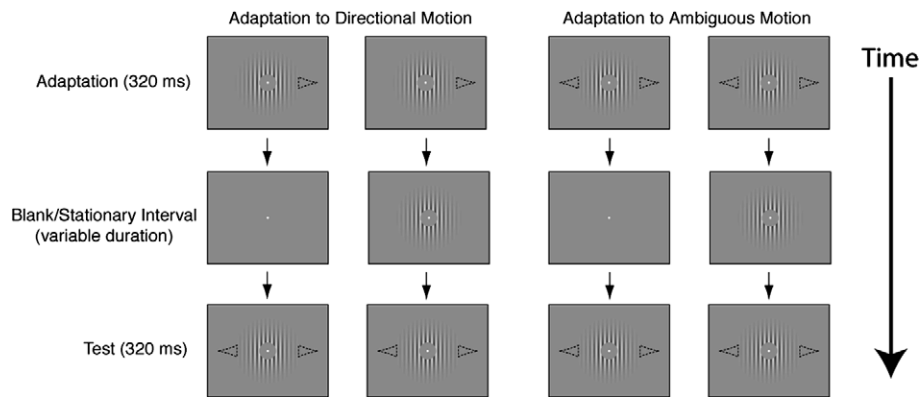
Fig. 1. Design of Experiment 1. There were four stimulus conditions in Experiment 1. Each is illustrated by one of the columns. (Top row) Adaptation stimulus was either directional (left two columns) or ambiguous motion (right two columns). The single dotted arrows indicate directional motion (defined by consecutive 90 degrees phase shifts). Here only rightward motion is shown as an example, but leftward motion was also used for adaptation on half of the trials. The bidirectional dotted arrows indicate ambiguous motion which could be perceived as moving to the right or to the left. (Middle row) Either a blank display or a stationary stimulus was continuously shown during the variable interval between the adaptation and test. (Bottom row) The test stimulus was always ambiguous motion.
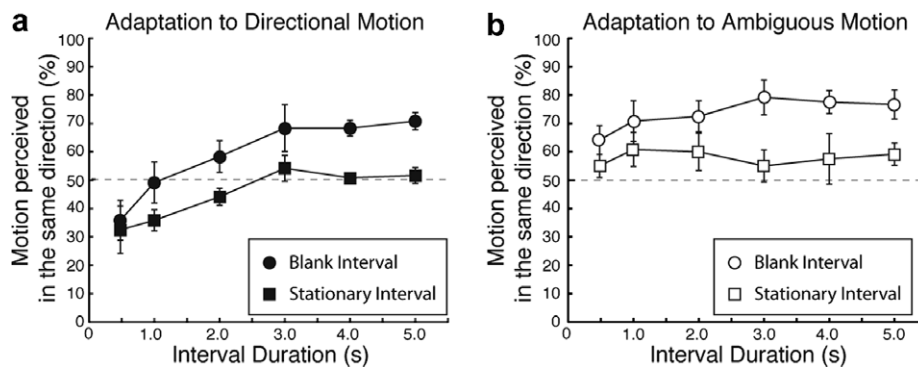

Fig. 2. Rapid adaptation to (a) directional stimuli and (b) ambiguous stimuli. The percentage of trials where the test stimulus was perceived in the same direction as the adapting stimulus is plotted as a function of the duration of the adaptation–test interval. (a) Results of adaptation to directional motion. The solid circles indicate the results for blank intervals, and the solid squares for stationary intervals. (b) Results for adaptation to ambiguous motion. The open circles indicate the results for blank intervals, and the open squares for stationary intervals. Error bars indicate one standard error of the mean (SEM) across observers ($n = 10$).

and test stimulus were perceived to move in the same direction is shown as a function of the interval between adaptation and test (ISI). The solid circles indicate the results of adaptation to directional motion followed by the blank intervals. In this condition, the exposure to directional motion produces the rapid motion aftereffect (rMAE; see, Kanai & Verstraten, 2005) for short ISIs (<1 s). For ISIs longer than 3 s, the percept is biased towards the same direction as the adaptation stimulus. This shows that both the rMAE and PS are induced by the same unambiguous stimulus. They manifest themselves at different ISIs (Fig. 2a), indicating a gradual transition from rMAE to PS over time.

On the other hand, adaptation to ambiguous motion did not produce a negative bias (<50%) for all ISIs tested. Instead, it primes the percept to the same direction. Again, the PS gradually developed with increasing the ISI (open circles in Fig. 2b), replicating the previous results (Kanai & Verstraten, 2005; Leopold et al., 2002). These results show that adaptation to both directional and ambiguous

motion produces the sensitization effect. In both cases, the effect steadily increased without decay at least up to 5 s, the longest ISI tested.

More relevant to the purpose of this experiment is to see whether the stationary stimulus during the interval affected the development of sensitization. Our results show that sensitization is disrupted when the period between the adaptation and test was filled with a stationary stimulus, instead of a blank. This was observed both for adaptation to directional motion (Fig. 2a, solid squares) and adaptation to ambiguous motion (Fig. 2b, open squares).

The stationary intervals seem to selectively disrupt the PS, but not the rMAE. As said, adaptation to directional motion causes both rMAE and PS. In the stationary-interval condition (Fig. 2a, solid squares), the PS seems to be completely abolished; no positive bias (>50%) was found for the tested ISI range. On the other hand, the rMAE was not disrupted by the stationary intervals. Rather, the duration of rMAE extended to 2 s by presenting a stationary stimulus during the interval. This apparent facilitation

of the rMAE is probably due to the fact that in the blank intervals, the PS, which starts developing even at short ISIs, effectively canceled out the rMAE at short ISIs.

The disruption of the PS by a stationary stimulus was also observed when the adaptation stimulus was ambiguous (Fig. 2b, open squares). Although the disruption was not complete (the mean over all ISIs is 57.9%, so slightly above 50%, one-tailed *t*-test, $P = 0.033$), the effect size was significantly reduced as compared to the blank-interval condition (one-tailed *t*-test, $P < 0.01$). The gradual increase observed for exposure to ambiguous motion with the blank interval (Spearman's rank-order correlation, Rs = 0.4173, $P < 0.01$) disappeared in the stationary-interval condition (Spearman's rank-order correlation, Rs = 0.0121, $P = 0.4715$). In sum, our results so far indicate that the development of the PS is disrupted by the presence of a stationary stimulus during the interval.

The disruption of the PS poses an apparent contradiction with previous studies showing the robustness of the effect. For example Maier et al. (2003) showed that the effect is not disrupted even when other types of bistable stimuli are interleaved between the blank periods. The discrepancy may arise from a difference in the nature of the stimuli presented during the intervals. Maier et al. inserted other ambiguous stimuli or the same type of stimuli but in 'orthogonal' directions, which could have resulted in independent effects. Our manipulation of displaying stationary stimuli seems to supply additional information to the visual system that the moving grating has halted. This could be used as a cue to recalibrate and remove the PS in the visual system. Another possibility is that while Maier et al. presented another stimulus only briefly during the intervals, our stationary stimuli were presented for the whole ISI period. The disruption of the PS may require that a stimulus be presented for a long time during the interval. In Experiments 2 and 3, we examine these two possibilities.

3. Experiment 2: Orthogonal stationary stimuli

Our primary interest now is whether the disruption is specific to a stationary stimulus which has the same pattern as the motion stimuli (i.e., vertical grating) or it can be induced by any stationary stimulus. The presentation of a stationary stimulus with the same orientation perceptually indicates that the moving grating has stopped. This could provide the cue, which disrupts the PS. On the other hand, presenting an orthogonal grating is more similar to the blank interval in that the moving grating disappears and reappears abruptly.

To examine whether the disruption is caused by the signals for (1) *the halt of motion* or (2) *the presence of a stationary stimulus*, we conducted the following two experiments. The first is the *orthogonal orientation* condition in which the stationary grating during the interval was orthogonal (i.e., a horizontal grating). The second is the *same orientation* condition in which the stationary grating had the same

orientation as the motion stimuli. This condition is needed for comparison and is essentially identical to Experiment 1.

A second purpose of this experiment is to replicate the results of Experiment 1 using a different task in which observers explicitly indicate the directions of the adaptation and test stimuli. In Experiment 1, the observers judged whether the first and the second stimuli moved in the same direction or in the opposite directions. This procedure does not allow observers to report ambiguous percept such as flicker or oscillatory motion. In order to ensure that the result observed in Experiment 1 is not restricted to this particular instruction, we now allow the observers to report the ambiguous percept as well.

3.1. Methods

3.1.1. Apparatus
The apparatus was identical to Experiment 1.

3.1.2. Observers
A total of 10 observers participated. Two observers were excluded from the analysis, because they reported ambiguous percept (flicker or oscillatory motion) on more than 80% of trials. The remaining eight observers participated in the same orientation experiment and/or the orthogonal orientation experiment. For each experiment the data were obtained from a total of six observers. Four out of the six participated in both experiments, and the remaining four observers participated in either of the two experiments. The order of the two experiments was counterbalanced for the four observers that participated in both experiments.

3.1.3. Stimuli
In both experiments, both directional and ambiguous motion was used as the adaptation stimulus, and they were mixed across trials. We used five different interval durations (1000, 2000, 3000, 4000, and 5000 ms) in both experiments. The details of the stimulus parameters are identical as described in Section 2.1.

3.1.4. Procedure
The task was to report the direction of the first and second (i.e., adaptor and test) stimuli after each trial. In addition to 'leftward' and 'rightward' reports, the observers were allowed to report the motion as 'ambiguous' when they perceived a flicker or oscillatory movement instead of unidirectional motion.

For each experiment (same and orthogonal orientation conditions), there were 20 conditions in total; 2 adapting stimulus types [directional or ambiguous] × 2 interval types [blank or stationary] × 5 (ISIs). Each observer performed 40 trials per condition. These conditions were randomized across trials.

3.1.5. Analysis
The trials in which observers reported an ambiguous percept either for the adaptation or the test stimulus were

excluded from the analysis. After excluding the two observers mentioned above, the percentage of the valid trials in which observers reported unambiguous percept (either leftward or rightwards for ambiguous stimuli) was 83.2% ± 7.9% (SEM) for the orthogonal condition, and 87.9% ± 4.1% (SEM) for the same condition. Only these conditions were used for the analysis. The percentage of valid trials did not differ between the two experiments (t-test, $P = 0.635$).

3.2. Results and discussion

The results are summarized in Fig. 3: the percentage of trials in which observers reported same direction for the adaptation and test stimulus as a function of the interval duration. Figs. 3a and b show the results of the same orientation condition. It shows that the results of Experiment 1 can be replicated for the task in which observers were allowed to report ambiguous percept as such, and therefore the robustness of the effects.

More germane to our primary aim is the orthogonal orientation condition. The results shown in Figs. 3c and d indicate that the orthogonal stationary grating also disrupts the development of the PS. This means that the disruption is not specific to the percept of the halt of the adapting stimulus, but that the presence of a stationary pattern *as such* is critical for the disruption.

4. Experiment 3: The disruption depends on the duration of stationary stimuli

As discussed, the presentation of a brief stimulus alone is usually not sufficient to disrupt the stabilization of bistable percept (Maier et al., 2003). The difference of our stimulus conditions from Maier et al.'s is that the stationary stimulus we presented during the interval was present throughout. Thus, the disruption of the stabilization may require that the stationary stimulus be viewed for a sufficiently long time. If so, the disruption should become gradually effective with increasing presentation duration. In this experiment, we will directly address this possibility by varying the presentation duration of the stationary stimulus.

4.1. Methods

4.1.1. Apparatus
The apparatus was identical as Experiments 1 and 2.

4.1.2. Observers
Six observers participated in this experiment. One of them was the author (R.K.), but the others were naïve as to the purpose of the experiment.

4.1.3. Stimuli
The interval duration was fixed at 4000 ms, because this duration produces a strong PS. Only the directional
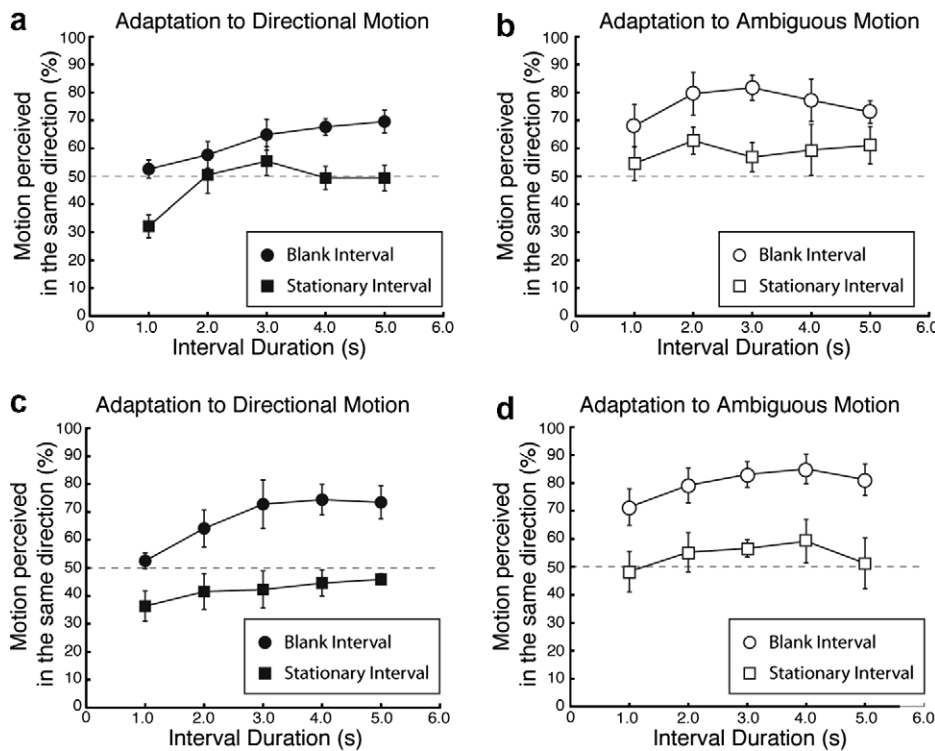

Fig. 3. Results of Experiment 2: (a and b) stationary stimulus with the same orientation. (a) Results of adaptation to directional motion. (b) Results for adaptation to ambiguous stimuli. (c and d) Stationary stimulus with the orthogonal orientation. (c) Results of adaptation to directional motion. (d) Results for adaptation to ambiguous stimuli. Disks denote the results for blank intervals, and the squares for stationary intervals. Error bars indicate one SEM across observers ($n = 6$).
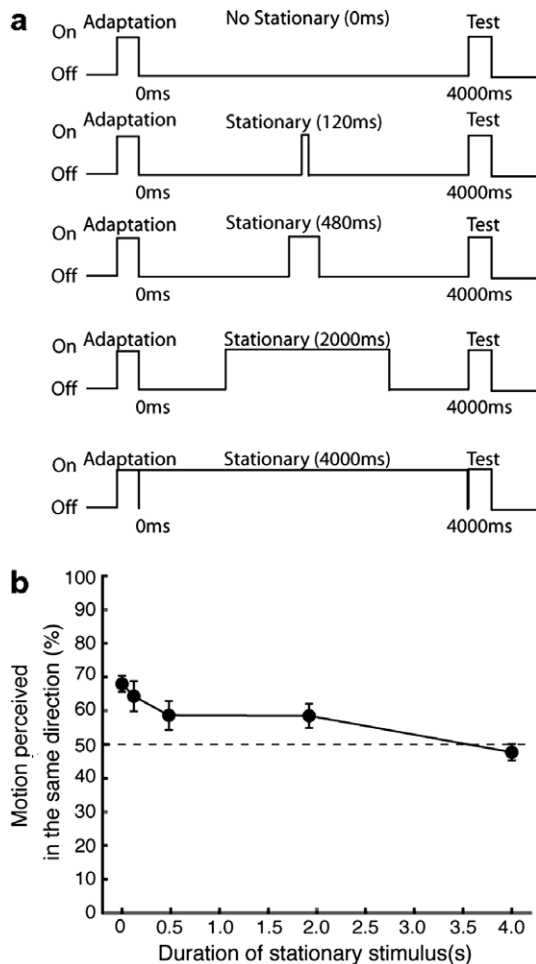
Fig. 4. Schematic representation of the time sequence of stimulus presentation and results of Experiment 3. (a) Five different presentation durations of the intervening stationary stimulus in Experiment 3 are diagrammed. The timing of the presentation was centered at the middle of the interval (2000 ms). (b) The percentage of trials in which the test stimulus was perceived in the same direction as the directional adaptation stimulus is plotted as a function of the presentation time of the stationary stimulus. Error bars indicate one SEM across observers ($n = 6$).

motion was used for adaptation, since our previous results show that directional motion induces the PS reliably with the 4000 ms interval. The reason why we used the directional motion is to avoid discarding many trials due to ambiguous percept for the adaptation stimulus. The stationary stimulus had the same orientation as the motion stimuli.

The duration of the stationary stimulus was varied between 0 ms (that is, no stationary stimulus), 120, 480, 2000, and 4000 ms (Fig. 4a). The timing of the presentation was centered at the 2000 ms after the offset of the adaptation stimulus. For example, for the presentation duration of 2000 ms, the stationary stimulus was presented from 1000 to 3000 ms from the offset of the adaptation stimulus. Except for these points, the details of the stimuli were identical to Experiments 1 and 2.

4.1.4. Procedure

The task was the same as in Experiment 2; the observers were asked to judge the direction of the first and second stimulus. They were allowed to report ambiguous percepts as such. The direction of the adaptation motion was randomly intermixed.

There were 10 conditions; 5 (ISIs) × 2 (directions for the adaptation stimulus [leftward or rightward]). Ten samples were made for each condition and the data for the two directions were merged so that 20 samples were made for each stationary duration per observer.

4.2. Results and discussion

The results are shown in Fig. 4b. The positive bias induced by the adaptation stimulus gradually decreased as the presentation time of the stationary stimulus increased (Spearman rank-order correlation, Rs = −0.658, $P < 0.01$). This implies that the disruption of the stabilization does require prolonged viewing of a stationary stimulus.

Although the disruption occurred gradually with increasing the presentation time of the stationary pattern, complete disruption was attained only when the stationary pattern was presented for the entire interval duration (4 s). One-tailed t-test performed for each presentation duration shows that the percentage of trials perceiving the same direction was significantly larger than 50% for the durations of 0, 120, 480 and 2000 ms (pair-wise t-test, $P < 0.05$), but it was not for the presentation time of 4000 ms.

In light of these results, we can now explain why the presentation of another object during the interval does not disrupt the stabilization. In order to obtain the disruption of the stabilization reliably, the interleaved stimulus needs to be presented for a long duration and the mere presentation of another stimulus is not sufficient. This suggests that the disruption is not an all-or-none phenomenon, but involves an active, continuous process.

5. Experiment 4: A case of binocular rivalry

So far, we have shown the disruption of perceptual sensitization for a particular type of bistable motion stimulus, namely, ambiguous apparent motion. However, it remains unclear whether our disruption method can be generalized to other types of multistable stimuli. In this experiment, we examine if presenting a neutral stimulus during the adapt–test interval can disrupt stabilization in binocular rivalry.

5.1. Methods

5.1.1. Apparatus
Observers viewed stimuli through a stereoscope.

5.1.2. Observers
Six observers participated in the experiment. Two of them were the authors (R.K. and T.K.) and the other observers were naïve as to the purpose of the experiment.

5.1.3. Stimuli

Stimuli and conditions are illustrated in Fig. 5a. The binocular rivalry stimulus consisted of a pair of orthogonal gratings (45 and 135) presented dichoptically within a white 1.6-by-1.6 square frame (70.1 cd/m^2). The gratings were half-rectified sine waves (35.0 cd/m^2) with a spatial frequency of 1.6 cycles per degree and were presented against a black background (0 cd/m^2). The contingency between the eye and orientation was counterbalanced across trials.

The rivalry stimuli were presented for 707 ms in the adaptation phase, and after a variable duration (107, 253, 507, 1000, 2000, 3000, 4000 or 5000 ms), the same stimuli were presented again for 800 ms. On half of trials, a plaid pattern (additive superposition of the two gratings) was presented to both eyes during the adapt–test interval. On the other half of trials, the interval was blank except that a red fixation cross was shown to indicate the continuation of the blank period.

5.1.4. Procedure

The task was to report whether the first and second stimuli has the same orientation or different orientations. There were a total of 16 conditions; 8 (ISIs) × 2 (presence or absence of an intervening stimulus). Sixteen samples were made for each condition, resulting in a total of 256 trials per session.

5.2. Results and discussion

The results are shown in Fig. 5b. Consistent with the previous experiments with ambiguous apparent motion, the probability of perceiving the same pattern increased with the interval duration. This was the case both for the blank-interval condition (Rs = 0.5671, $P < 0.001$) and the plaid interval condition (Rs = 0.5015, $P < 0.001$). However, stabilization was disrupted by the presentation of a plaid pattern. This observation was confirmed statistically: a repeated measures ANOVA revealed main effects of ISI duration ($F(7, 35) = 14.09$, $P < 0.001$) and the presence or

absence of the intervening plaid stimulus ($F(1, 35) = 10.14$, $P < 0.05$), but there was no interaction between the two factors ($F(7, 35) < 1$).

These results confirm that stabilization in binocular rivalry develops in a similar time course as in ambiguous apparent motion and that it can be attenuated by continuously presenting a neural stimulus during adapt–test intervals.

6. General discussion

We have shown that presenting a stationary intervening stimulus during the interval between adaptation and test disrupts perceptual stabilization/sensitization. Disruption was induced regardless of the orientation of the stationary stimulus, and becomes more effective as the presentation time of the stationary stimulus increased. These findings indicate that the suppression of stabilization was not specific to halt signals of the motion stimuli, but was dependent solely on the signals indicating the absence of motion. Moreover, we confirmed that the development of the perceptual sensitization is also disrupted in binocular rivalry by presenting a neutral stimulus, suggesting the possibility that our conclusions may be extended to other types of multistable stimuli.

In the report by Maier et al. (2003), the mere presence of an intervening stimulus was not sufficient to disrupt the stabilization of the bistable percept, whereas in our present report, more continuous, as opposed to brief, presentation of a neutral stimulus caused a reduction of the perceptual bias. Care must be taken regarding the differences between the two studies when compared. In Maier et al.'s study, bistable stimuli were intermittently presented for a prolonged period, whereas in the present study, unambiguous stimuli were interleaved as the adapting stimuli on half of the trials. The difference in the experimental design could potentially be important. One reason for the precaution comes from our preliminary observation. We noticed that stabilization was much more persistent when only ambigu-
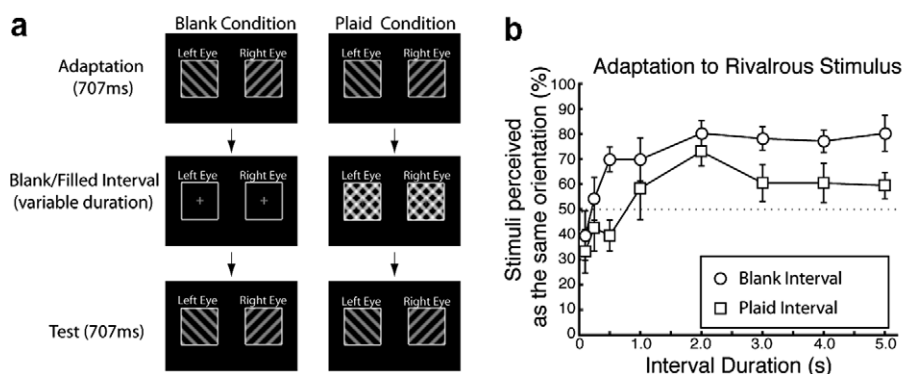

Fig. 5. Design and results of Experiment 4. (a) Two main conditions are illustrated. After brief adaptation to binocular rivalry gratings, the gratings were replaced by a blank (the left column) or a plaid pattern (the right column) for a variable duration, and then the original rivalry gratings were displayed again to test the strength of perceptual memory from the first presentation. (b) The percentage of trials in which the test stimulus was perceived as the same orientation as the adapting stimulus is plotted as a function of the adapt–test interval. The open circles indicate the data from the blank interval condition and the open squares the data from the plaid interval condition. Error bars indicate one SEM across observers (n = 6).

ous motion was used as the adapting stimulus. The presentation of unambiguous stimuli as the adapting stimulus on half of the trials may have contributed to the reduction of stabilization.

At a superficial level, our present results are reminiscent of the storage effect known in motion aftereffect (MAE), where MAE does not decay substantially while viewing a blank screen (Spigel, 1960; van de Grind, van der Smagt, & Verstraten, 2004; Wohlgemuth, 1911). Both in MAE and in sensitization, the effects are maintained while viewing a blank screen, and manifest themselves on test patterns. However, one must be careful to make a direct connection between the two phenomena. First, MAE and sensitization have opposite effects. Second, MAE typically requires a longer adaptation, while sensitization arises from a brief exposure to a stimulus. Third, MAE is strongest immediately after adaptation, while sensitization appears to develop over a few seconds. While these qualitative differences suggest that the MAE storage and sensitization are mediated by distinct mechanisms, both effects seem to be involved in dynamic calibration of the motion system depending on incoming signals. The storage of MAE has been discussed in the context of calibration previously (van de Grind et al., 2004). The nullification of sensitization while viewing a stationary stimulus may be regarded as a similar calibration mechanism for the visual system.

Could the reduction of sensitization be due to perceived motion during a stationary interval? If one perceived a MAE while viewing the stationary stimulus, that percept might create a bias opposite to the adapting stimulus. Since we have not directly tested the possibility of perceiving motion during the stationary intervals, we cannot completely exclude this possibility. However, the parallel results in the binocular rivalry experiment, which does not have the issue of perceived motion during the plaid blanks, give us some support that potential percept of motion is not the only reason for canceling sensitization.

In experiments with binocular rivalry, Pearson and Clifford (2005) argued that unambiguous stimuli produce aftereffects, whereas ambiguous stimuli produce priming. Although our present study mainly used a different type of bistable stimuli (i.e., ambiguous motion), our results suggest that the difference between ambiguous and unambiguous primes may not be qualitative, but could be a quantitative difference in the temporal pattern of the priming effect following an exposure to ambiguous and unambiguous stimuli. Our results of Experiment 1 and Experiment 4 indicate that adaptation to unambiguous motion leads to both aftereffect and priming depending on the adaptation–test interval. With short ISIs, unambiguous motion indeed produces an aftereffect, but later the effect of adaptation switches to priming. A number of studies in the past consistently revealed that a brief exposure produces a priming effect, whereas prolonged viewing of the same stimulus produces an opposite effect (Huber & O'Reilly, 2003; Kanai & Verstraten, 2005; Long, Toppino, & Mondin, 1992; Pinkus & Pantle, 1997). In the study by

Pearson and Clifford, the blank interval was relatively short (1 s), where a predominant negative bias is expected to occur after adapting to an unambiguous prime. Thus, it is plausible that an unambiguous prime turns to a positive bias with a longer inter-stimulus interval. Parsimoniously, this would obviate the need to assert the existence of two categorically distinct priming or adapting mechanisms depending on the ambiguousness of the priming stimulus.

We found that sensitization is hardly disrupted by flashing a stationary stimulus. This contrasts with the finding that presenting a visual transient during the observation of a multistable stimulus triggers a perceptual alternation by resetting the internal states sustaining the current percept (Kanai & Kamitani, 2003; Kanai, Moradi, Shimojo, & Verstraten, 2005; Wilke, Logothetis, & Leopold, 2003). This disparity suggests that sensitization involves a mechanism that is distinct from the sustention of a percept during continuous observation (Carter & Cavanagh, 2007). Instead, the absence of disruption by brief stimuli during the blank period is consistent with a previous finding that stabilization is maintained for multiple stimuli when each of the ambiguous stimuli was only briefly presented.

Visual perception is inherently an inference process, as the peripheral visual information inevitably contains ambiguity. In order for the visual system to resolve the ambiguity and reach a probable interpretation, the system ought to make certain assumptions as to the structure of the environment. In this view, perceptual bias created by past percepts may be regarded as calibration of the implicit assumption for resolving ambiguity. In the context of our experiments, when we have perceived a motion stimulus in one direction in the recent past, this experience changes the implicit assumption of motion perception towards that direction, resulting in a positive bias. On the other hand, perception of a neutral stimulus (stationary stimuli for apparent motion or a plaid for binocular rivalry) sets the visual system to reduce the internal bias. This production and cancellation of internal bias may serve an important function in achieving an optimal internal bias for resolving ambiguity.

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