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Vision Research 45 (2005) 3109–3116
Vision Research
www.elsevier.com/locate/visres

Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization

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Received 26 October 2004; received in revised form 1 April 2005

Abstract

Visual neurons show fast adaptive behavior in response to brief visual input. However, the perceptual consequences of this rapid neural adaptation are less known. Here, we show that brief exposure to a moving adaptation stimulus—ranging from tens to hundreds of milliseconds—influences the perception of a subsequently presented ambiguous motion test stimulus. Whether the ambiguous motion is perceived to move in the same direction (priming), or in the opposite direction (rapid motion aftereffect) varies systematically with the duration of the adaptation stimulus and the adaptation-test blank interval. These biases appear and decay rapidly. Moreover, when the adapting stimulus is itself ambiguous, these effects are not produced. Instead, the percept for the subsequent test stimulus is biased to the perceived direction of the adaptation stimulus. This effect (perceptual sensitization) builds gradually over the time between the adaptation and test stimuli. Our results indicate that rapid adaptation plays a role mainly within early motion processing, whereas a slow potentiation controls the sensitivity at a later stage.

Keywords: Motion; Adaptation; Plasticity; Bistable; Aftereffect

1. Introduction

After viewing a moving pattern continuously, we perceive a subsequently presented stationary pattern as moving in the opposite direction. This phenomenon—known as the motion aftereffect (MAE)—has been widely studied to gain insights into adaptation characteristics of motion-sensitive neurons in the visual system (see Anstis, Verstraten, & Mather, 1998 for an overview). Typically, the MAE is induced by using adaptation durations that last several to tens of seconds. Neurons showing similar time courses have been considered as the neuronal substrates underlying the MAE (Barlow & Hill, 1963; Hammond, Mouat, & Smith, 1988a, Hammond, Mouat, & Smith, 1988b; Kohn & Movshon, 2003).

In contrast to the relatively slow dynamics of adaptation resulting in the MAE, much faster forms of adaptation—on the order of a few hundreds of milliseconds—have been reported in electrophysiological studies. For example, when the same stimulus is presented twice in close temporal succession, the neural response to the second presentation is considerably reduced (Nelson, 1991; Chance, Nelson, & Abbott, 1998; Finlayson & Cynader, 1995; Stratford, Tarczy-Hornuch, Martin, Bannister, & Jack, 1996). This pattern is also observed in area MT (Lisberger & Movshon, 1999; Priebe, Churchland, & Lisberger, 2002), which is apparently closely linked to the subjective experience of visual movement (Newsome, Britten, & Movshon, 1989; Zeki, Watson, & Frackowiak, 1993; Logothetis & Schall, 1989; Bradley, Chang, & Andersen, 1998).

Moreover, neuronal plasticity exists not only in depressive forms—leading to a decrease in responsiveness—but also shows potentiation in response to brief

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0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.05.014

stimulation. Prior stimulation of a neuron increases its responsiveness to a subsequent stimulation (e.g., Castro-Alamancos & Connors, 1996; Hempel, Hartman, Wang, Turrigiano, & Nelson, 2000). The presence of these two opposite adaptive mechanisms implies that they play distinct functional roles in the nervous system. However, given the diversity of the forms of plasticity and the complexity of their induction conditions, it is difficult to infer how these different types of plasticity orchestrate the perceptual outcome. Although depth of adaptation and MAE duration are closely related (e.g., Verstraten, Fredericksen, Grüsser, & van de Grind, 1994), no firm relationship has been drawn between these fast patterns of neurophysiological plasticity and patterns of psychophysical behavior.

In psychophysics, studies using brief stimulus presentations have produced two opposite effects: aftereffects and priming. A few studies have shown that a brief presentation of a stimulus results in a suppressive effect in the perception of subsequently presented stimuli (e.g., Sekuler & Littlejohn, 1974; Raymond & Isaak, 1998). On the other hand, many other studies use brief presentations to produce priming effects—a facilitatory effect on the perception of a subsequently presented stimulus. In the motion domain, briefly presenting unidirectional motion facilitates the percept of that direction for the next presentation (Pinkus & Pantle, 1997; Raymond, O'Donnell, & Tipper, 1998). It is puzzling that, while the general procedures to induce aftereffects and priming in these studies are almost identical, they result in opposite effects in terms of perceived direction. This apparent conflict needs to be resolved, but methodological differences between the studies make direct comparison of the results difficult.

In the present study, we systematically vary the timing between a particular pair of adaptation and test stimuli. This way, we attempt to find out which conditions lead to negative aftereffects, and which lead to priming. Furthermore, we deduce the location of the effects in the processing hierarchy by comparing the results with those obtained from adaptation to an ambiguous stimulus. These time courses and locations are then related to the known neurophysiological dynamics and anatomy.

Our results show that there are at least three types of psychophysical adaptations.

- The first is known as visual motion priming (or VMP) as reported by Pinkus and Pantle (1997). They showed that an extremely brief exposure (80 ms) to energy-based motion causes a strong bias toward the same direction.
- The second is a very rapid form of MAE (rMAE), in which slightly longer adaptation (e.g., 320 ms) produces a strong bias toward the opposite direction.
- The third is what we call perceptual sensitization (PS), in which an ambiguous stimulus lacking energy based motion causes subsequent percepts to follow the direction of the preceding percept.

The VMP and the rMAE occur almost immediately after exposure to the adaptation stimulus and decline quickly over a second. PS, on the other hand, develops gradually over the course of a few seconds. The distinct time courses of these effects suggest the involvement of different types of neural plasticity at different processing levels.

2. Experiment 1: Adaptation to brief directional motion

We presented an adaptation stimulus consisting of unidirectional motion, and measured its effect on the percept of the subsequently presented directionally ambiguous test stimulus. By varying both the duration of the adaptation stimulus as well as the blank interval between the adaptation and test stimulus, we characterize the temporal dynamics of aftereffect and priming.

3. Methods

3.1. Apparatus and observers

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.

Ten observers including one of the authors (RK) participated in this experiment. Other observers were naïve as to the purpose of the experiment. All observers had normal or corrected-to-normal visual acuity.

3.2. Stimuli and procedure

The stimuli were sine-wave luminance gratings with a contrast of 0.5 (Michelson contrast) and a spatial frequency of 1 cpd. The gratings were spatially enveloped by a 2-D Gaussian with a sigma of 4°. To aid fixation, the central part of the stimuli was replaced by a disk (2° in radius) with the same luminance of the background, and a white fixation point was drawn in the center of the display.

Both the directional and ambiguous stimuli were created by shifting the phase of the sine-wave stimulus. To create the directional stimuli, the phase was shifted by ±90° every 40 ms. The direction of motion was horizontal either to the right or to the left. Ambiguous stimuli were created by shifting the phase 180° every 80 ms (Fig. 1A). This way, the speed of the test stimulus matched that of the adaptation stimulus (6.25 deg/s).

The direction of the adaptation stimulus was randomized across trials. We varied the adaptation duration between 80, 160, 320, and 640 ms, which corresponded to 2, 4, 8, and 16 frames, respectively. After a variable ISI (40, 120, 480, 1000, and 2000 ms), during which the display was blank, the test stimulus was always presented for 320 ms.

The task was to indicate whether the test stimulus was moving in the same direction or in the opposite direction as compared to the adaptation stimulus. There were a total of 20 conditions; 4 (adaptation durations) × 5 (ISIs). Forty trials were performed for each condition, and the order of conditions was randomized.

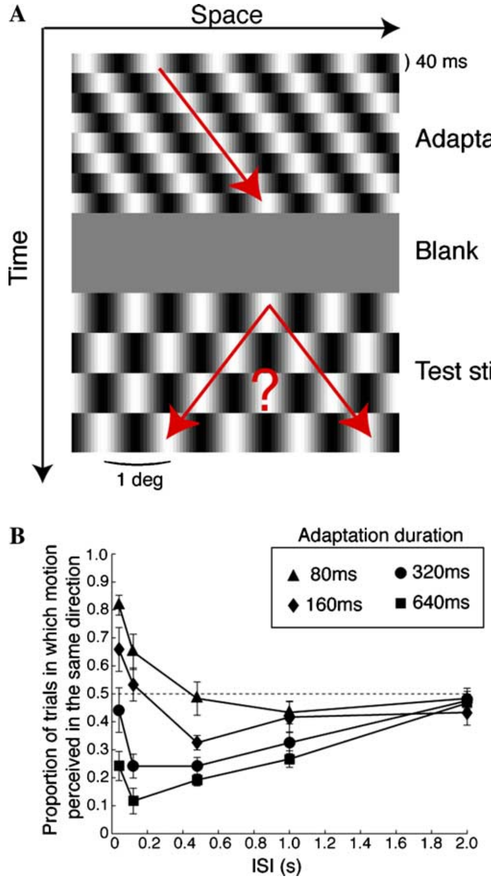

Fig. 1. (A) Illustration of the stimuli. The adaptation stimulus was directional apparent motion created by 90° phase shifts. Here, an example of 320 ms adaptation is shown. After the adaptation, a blank image was presented for 40, 120, 480, 1000, or 2000 ms. This was followed by ambiguous motion made of 180° phase shifts. The duration of the test stimulus was constant (80 ms × 4 frames = 320 ms). Both for the adaptation stimulus and the test stimulus, the luminance contrast was 0.5 (Michaelson contrast). (B) Results from experiment 1 ($n = 10$). For each adaptation duration, the proportion of trials in which observers perceived the test stimulus as moving in the same direction as the adaptation stimulus is shown as a function of blank duration. The results are shown for four adaptation durations; 80 ms (solid triangle), 160 ms (solid diamond), 320 ms (solid circle), and 640 ms (solid square). Error bars indicate one s.e.m.

4. Results

The results are shown in Fig. 1B. For each adaptation duration, the percentage of trials in which the test stimulus was perceived to move in the *same* direction is shown as a function of the adaptation-test ISI. With the shortest adaptation duration (80 ms, solid triangle), there was a strong perceptual bias for perceiving the ambiguous motion in the same direction as the adaptation stimulus. This effect—known as visual motion priming (or VMP)—decayed rapidly as a function of the ISI. This is quantitatively consistent with the earlier reports by Pinkus and Pantle (1997).

As the adaptation duration increased, the VMP vanished and was replaced with an opposite effect. That is to say, after adapting to directional movement for a slightly longer duration, the test stimulus tended to be perceived as moving in the opposite direction. Although the effect resembles the classical MAE, we call it rapid MAE (rMAE) for two reasons. First, given the temporal characteristics, we do not know whether the rMAE results from the same neural adaptation responsible for the classical MAE. Second and more importantly, the classic MAE exhibits "storage", in that it survives even after extended viewing a blank display after adaptation (Spigel, 1960; but see also, van de Grind, van der Smagt, & Verstraten, 2004) whereas the rMAE does not. It has decayed completely after a blank of 2–3 s. These observations suggest that a different type of neural plasticity may underlie the rMAE.

Our results demonstrate that the contradictory effects, namely the VMP and (r)MAE can arise from the same stimulus and task, and the effect flips depending on small differences in adaptation duration and ISI. Both effects recovered to the baseline level (indicated by the dashed line in Fig. 1B) quickly, but with different rates. The VMP vanished within one second, whereas the rMAE recovered more gradually over 2–3 s.

5. Experiment 2: Brief adaptation to ambiguous motion

Where does the rMAE take place in the hierarchy of visual motion processing stages? In functional terms, at least two stages can be distinguished. The early stage involves the detection of local motion energy inherent in the stimulus. In other words, the activation is stimulus-driven in the early stage. On the other hand, the late stage is related to perceptual decision-making based on the integration of the local motion signals. A counterphase grating, for example, activates motion detectors for opposite directions simultaneously at the early stage.

However, only one of the two directions is usually perceived. This perceived direction is determined and represented in the later stage (Williams, Elfar, Eskandar, Toth, & Assad, 2003).

Does the rMAE take place at the early stage or the late stage? To answer this question, we used directionally ambiguous motion as an adaptation stimulus. The rationale behind using ambiguous motion is to bypass the directional biases induced by adaptation in the early stage. Since the local motion energy of ambiguous motion is balanced between the two opponent directions, exposure to ambiguous motion will not cause a directional bias at the early stage. This allows us to extract effects specific to the late stage. If rMAE occurs in the late stage without involving the early stage, the rMAE should be observed even when the adaptation does not contain a bias in motion energy. If rMAE is specific to the early stage and absent in the late stage, no rMAE will be observed.

6. Methods

6.1. Apparatus and observers

The same experimental setup was used for this experiment. Eight observers including one of the authors (RK) participated. All observers had normal or corrected-to-normal visual acuity.

6.2. Stimuli and procedure

Stimuli were the same sine-wave gratings as in experiment 1. Here, the difference is that on half the trials, the adaptation stimulus was ambiguous motion instead of directional motion. For both the ambiguous and directional adaptation stimuli, the duration was 320 ms. Again, we varied the blank duration between the adaptation and the test (40, 120, 480, 1000 and 2000 ms). Thus, half of the trials with a directional motion replicate the 320 ms adaptation condition of experiment 1, and the other half are equivalent conditions but with ambiguous motion.

The task was the same as for experiment 1. Observers were asked to indicate whether the test stimulus was moving in the same direction or in the opposite direction with respect to the direction of the adaptation stimulus. There were a total of 10 conditions; 2 (ambiguous adaptation and directional adaptation) X 5 (ISIs). Forty trials were performed for each condition, and the order of conditions was randomized across trials.

7. Results

The results are shown in Fig. 2. For each type of adaptation stimulus (ambiguous vs. directional), the percentage of trials, in which the test stimulus were perceived to move in the same direction is shown as a function of the blank duration. The rMAE was observed when the adaptation stimulus was directional: the subsequent percept was biased in the opposite direction, corroborating the results of the previous experiment. On the other hand, adaptation to ambiguous motion did not lead to negative bias (or the rMAE). This implies that the rMAE is primarily mediated by the early motion processing stages.

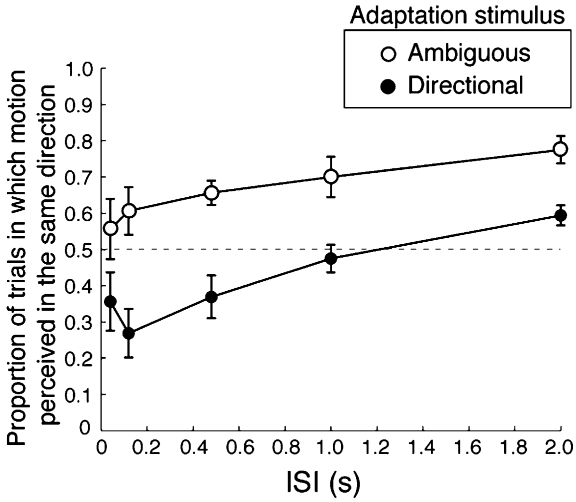

Fig. 2. Results of experiment 2 ($n = 8$). For each of the two types of adaptation stimuli, the proportion of trials in which the test was perceived to move in the same direction as the adaptation stimulus is plotted as a function of the adaptation-test ISI. Solid circles show the data from the conditions in which the adaptation stimulus was directional (unambiguous), replicating the results of experiment 1 (i.e., Fig. 1B, solid circles). Open circles indicate the data from the conditions in which adaptation stimulus was ambiguous. Error bars indicate one s.e.m.

The ambiguous motion produced a positive bias, in which the percept of the same direction as the previously perceived direction is facilitated (*t* test on the pooled data across all ISIs, $P < 0.001$). In other words, a brief exposure to ambiguous motion caused a facilitation effect similar to priming. This means that the responsiveness of the neuronal substrates seems to be enhanced when they are perceived. This plasticity gradually develops over the few seconds that follow the adaptation stimulus (Spearman rank-order correlation $R_s = 0.29$, $P < 0.05$). This slow time course distinguishes itself from the VMP which decays quickly, and shows that a different kind of plasticity exists at a later stage.

8. Experiment 3: Long intervals

In the previous experiment, perception of one motion direction produces a positive bias on the perception of a subsequent ambiguous motion—the effect we refer to as perceptual sensitization (PS). We did not obtain the positive bias from adaptation to directional motion. However, directional motion also induces a subjectively very similar percept of movement. Thus, if the PS is induced by the percept of directional movement, unambiguous motion should also produce the PS. The failure to find the PS with adaptation to directional motion can be attributed to the dominance of the simultaneously induced rMAE. Since the PS grows gradually over a few seconds, and the rMAE seems to decline more rapidly, we expect that with longer blank durations we can isolate the PS component from the rMAE. Based on these lines of reasoning, we conducted the same experiment as Section 5, but including longer ISIs up to 5 s.

9. Methods

9.1. Apparatus and observers

The same experimental setup was used for this experiment. Six observers including one of the authors (RK) participated. All observers had normal or corrected-to-normal visual acuity.

9.2. Stimuli and procedure

Stimuli and procedure were identical as Section 5. In addition to the ISIs used in experiment 2 (40, 120, 480, 1000, and 2000 ms), we added the ISIs of 3000, 4000, and 5000 ms. Both directional motion and ambiguous motion were used as adaptation stimulus (320 ms).

There were a total of 16 conditions; 2 (ambiguous adaptation and directional adaptation) × 8 (ISIs). Forty trials were performed for each condition, and the order of conditions was randomized across trials.

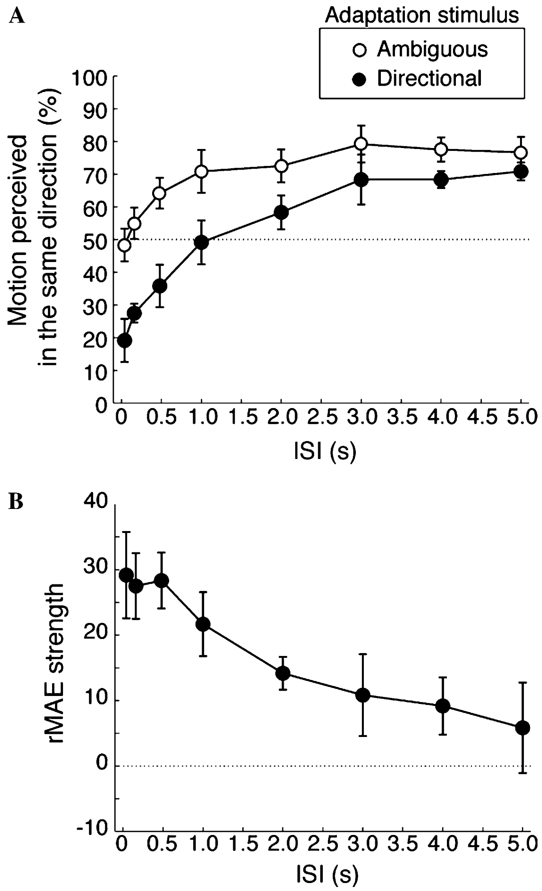

Fig. 3. Results of experiment 3 ($n = 6$). (A) For each of the two types of adaptation stimuli, the proportion of trials in which the test was perceived to move in the same direction as the adaptation stimulus is plotted as a function of the adaptation-test ISI. Solid circles show the data from the conditions in which the adaptation stimulus was directional (unambiguous). Open circles indicate the data from the conditions in which adaptation stimulus was ambiguous. Error bars indicate one s.e.m. (B) The strength of rMAE after subtraction of the PS. Subtraction was performed for individual data and then averaged across the observers. Error bars indicate one s.e.m.

10. Results

The results are shown in Fig. 3A. Consistent with experiment 2, adaptation to ambiguous motion induced a positive bias throughout the ISIs. The PS gradually developed with increasing the ISI (Spearman rank-order correlation $R_s = 0.602$, $P < 0.001$) without showing any decline even with the long ISIs.

Exposure to directional motion produced a negative bias (or rMAE) for short ISIs. However, increasing the ISI (> 3 s) resulted in a positive bias, i.e., the percept for the same direction was promoted. The percept of the same direction steadily increased as the ISI increased (Spearman rank-order correlation $R_s = 0.804$, $P < 0.001$). This shows that both the rMAE and PS are induced by the same stimulus (i.e., directional motion), but they manifest themselves at different times.

The coexistence of the rMAE and PS suggests that the apparently fast recovery of the rMAE (in Sections 2 and 5) can actually be slower, because the weak rMAE after a long ISI must be counteracted by the PS. Fig. 3A shows the difference between the data for adaptation to ambiguous motion and the data for adaptation to directional motion. This provides us a rough idea about the time course of the rMAE alone (the underlying assumption is that both directional motion and ambiguous motion induced equally strong PS). The subtraction shows that the rMAE component gradually decayed with increasing the ISI, and the time constant for the rMAE to decay to 50% of the initial maximum strength is about 2 s. Indeed, the best fit of exponential decay function was obtained when the time constant was 2007 ms and the maximum amplitude 32.58.

11. General discussion

In summary, we have shown that three distinct types of adaptation can be induced in response to a brief stimulus; (1) visual motion priming (VMP), (2) rapid MAE (rMAE), and (3). perceptual sensitization (PS). These effects are characterized by the time course and effect on the perceived direction.

Section 2 shows that a brief stimulus presentation works as a prime despite its similarity to a typical adaptation paradigm used for the MAE. In fact, our results show that the VMP and (r)MAE occur in the same stimulus configuration, producing opposite effects due to a slight change in adaptation duration. If adaptation is very brief ($80 \sim 160$ ms), VMP is produced. With longer durations, the rMAE becomes dominant. Both the VMP and the rMAE are absent with adaptation to energy-balanced motion, suggesting these two effects result from early motion processing (Section 5).

The classical MAE has been attributed to adaptation of direction-selective neurons with a time constant of several seconds (see Verstraten et al., 1994; Wade & Verstraten, 2005, for an overview). However, the rMAE is induced by very brief adaptation duration. Given the speed of adaptation, the rMAE seems to involve neural substrates with distinct rapid plasticity, which cannot be directly studied using the classical MAE.

Our experiments show that this rapid plasticity takes place primarily in the early motion processing stage responsible for motion energy detection. However, in the later stage of perceptual processing the rMAE seems to be absent or present, but so weak that it is concealed by the PS. The earlier and later stages are usually considered to correspond to the primary visual cortex (or V1) and medial temporal area (or MT/V5), respectively. These neuro-anatomical correspondences suggest that the rapid depression responsible for the rMAE probably takes place at the level of V1, and possibly even earlier at the synapses from LGN to V1 (see, Carandini, Heeger, & Senn, 2002; Chung, Li, & Nelson, 2002; Chance et al., 1998).

The later stage shows, instead, a gradual development of potentiation, and no decay at least up to 5 s. This slow time course implies the involvement of a different type of neural plasticity. Related to this phenomenon is the perceptual stabilization of intermittently presented multistable stimuli. Normally, when a multistable stimulus is continuously presented, observers experience incessant spontaneous alternations between the possible percepts. However, if the stimulus is presented only intermittently with blank intervals of 3–5 s, the percept for that stimulus is stabilized for a long duration (Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Chen & He, 2004; see also Ramachandran & Anstis, 1985). The sensitization we report here may fundamentally be the same phenomenon. The time course of the perceptual sensitization in which the facilitation gradually increases with longer blank durations may provide the basis for the perceptual stabilization and account for the necessity of the 3–5 s blank intervals. In the case of stabilization, each presentation of a stimulus serves as the adaptation stimulus for inducing the sensitization for one percept. Then, during the extended blank interval, the sensitization develops sufficiently strong to consistently bias the subsequent percept to the same interpretation. Then, the percept of the new stimulus works as another adaptation stimulus for causing the bias in the same direction, and so on.

In the classical MAE, two types of MAEs—static and dynamic–have been used to illuminate the two distinctive motion processing stages (Culham, Verstraten, Ashida, & Cavanah, 2000; Nishida & Ashida, 2000; Verstraten, van der Smagt, Fredericksen, & van de Grind, 1999). The static MAE is obtained after an observer views a motion stimulus with directional energy. It is observed regardless of whether the test stimulus is static or dynamic. However, when the adapting stimulus is energy-balanced (or bistable), the MAE is observed only with dynamic test stimuli. These two types of MAEs show the independent motion processing stages.

The motivation behind Section 5 and Section 8 is analogous to these studies. However, the results obtained from brief exposures to motion stimuli are qualitatively different from those using extended adaptation. First, the rMAE was observed only with a dynamic pattern as a test. When adaptation is extremely brief as in our rMAE, static test patterns did not produce any measurable MAE, even when the adapting stimulus contained directional motion energy (Section 2). This contrasts with the classical static MAE where MAE from directional motion can be observed both with static and dynamic test patterns. One possible reason for this is that the adaptation resulting in an rMAE is not as strong as the classical MAE due to the brief adaptation and can be revealed only by a dynamic test, which is generally considered to be more sensitive. Second, our brief presentation of energy-balanced motion did not produce any MAE analogous to the dynamic MAE. Instead, we found the perceptual sensitization, an opposite effect. These differences imply differences in the underlying neural mechanisms mediating various types of perceptual adaptations.

The PS showed a gradual development over the blank interval. In fact, this steady increase can be interpreted in two ways. One interpretation is that the plasticity responsible for the PS itself increases gradually. Alternatively, the PS is established just after the adaptation stimulus, but is effectively cancelled by another short-lasting negative bias (or an aftereffect) driven by perception. Our present experiments cannot clearly distinguish between these two possibilities. Further study is needed to elucidate the time courses of possibly multiple types of plasticity underlying the slowly increasing PS.

Finally, the present results show the perceptual manifestations of fast neuronal plasticity and for the first time relates them to fast adaptation characteristics, previously reported in electrophysiological studies (Nelson, 1991; Stratford et al., 1996; Lisberger & Movshon, 1999). They indicate that at least two opponent sensory adaptations coexist at different levels of visual motion processing; fast rapid depression at the early motion detection stage, and slow gradual potentiation at the perceptual stage. These two types of rapid plasticity may play a functional role in visual perception. For example, the early rapid depression would be useful for gain control at the input level (Abbott, Varela, Sen, & Nelson, 1997) as well as for detecting a temporal contrast (Kanai & Verstraten, 2004). On the other hand, the late gradual potentiation may help us to maintain perceptual continuity across disruptions by other objects or saccades, and also serves as a foundation for rapid perceptual learning (Hawkey, Amitay, & Moore, 2004) by enhancing the sensitivity to perceptually confirmed interpretations.

Acknowledgments

We thank Chris Paffen and Daw-An Wu for discussion and comments on earlier versions of the manuscript.

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