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Cross-fixation transfer of motion aftereffects with expansion motion

Xin Meng [a,1], Pietro Mazzoni [b], Ning Qian [a,*]

[a] *Center for Neurobiology and Behavior, Department of Physiology and Cellular Biophysics, Columbia University, New York, NY 10032, USA*
[b] *Motor Performance Laboratory, Department of Neurology, Columbia University, New York, NY 10032, USA*

Abstract

It has been shown that motion aftereffect (MAE) not only is present at the adapted location but also partially transfers to nearby non-adapted locations. However, it is not clear whether MAE transfers across the fixation point. Since cells in area MSTd have receptive fields that cover both sides of the fixation point and since many MSTd cells, but not cells in earlier visual areas, prefer complex motion patterns such as expansion, we tested cross-fixation transfer of MAE induced by expanding random-dots stimuli. We also used rightward translational motion for comparison. Subjects adapted to motion patterns on a fixed side of the fixation point. Dynamic MAE was then measured with a nulling procedure at both the adapted site and the mirror site across the fixation point. Subjects' eye fixation during stimulus presentation was monitored with an infrared eye tracker. At the adapted site, both the expansion and the translation patterns generated strong MAEs, as expected. However, only the expansion pattern, but not translation pattern, generated significant MAE at the mirror site. This remained true even after we adjusted stimulus parameters to equate the strengths of the expansion MAE and translation MAE at the adapted site. We conclude that there is cross-fixation transfer of MAE for expansion motion but not for translational motion.

1. Introduction

After prolonged viewing of motion in a given direction, a static pattern or a dynamic noise pattern appears to move in the opposite direction. This is the well-known motion aftereffect (MAE) or waterfall illusion (Mather, Verstraten, & Anstis, 1998). MAE has been explained as an imbalance of neural activities tuned to different directions (Barlow & Hill, 1963; Sutherland, 1961). Specifically, before motion adaptation, cells tuned to different directions produce roughly equal responses. During exposure to a particular direction of motion, neurons tuned to that direction will fire maximally and adapt, and their response to subsequent

stimuli will be reduced for a certain period of time after the exposure (Kohn & Movshon, 2003; Petersen, Baker, & Allman, 1985; Van Wezel & Britten, 2002). Consequently, a test pattern without net motion elicits more response in the opposite direction than the adapted direction, and thus the illusion.

MAE is strongest at the location where the adapting motion stimulus was presented, but it also transfers partially to adjacent, non-adapted regions (Bex, Metha, & Makous, 1999; Bonnet & Pouthas, 1972; Price, Greenwood, & Ibbotson, 2004; Snowden & Milne, 1997; Weisstein, Maguire, & Berbaum, 1977). In the literature, MAE at the adapted site is referred to as 'concrete' or 'local' MAE whereas the transfer to non-adapted sites is termed 'phantom' or 'remote' MAE.

In the primate visual system, directionally tuned cells have been found at several cortical stages, including areas V1, V2, MT, and MSTd, with progressively larger and more complex receptive fields along the hierarchy

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* Corresponding author. Fax: +1 212 543 5816.
  E-mail address: nq6@columbia.edu (N. Qian).
  URL: http://brahms.cpmc.columia.edu (N. Qian).
[1] Present address: SUNY College of Optometry, 33 W 42nd Street, New York, NY 10036, USA.

(Andersen, 1997). Remote MAE is thought to reflect adaptation in area MSTd where the very large receptive fields can explain the transfer of MAE from the adapted to non-adapted locations. However, remote MAE is usually demonstrated at locations adjacent to the adapted location. Since each visual cortical area has a broad distribution of receptive field sizes, relatively large receptive fields in V1, V2, or MT centered at the border between the adapted and non-adapted regions must cover both regions to some degree and thus can potentially explain remote MAE. Therefore, although remote MAE is consistent with MSTd physiology, it is hard to rule out the alternative explanation based on the responses of the earlier visual areas.

A distinctive property of MSTd receptive fields is that they are not only large but also often cover both sides of the fixation point *extensively* (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Saito et al., 1986). In contrast, none of the earlier visual areas have receptive fields extended significantly beyond the fixation point. For example, receptive fields of V1 and MT cells along vertical meridian only cross over slightly to the other side of fixation, and those away from vertical meridian usually do not cross at all (Dow, Snyder, Vautin, & Bauer, 1981; Maunsell & Van Essen, 1987). Therefore, if MSTd is responsible for the MAE generated by a particular stimulus, then the MAE should transfer not only to adjacent regions on the same side of the fixation but also across the fixation point. Previous studies on remote MAE cannot address this issue conclusively because in those studies, the adapting and test stimuli covered both sides of the fixation point.

In this study, we investigated whether there is cross-fixation transfer of MAE by restricting motion adaptation on one side of the fixation and then measuring MAE on both the adapted location and the mirror location across the fixation point. The presence of significant across-fixation transfer would provide more conclusive evidence for the involvement of MSTd (or higher areas) in MAE. MSTd cells are sensitive to complex motion patterns, such as radial, circular, or spiral motions, in addition to translational motion, whereas the earlier visual areas prefer translational motion only (Duffy & Wurtz, 1991; Geesaman & Andersen, 1996; Graziano et al., 1994; Saito et al., 1986). Among the complex motion patterns, there is a strong bias of MSTd tuning to expansion motion. We therefore tested cross-fixation transfer with expansion motion. For comparison, we also used rightward translational motion. Although some other perceptual phenomena related to MSTd physiology have been reported (Bex & Makous, 1997; Geesaman & Qian, 1996; Morrone etal., 1995), to our knowledge, the question of cross-fixation transfer of MAE has not been addressed.

MAE can be observed with either a static test pattern (static MAE) or a dynamic noise test pattern (dynamic MAE) after motion adaptation. Since dynamic MAE appears to be more sensitive than static MAE and is indistinguishable from real motion (Blake & Hiris, 1993; von Grunau, 1986; Wright & Johnston, 1985), we measured dynamic MAE by nulling it with real motion in our experiments.

2. Experiment 1

In this experiment, we generated expanding and rightward translating random-dot patterns with well-matched stimulus parameters including dot density, adaptation durations, and mean speed, and used them to measure dynamic MAE both at the adapted location and at the mirror location across the fixation point.

2.1. Methods

2.1.1. Observers
The observers included the first author and two individuals who were naïve about the purpose of the study. All had normal or corrected-to-normal acuity. All experiments were undertaken with the understanding and written consent of each observer, and approval from our Institutional Review Board.

2.1.2. Apparatus and stimuli
The experiment was conducted on a 21′ ViewSonic P225f monitor controlled by a Macintosh G4 computer. The vertical refresh rate was 120 Hz, and the spatial resolution was 1024 by 768 pixels. In a dark room, observers viewed the monitor from a distance of 76 cm, using a chin rest to stabilize the head position. The eye position was measured with an ASL head-mounted Eye Tracking System (see details below).

The monitor screen had a constant veiling luminance of 42.1 cd/m². A pair of white (85.6 cd/m²) circular apertures, each 10 deg in diameter, was presented on the monitor side by side. The separation between the nearest points of the two apertures was 4 deg. A black ($\sim$0 cd/m²) fixation dot, 0.5 deg in diameter, was placed mid way between the apertures. Thus, the aperture edges were at least 2 deg away from the vertical meridian through the fixation point, and stimuli within the apertures are unlikely to generate cross-fixation activities in early visual cortical areas such as V1 or MT (Dow et al., 1981; Maunsell & Van Essen, 1987).

Each stimulus consisted of 20 black dots displayed within one of the apertures only. Each dot was a 3×3 pixel square (approximately 5.1 arc min on each side) with limited lifetime (167 ms, or 20 frames). At the end of the lifetime, each dot was assigned a new random location within the aperture. The dots lifetimes were set asynchronously in the first frame to avoid a coherent blinking of the stimulus every 167 ms. If the dot moved outside the bounds of the aperture, it was immediately assigned a new, random location within the aperture, whether or not it had completed its entire life circle. This prevented any fluctuation in the dot density across the pattern from frame to frame.

Expansion and rightward motion patterns were used as adaptation stimuli to induce MAE. These stimuli were 100% coherent, with all the dots moving either outward or rightward (Fig. 1A). The corresponding test stimuli for measuring MAE had varying percentages of dots moving coherently (signal dots); the remaining dots moved in random directions (noise dots) (Fig. 1B and C). We use positive percentage numbers to denote the test stimuli whose signal dots moved in the same direction as the corresponding adaptation stimuli (expansion or rightward translation), and negative percentage numbers to denote the test stimuli whose signal dots moved in the opposite direction (contraction or leftward translation). For expansion and contraction stimuli, the speed of each dot (signal or noise) was a linear function of its distance r from the center of the aperture according to the formula $s = 0.21 * r$ where s is in deg/s and r is in deg. The resulting mean speed was 4.5 deg/s. For translational motion stimuli, the speed of all dots was the same and was set to 4.5 deg/s.

The range of signal-dot percentages of the test stimuli depended on whether the test stimuli were used to measure MAE at the adapted location (adapted-site MAE) or at the mirror location across the fixation point (cross-fixation MAE). This was necessary because our pilot study revealed that the adapted-site MAE was much stronger than the cross-fixation MAE (if any). Likewise, the range depended on whether expansion MAE or translation MAE was measured because the former is much stronger than the latter (Bex et al., 1999; Snowden & Milne, 1997; Steiner, Blake, & Rose, 1994). In each case, a set of seven test stimuli was generated. For adapted-site expansion MAE, the signal percentage of the test stimuli varied from 30% (expansion) to 90% (expansion), in steps of 10%. For cross-fixation expansion MAE, the signal percentage varied from −10% (contraction) to 50% (expansion). For adapted-site translation MAE, the signal percentage of the test stimuli varied

from −10% (leftward) to 50% (rightward). Finally, for cross-fixation translation MAE, the signal percentage varied from −30% (leftward) to 30% (rightward).

All stimuli were generated in advance by our anti-aliasing program in Matlab (Matthews, Liu, Geesaman, & Qian, 1999), using Psychophysics Toolbox extensions generously provided by Brainard and Pelli (Brainard, 1997; Pelli, 1997). Due to the limited computer memory, the maximum length of a stimulus was 10 s. If a stimulus needed to be shown for more than 10 s, it was started over from the first frame.

2.1.3. Procedure

For each subject, we measured both expansion and rightward translation MAEs at both the adapted site and the mirror site across the fixation. In each of the four cases, a psychometric curve was obtained through a constant-stimuli procedure, and the signal percentage needed to null the illusory movement of the MAE was taken as the strength of the MAE (Blake & Hiris, 1993).

For each motion type (expansion or translation), the trials for measuring the adapted-site and cross-fixation MAEs were randomly interleaved. There were 10 trials for each of the 7 test stimuli, resulting in a total of $10 \times 7 \times 2 = 140$ trials. These trials were divided into two 70-trial blocks. The blocks for expansion and the blocks for translation were randomly interleaved, with at least a 5-min break between every two blocks.

The fixation point and the two apertures were always shown on the screen. After fixating, an observer started a block of trials by pressing a mouse button. An adapting stimulus then appeared in one of the apertures for 60 s. After that, a 1-s test stimulus was shown in either the left or right aperture. The observers were required to report the directions (contraction or expansion in the case of expansion adaptation; leftward or rightward motion in
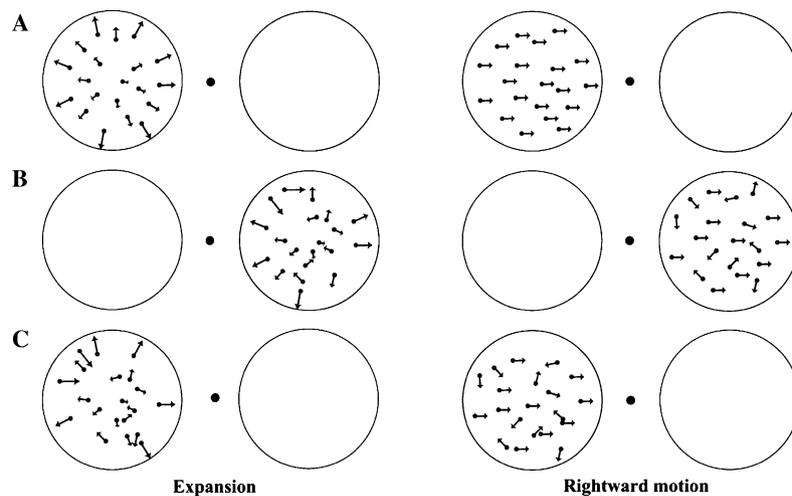
Fig. 1. Schematic illustration of the stimuli used in the Experiments. A fixation point and two apertures were always shown on the screen during the experiments. (A) patterns used for expansion (left panel) and rightward translational motion (right panel) adaptation; (B) patterns for testing cross-fixation MAE; (C) patterns for testing adapted-site MAE. In this schematic, the test patterns have 50% signal strength; in the actual experiments, a range of signal percentages was used.

the case of rightward motion adaptation) of the test stimuli by pressing the left or right button of a mouse. In subsequent trials, a test stimulus was always preceded by a 10-s top-up re-adaptation. The interval between (re-)adaptation stimulus and test stimulus in a trial was 200 ms, and the interval between successive trials was 500 ms. To minimize eye movements during stimulus presentation, after every 10 trials, observers had to take a 1-min break to look around freely. Then, they fixated again, and pressed a mouse button to start the next 10 trials. In the first trial after the break, the re-adaptation was 30 s instead of the usual 10 s. The adaptation stimuli (expansion and rightward translation) were always shown in a fixed aperture, randomly selected for each observer whereas the test stimuli were shown in either aperture to measure both the adapted-site and cross-fixation MAEs (Fig. 1).

2.1.4. Fixation and eye position monitoring

Fixation during the stimulus presentation was important to ensure that the adapting and test stimuli appeared on the intended side of the fixation point. Subjects were asked to fixate as well as they could during stimulus presentation and to move eyes freely during the frequent break periods. The eye movements of all observers were monitored with an ASL head-mounted Eye Tracking System (Model 501). The precision of the system is better than 0.5 deg within the 50 deg by 35 deg range. The horizontal and vertical eye positions were recorded at 120 Hz during stimulus presentation. The data were analyzed with the software from ASL. We measured the time during which the eye position was more than 2 deg away from the fixation point in any direction. If such periods constituted more than 10% of the total stimulus presentation period, the entire block was excluded and re-run. Like most video-based eye trackers, recordings from the ASL system contained artifacts that do not correspond to real eye movements. Thus, the actual periods of broken fixation in the accepted blocks were significantly less than 10%. In fact, we always monitored the camera image of subjects' eyes on a computer screen, and found that subjects rarely broke fixation during stimulus presentation.

2.1.5. Data analysis

For each observer, the data were sorted offline according to the adapting motion type (expansion or rightward motion) and the test stimulus location (adapted site or the mirror site across fixation). In each of the four conditions, the proportion of 'expansion' or 'rightward motion' responses was plotted against the signal percentage of the test patterns, and the curve was fitted by the logistic function ($f(x) = \frac{1}{1+e^{-(x-x_0)/\tau}}$). The signal percentage corresponding to the 50% proportion is the point of subjective equality (PSE) where the signal-dot motion cancelled the MAE and provides a measure of the MAE.

To determine if a MAE is significantly different from zero, we need to calculate the confidence interval around the PSE. This was done using a bootstrap method based on a large number of simulated repetitions of the real experiments (Efron, 1979; Efron & Tibshirani, 1991; Geesaman & Qian, 1998; Wichmann & Hill, 2001). It is a Monte Carlo technique that does not make unwarranted assumptions about the underlying probability distribution of the PSE. The procedure we used was identical to that described by Geesaman and Qian (1998). For each measured psychometric curve of each subject, we first fit a logistic function to the curve. We then read off, from the fitted function, the seven proportion-of-response values at the seven signal percentages of the test patterns. These values were used to generate simulated data. Specifically, for each signal percentage, the corresponding proportion-of-response value was used as the probability (p) of Bernoulli trials in a binomial distribution and the number of trials (N) in the binomial distribution was set to 10, identical to the trial number for each real datum point. To generate a simulated data set, we drew one random number from each of the seven binomial distributions, and divided that number by N to obtain a simulated proportion of response. We then fit a logistic function to the seven simulated proportions of response and determined the simulated PSE just as we did for the real data. By repeating this procedure 1000 times, we obtained a distribution of the PSE. The 95% confidence interval of the PSE (marked by dotted vertical lines in Figs. 2–5) was then determined by eliminating 25 (2.5% of 1000 repetitions) simulated PSE points from each end of the distribution.

2.2. Results

The psychometric curves (the proportion of expansion or rightward motion responses as a function of the signal percentage of the test patterns) for three observers are presented in the three columns of Fig. 2. The positive and negative values of signal percentages represent motion of the signal dots in the adapted direction and the opposite direction, respectively. The top and bottom rows show the results for the expansion adaptation and the rightward translation adaptation, respectively. The two curves in each panel are the results for the adapted site (solid curve) and the mirror site across the fixation point (dashed curve). The 50% point or PSE of each curve is marked by a solid vertical line and indicates the strength of the MAE as the percentage of signal dots needed to null the illusory motion caused by the adaptation. The two vertical dotted lines around each solid vertical line indicate the 95% confidence interval of the PSE, calculated with the bootstrap method.

Although there was considerable inter-subject variability, the results were qualitatively consistent across subjects. At the adapted site, all three observers had significant MAEs for both expansion and translation-motion adaptation, and the expansion MAE was significantly larger than translation-motion MAE. These results are expected based on previous reports (Bex et al., 1999; Snowden & Milne, 1997). The new finding is that at the mirror site across the fixation point, there was a sizable partial transfer of
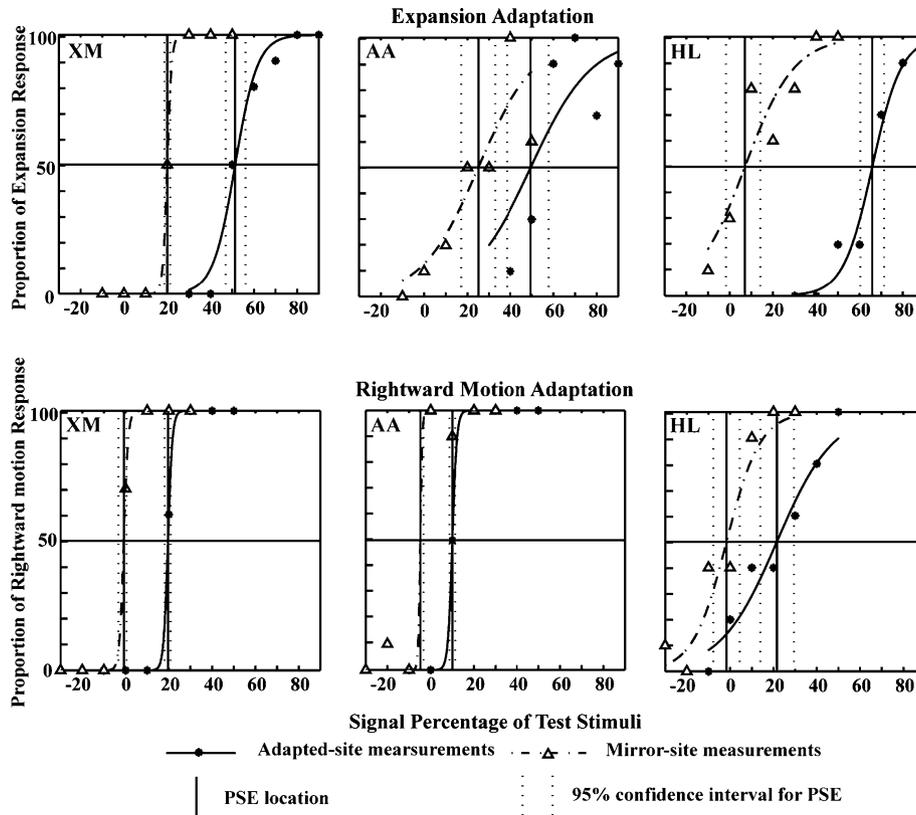
Fig. 2. Psychometric curves of three observers from Experiment 1. Results from expansion adaptation and rightward motion adaptation are shown in the top and bottom rows, respectively. In each panel, the solid and dashed curves represent measurements at the adapted site and the mirror site across the fixation, respectively. The solid vertical line on each curve indicates the signal percentage for at the 50% point (PSE) for nulling the MAE. The two dotted vertical lines around each solid vertical line indicate the 95% confidence interval for the PSE.
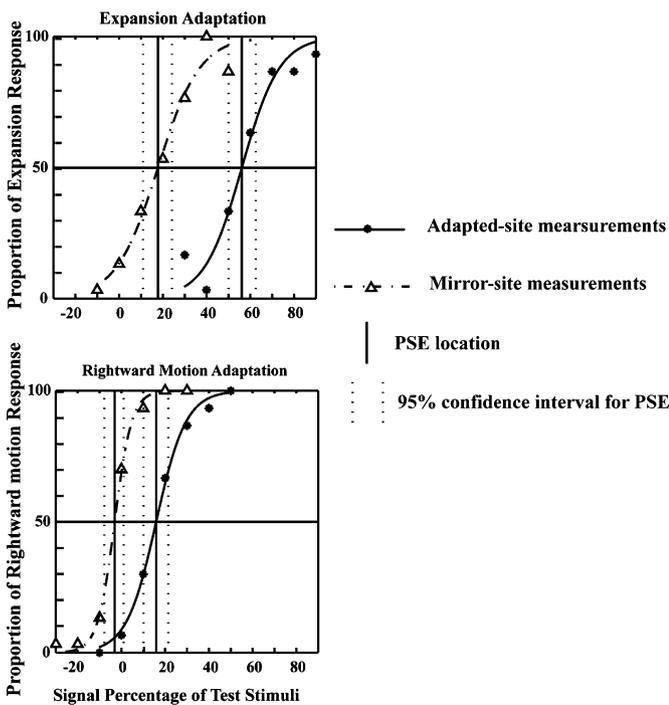
Fig. 3. Pooled results from all three observers of Experiment 1. The presentation format is identical to that of Fig. 2.

MAE for the expansion motion. Based on the 95% confidence intervals, the cross-fixation MAE was significant for observers XM and AA, and nearly significant for observer HL. In contrast, there was little cross-fixation MAE for the translational-motion adaptation. Observer AA actually showed a small but significant MAE in the 'wrong' direction, presumably due to a small bias in directional judgement.

The pooled data for all three observers are shown in Fig. 3. At the adapted site, the mean MAEs for the expansion and translation were 56.1% and 15.9% of the signal dots, respectively; both MAEs were significantly different from 0. At the mirror site across the fixation, the mean MAEs for expansion and translation were 17.8% and −3.1%, respectively; only the expansion MAE at the mirror site was significantly different from 0.

This experiment demonstrates the transfer of MAE to the mirror site across the fixation point for expansion motion. However, the comparison between expansion and translation MAEs at the mirror site is less conclusive. The reason is that with the matched stimulus parameters (number of dots, mean speed, adaptation durations etc.) for the expansion and translation stimuli in this experiment, the expansion MAE was much larger than the translation MAE at the adapted site. For translation
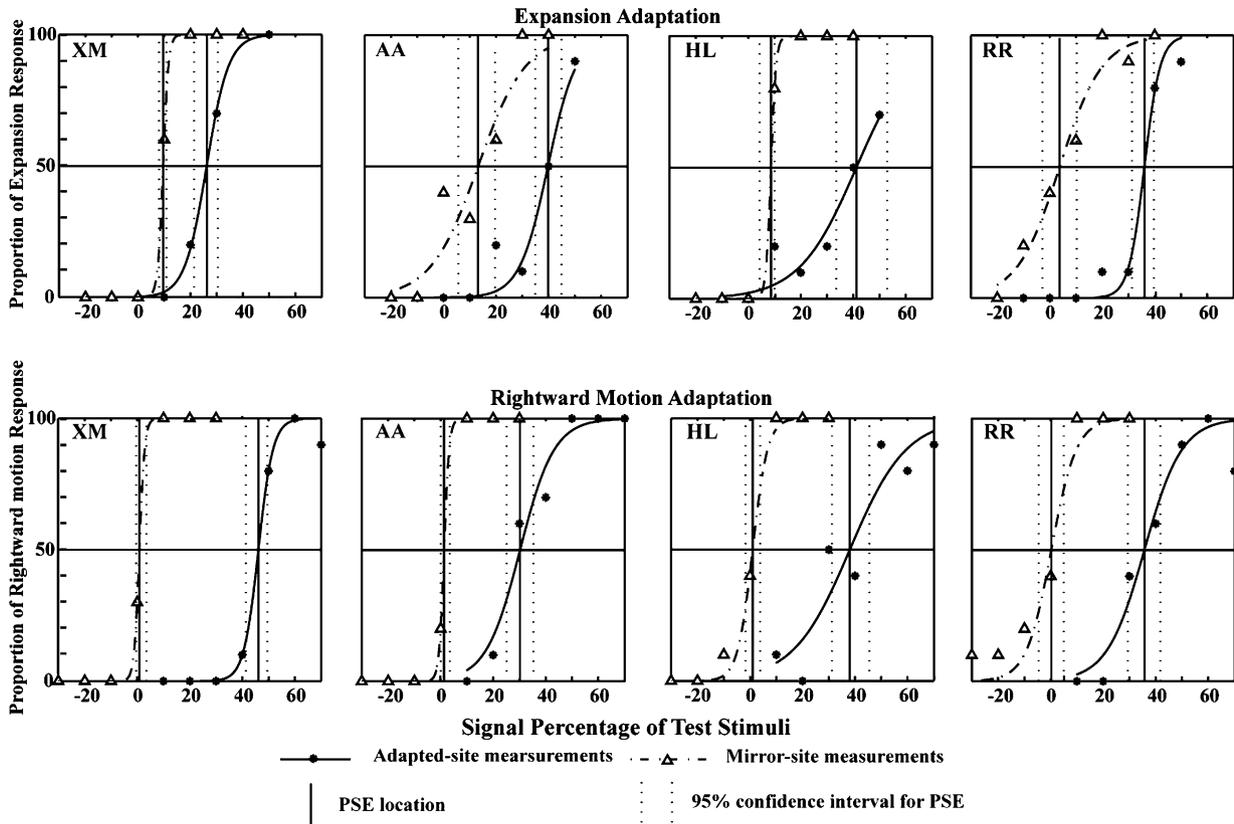
Fig. 4. Psychometric curves of four observers from Experiment 2. The presentation format is identical to that of Fig. 2.
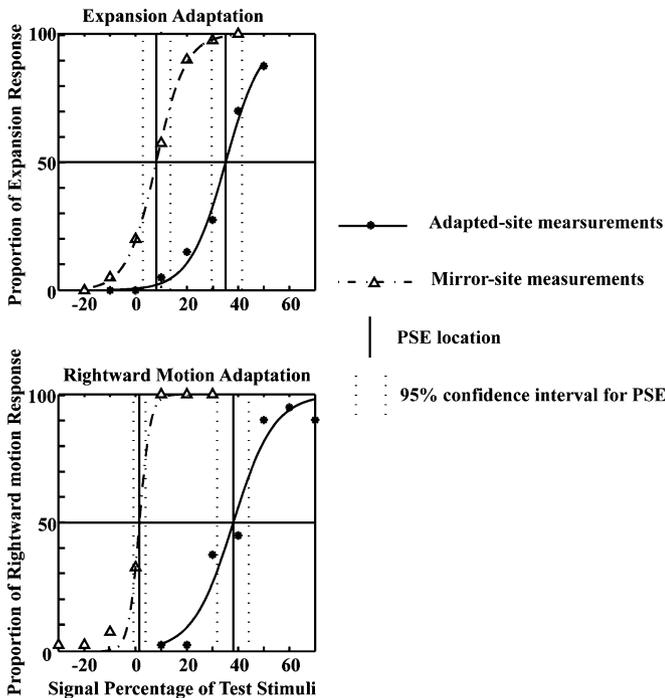
Fig. 5. Pooled results from all four observers of Experiment 2. The presentation format is identical to that of Fig. 2.

3. Experiment 2

In this experiment, we reduced the adaptation duration for the expansion motion and increased the dot density for the rightward translational motion such that at the adapted site, the expansion and translation MAEs were of similar magnitudes. This allowed a fair comparison of the cross-fixation transfer of the two types of MAEs at the mirror site.

3.1. Methods

The same three observers in Experiment 1 and a new naïve observer participated in this experiment. All aspects of the experiment were identical to those of Experiment 1 except for the following adjustments.

To reduce expansion MAE at the adapted site, we could reduce either the adaptation durations or the dot density for expansion stimuli. Since the dot density in Experiment 1 was already low, we decided to reduce the durations to one tenth of the values used in Experiment 1. That is, the initial adaptation at the beginning of a block was reduced to 6 s, and the re-adaptation was reduced to 3 s (for the first trial after a 1-min break) or 1 s (for the other trials). The signal-percentage ranges of the test stimuli were 10% (expansion) to 70% (expansion) at the adapted site, and from −20% (contraction) to 40% (expansion) at the mirror site across the fixation.

adaptation, the lack of significant cross-fixation MAE might be due to the weaker MAE at the adapted site. The next experiment addressed this problem.

To increase translation MAE at the adapted site, we could increase either the adaptation durations or the dot density for translation stimuli. Since increasing durations would make it harder for subjects to maintain fixation, we chose to increase the dot density. For translation, the mean adapted-site MAE in Experiment 1 was only 15.9% of signal dots, much smaller than the 40% value reported by Hiris and Blake (1992). In this experiment, we increased the dot density to 13 dots/deg^2 (1000 dots in an aperture), similar to the density (12 dots/deg^2) used by Hiris and Blake. To avoid overlap of the dots, the dot size was decreased to a 1×1 pixel square (approximately 1.7 arc min on each side). The dot size for the expansion stimuli remained at 3×3. The signal-percentage range was 10% (rightward motion) to 70% (rightward motion) at the adapted site, and was −30% (leftward motion) to 30% (rightward motion) at the mirror site across the fixation.

3.2. Results

The results from each of the four observers are shown in Fig. 4, and the pooled data from all observers in Fig. 5. The format of presentation is identical to that of Figs. 2 and 3. Like Experiment 1, there was considerable inter-subject variability but the results were qualitatively consistent across subjects.

Compared with Experiment 1, the expansion MAE at the adapted site was significantly *smaller* due to the reduced adaptation durations. The values varied from 26.2% to 41.2% of signal dots for the four observers, with a mean of 35.8%. At the adapted site, the translation MAEs were significantly *larger* compared with Experiment 1 due to the increased dot density. The values varied from 30.2% to 46.1% for the four observers, with a mean of 37.5%, which is consistent with results of Hiris and Blake (1992). Overall, we achieved the goal of matching the expansion and translation MAEs at the adapted site.

Let us now examine the MAEs at the mirror site across the fixation point. For the expansion motion, the cross-fixation MAEs ranged from 3.8% to 13.2% of signal dots for the four observers (Fig. 4). They are significantly different from 0 for all observers except RR. The mean MAE of the pooled data was 8.8% (Fig. 5), which is also significantly larger than zero. In contrast, for the rightward motion, the cross-fixation MAEs ranged from 0.2% to 1.3% of signal dots for the four observers, and none was significantly different from 0. The mean MAE of the pooled data was only 0.9%, again not significantly different from 0.

We conclude that even with matched MAEs for the expansion and translation motion at the adapted site, expansion MAE transfers across the fixation point whereas translation MAE does not.

4. Discussion

The main goal of this study is to show the presence of cross-fixation transfer of MAE and thus to establish the involvement of area MSTd in MAE more conclusively. Since MSTd cells are tuned to complex motion patterns with a strong bias to expansion whereas earlier visual cortical areas are tuned to translational motion only, we used expanding and rightward translating random-dot stimuli to probe MAEs both at the adapted site and the mirror site across the fixation point. In Experiment 1, the stimulus parameters for the two types of motions were well matched. We found a significant cross-fixation transfer of MAE for the expansion motion but not for translation motion. However, at the adapted site, the expansion MAE was much stronger than translation MAE. Although this is consistent with previous reports (Bex et al., 1999; Snowden & Milne, 1997; Steiner et al., 1994), it raised the possibility that the lack of cross-fixation transfer of translation MAE were due to the weak MAE at the adapted site. Experiment 2 ruled out this possibility. In this experiment, we adjusted stimulus parameters to increase translation MAE and to decrease expansion MAE at the adapted site. We found that even when the expansion and translation MAEs were virtually identical at the adapted site, there was still significant cross-fixation MAE for expansion but not for translation. In addition to establishing cross-fixation transfer of MAE induced by expansion motion, our results also suggest that although MAE induced by translational motion transfers to non-adapted sites (Bex et al., 1999; Snowden & Milne, 1997; Steiner et al., 1994), it does not transfer across the fixation point.

The lack of cross-fixation transfer of translation MAE seems puzzling since many MSTd neurons are tuned to translational motion as well as complex motion patterns (Duffy & Wurtz, 1991; Graziano et al., 1994; Orban et al., 1992). We do not have a convincing explanation for the puzzle, but the following speculative considerations on expansion and translation adaptation might help.

For an expansion stimulus, an MSTd cell tuned to expansion will fire maximally. A cell in an earlier area such as V1 or MT whose preferred direction matches the local direction within the cell's receptive field will also fire maximally. Since V1 is much larger than MSTd, one might conclude that overall, adaptation of the earlier areas combined must overwhelm any effect in MSTd. However, the following factor may greatly boost the relative significance of MSTd adaptation to expansion: MSTd is heavily biased toward representing expansion and the majority of MSTd cells respond strongly to stimuli with an expansion component (see, e.g., Fig. 9 of Graziano et al., 1994). In addition, MSTd cells have huge receptive fields; consequently, *all* the expansion cells in MSTd must be strongly activated by an expansion stimulus. In contrast, cells in the earlier areas such as V1 and MT have their preferred directions more or less uniformly distributed over the entire 360 deg range (Livingstone & Conway, 2003; Maunsell & Van Essen, 1987), and their receptive fields are much smaller. Therefore, only a small fraction of those cells whose receptive fields overlap the stimulus and whose preferred directions happen to match the local translational components

of expansion respond strongly; the majority of cells in the earlier areas do not respond well. Thus, although expansion adaptation of MSTd may still be less important than that of the earlier areas combined, it may not be negligible. This is consistent with our finding that for expansion adaptation, cross-fixation transfer of MAE (presumably mediated by MSTd) is significant but is only about a quarter of the adapted-site MAE (caused by the earlier areas as well as MSTd).

We now consider adaptation to translational motion. Although many MSTd cells do respond to translation, there is no bias toward representing rightward translation used in our experiment. Therefore, the reason cited above that may boast the relative significance of expansion adaptation in MSTd does not apply to translation. In addition, MSTd cells well tuned to complex motion patterns such as expansion do not respond strongly to translation. Thus, for translational motion, adaptation in MSTd may indeed have a negligible perceptual consequence simply because there are far more cells in the earlier areas. Since receptive fields of cells in the earlier areas do not cover both sides of the fixation point significantly, the translation MAE does not transfer significantly across the fixation point.

A recent fMRI study by Morrone et al. (2000) is relevant to the above discussion. Using well-controlled visual stimuli, these investigators found an area within the human V5/MT complex that responds selectively to optic flow patterns (including expansion) but not to translational motion. If this area is the human analog of MSTd, then the finding supports our argument above that MSTd's overall response to expansion may be much stronger than that to translation. However, Morrone et al. noted the importance of using changing stimuli in their work while we used constant-stimuli in our experiments. So the applicability of their fRMI data to our discussion remains unclear.

Acknowledgments

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