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Global-motion aftereffect does not depend on awareness of the adapting motion direction

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Abstract It has been shown that humans cannot perceive more than three directions from a multidirectional motion stimulus. However, it remains unknown whether adapting to such imperceptible motion directions could generate motion aftereffects (MAEs). A series of psychophysical experiments were conducted to address this issue. Using a display consisting of randomly oriented Gabors, we replicated previous findings that observers were unable to perceive the global directions embedded in a five-direction motion pattern. However, adapting to this multidirectional pattern induced both static and dynamic MAEs, despite the fact that observers were unaware of any global motion directions during adaptation. Furthermore, by comparing the strengths of the dynamic MAEs induced at different levels of motion processing, we found that spatial integration of local illusory signals per se was sufficient to produce a significant global MAE. These psychophysical results show that the generation of a directional global MAE does not require conscious perception of the global motion during adaptation.

Keywords Adaptation · Aftereffects · Motion integration · Visual awareness

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A hallmark of human motion perception is the ability to integrate locally ambiguous motion signals over space and time to perceive globally coherent motion patterns. Humans show not only high sensitivity to global motion (Amano, Edwards, Badcock, & Nishida, 2009; Freeman & Harris, 1992; Lee & Lu, 2010; Morrone, Burr, & Vaina, 1995), but also remarkable adaptability to the dynamics of the recent history of motion stimulation (Bex, Metha, & Makous, 1999; Lee & Lu, 2012; Scarfe & Johnston, 2011; Smith, Scott-Samuel, & Singh, 2000). The famous "waterfall" illusion is often used to demonstrate adaptation-induced aftereffects following prolonged exposure to global motion (for reviews, see Anstis, Verstraten, & Mather, 1998; Mather, Pavan, Campana, & Casco, 2008). In many seminal studies on global-motion adaptation, researchers employed visible and salient motion-adapting stimuli, so that observers were consciously aware of the global motion direction(s) during adaptation (Anstis & Reinhardtrutland, 1976; Bex et al., 1999; Blake & Hiris, 1993; Snowden & Milne, 1997; van der Smagt, Verstraten, & van de Grind, 1999). Even though the subsequent test stimulus did not display any coherent motion (i.e., a static image or random motion), it is possible that the clear awareness of the global motion during adaptation caused the perceived motion aftereffect (MAE) in the subsequent test. If awareness of the global motion direction were necessary for yielding adaptation-induced MAEs, we would expect such aftereffects to disappear when the global motion becomes invisible during adaptation.

To examine whether a global-motion aftereffect depends on visual awareness of the adaptor, previous research has used binocular rivalry to manipulate phenomenal invisibility of the adapting motion stimuli. Although a rival stimulus suppressed an adapting stimulus from visual awareness, researchers found that such invisible motion adaptors still elicited an MAE (Lehmkuhle & Fox, 1975; Maruya, Watanabe, & Watanabe, 2008; O'Shea & Crassini, 1981). Interestingly, with low contrast of the adapting stimuli, the strength of MAE weakened when the adapting stimulus was removed from visual awareness for a longer suppression duration (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Wiesenfelder & Blake, 1990).

These results provided important evidence that global-motion adaptation depends on visual awareness of the motion adaptors, and also suggested that the neural activity in V1 may contribute to the dependency of the visual aftereffect on the adapting contrast (Albrecht & Hamilton, 1982; Sclar, Maunsell, & Lennie, 1990). This finding is consistent with one aspect of a computational account in which low-contrast displays introduce more ambiguity in local motion analysis, which may modulate the activity pattern in V1. However, computational simulations also showed that low-contrast stimuli appear to elicit stronger dependency on the integration of local motion signals over space with guidance from generic priors, including the slow-and-smooth prior (Weiss, Simoncelli, & Adelson, 2002; Yuille & Grzywacz, 1988) and pattern-specific priors for complex motion (Wu, Lu, & Yuille, 2009). Hence, in a low-contrast display, the attenuated MAE during binocular suppression may result from the modulation of awareness related to neural activity at V1 that performs local motion analysis (Blake et al., 2006; Wiesenfelder & Blake, 1990), or from attention-related influences on the spatial integration of local signals at higher-level motion-processing areas (i.e., MT or MST; Bulakowski, Bressler, & Whitney, 2007; Huk & Heeger, 2000; Watanabe & Shimojo, 1998), or from both.

To specifically investigate how awareness affects global-motion aftereffects in the motion-processing hierarchy, we employed a stimulus that did not affect the responses of local-motion detectors, so that our study could focus on the influence of awareness at the integration stage. In our previous study (Lee & Lu, 2012), we had developed a psychophysical method to dissociate local adaptation at the low level of motion processing from global adaptation at the stage of motion integration. This method employed the multiple-aperture stimulus (Amano et al., 2009; Lee & Lu, 2010; Mingolla, Todd, & Norman, 1992; for a review, see Nishida, 2011), probing the visual system for MAEs at specifically selected test locations, so that the contributions from different levels of motion processing in adaptation could be measured (Lee & Lu, 2012; Scarfe & Johnston, 2011). In the present study, we investigated how awareness affects MAEs, using an extended psychophysical paradigm to render the global motion directions imperceptible during adaptation. We employed multidirectional motion to render global directions imperceptible during adaptation (Greenwood & Edwards, 2009; Treue, Hol, & Rauber, 2000). The goal of the present study was to examine whether the perception of a global MAE depends on seeing the global motion directions during adaptation.

In the experiments presented here, we first verified that humans are indeed unable to perceive the global directions embedded in multidirectional motion patterns. Next, we examined whether adapting to such stimuli without perceptible global motion directions can still yield the static MAE. Finally, we measured the dynamic MAE and compared the strengths of the MAEs induced at different levels of motion processing.

General method

Stimulus

The stimulus consisted of 264 drifting Gabor elements, as is shown in Fig. 1a. Each element was a sine-wave grating, windowed by a stationary Gaussian function with a sigma of 0.21º. Spatial frequency was kept constant at 2 cycles/deg. Each element subtended a visual angle of 1º. Orientations were randomly and independently sampled from a uniform distribution between 0º and 180º. Elements were arranged in a circular pattern inscribed in a 20 × 20 grid in which cells were tightly packed, so that the separation between any two adjacent cells was zero. As a result, the centers of any two adjacent Gabors were 1º apart. To minimize pursuit eye movements caused by drifting Gabors near fixation, elements that were too close to fixation were removed, resulting in a display annulus spanning from 4º to 10º around fixation. Contrast was fixed at a low level of 0.05 (Michelson contrast) for all experiments, in order to promote the spatial integration of the local motion signals to perceive global motion in the multiple-aperture stimulus (Takeuchi, 1998).

Elements were randomly assigned to different numbers of sets (at most five), depending on the experimental conditions (i.e., Fig. 1b illustrates a five-set pattern). Each set was assigned one global-motion velocity, with speed of v and direction of α. The local drifting speed u of each element was computed on the basis of the element's orientation θ and the global velocity of the set to which the element belonged:

$$u = v \sin(\alpha - \theta).$$

As a result, the local drifting velocities of elements within the same set were all consistent with the set's global velocity. In other words, the set's global velocity was the intersection-of-constraint (IOC) solution when combining the local motion signals from all elements within this set.

Apparatus

Stimuli were generated using MATLAB and PsychToolbox (Brainard, 1997; Pelli, 1997), and presented in a dim room on a Viewsonic CRT monitor, with refresh rate of 75 Hz and resolution of 1,024 × 768 pixels. Viewing distance was kept constant at 57 cm using a chinrest and forehead rest, so that each pixel on the screen subtended 2.01 arcmin. We used a Minolta CS-100 photometer to calibrate the monitor, and converted a luminance range of 0 to 146.5 cd/m^2 into a linear

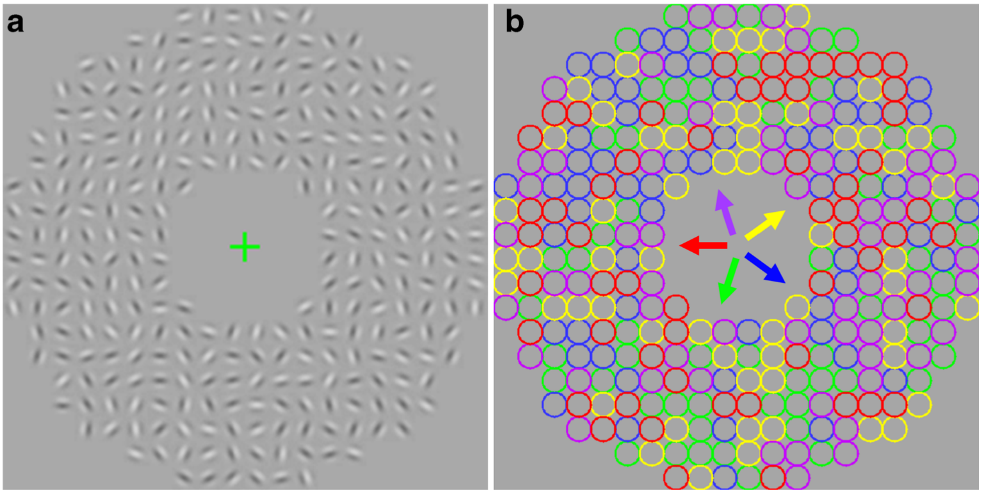

Fig. 1 Illustration of a five-direction stimulus. The parameters (e.g., contrast) have been modified for demonstration purposes. (A) Layout of the multiple-Gabor pattern. (B) Schematic illustration of a five-direction motion pattern. Colors indicate different sets of Gabor elements, and circles indicate the locations of the elements. The arrows at the center indicate the global velocities assigned to different sets

lookup table for 256 intensity levels. Participants were undergraduate students at the University of California, Los Angeles (UCLA), participating for course credit. All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiments. The experiments were approved by UCLA's Office for Protection of Research Subjects.

Experiment 1: Humans cannot perceive the global motion directions in a five-direction motion pattern in the multiple-aperture display

Previous psychophysical studies have provided evidence that humans are unable to discriminate motion patterns composed of four global directions from patterns with five directions (Edwards & Greenwood, 2005; Greenwood & Edwards, 2009). These findings suggest that a multidirectional motion pattern with four or more directions can "flood" the direction-selective global-motion detectors, so that the embedded directions of global motion will be rendered imperceptible. These psychophysical findings are consistent with results from electrophysiological studies with primates (Treue et al., 2000), suggesting that population responses of direction-selective neurons depend on the composition of embedding directions in a multidirectional-motion display. However, all previous studies used a random-dot display. In Experiment 1, we tested whether similar results would be obtained using a multiple-aperture display with randomly oriented Gabor elements.

Method

A group of 30 observers participated in Experiment 1. Half were tested on translational motion and the other half were tested on complex motion. For the translational-motion group, on each trial, observers viewed two motion stimuli (560 ms each) with an inter-stimulus interval of 500 ms. One of the two stimuli consisted of a random motion pattern, in which each Gabor element was assigned a random motion vector. The other stimulus was a multi-directional motion pattern with five conditions, in which Gabor elements were randomly grouped into one, two, three, four, or five sets, respectively. Each set contained the same number of elements. Elements within the same set were assigned the same global-motion vector. The global motion directions assigned to different sets were equally spaced over the 360° range. Observers were asked to judge which interval contained the random motion pattern. Each observer completed 40 trials for each condition, resulting in 200 trials in total. Trials in different conditions were randomly interleaved. Before running the 200-trial session, each observer ran a short version with five trials per condition as practice.

For the complex-motion group, stimuli and procedure were identical to those for the translational-motion group, except for the following details. The five conditions were (1) coherent clockwise, (2) coherent counterclockwise, (3) coherent inward, (4) coherent outward, and (5) "mixed" patterns. The first four "coherent" patterns were analogous to the one-direction pattern presented to the translational-motion group. Because the coherent patterns were obviously different from a random pattern, performance in those "coherent-versus-random" trials served as a benchmark. The "mixed" pattern was a four-set pattern, with each set being assigned one of the four complex global directions (i.e., clockwise, counterclockwise, inward contraction, and outward expansion).

Results

The results for Experiment 1 are shown in Fig. 2. For the translational-motion group (left panel), the mean accuracies

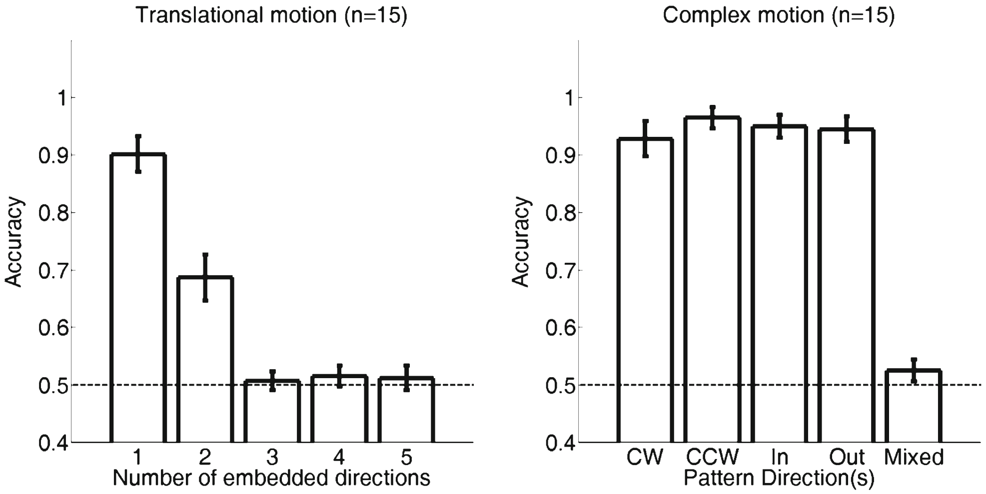

Fig. 2 Mean accuracies in distinguishing between a multiple-direction motion pattern and a random pattern: (Left) translational motion; (Right) complex motion. Error bars indicate the standard errors of the means

(with *SD*s in parentheses) for the five conditions were as follows: one-direction, 90 % (12 %); two-direction, 69 % (16 %); three-direction, 51 % (6 %); four-direction, 52 % (7 %); and five-direction, 51 % (8 %). Performance was above chance when the pattern contained one direction or two directions. However, performance dropped to chance level when the number of directions was increased to three, four, or five, consistent with previous findings using random-dot displays (Edwards & Greenwood, 2005; Greenwood & Edwards, 2009). For the complex-motion group (right panel), the mean accuracy was above 90 % for all coherent patterns, but dropped to chance level when the pattern was mixed, with four complex directions (mixed: mean = 53 %, *SD* = 7 %). These findings suggest that a multidirectional pattern, embedded with four or more directions, was perceptually indistinguishable from a random pattern, regardless of whether the underlying directions were translational or complex directions.

Experiment 2: Adapting to imperceptible motion directions yields perceptible static MAE

The objective of Experiment 2 was to examine whether the visual system can produce global MAE after adapting to a motion pattern with imperceptible global directions. We measured the perceived global MAE direction after adapting to a stimulus containing five global translational motion directions (i.e., the five-set translational pattern used in Exp. 1). In the test phase, we specifically selected a set of locations at which elements shared the same global velocities during adaptation (similar to the technique used in Lee & Lu, 2012; Scarfe & Johnston, 2011). If observers perceived a global MAE direction opposite to the tested set's adapting direction, it would imply that the conscious perception of the global adapting directions is not a necessary requirement for perceiving a global directional MAE.

Method

Stimulus

We used the imperceptible, five-direction motion pattern in Experiment 1 as the adapting stimulus, and measured the perceived MAE direction under two conditions. Similar to our previous work (Lee & Lu, 2012), the two experimental conditions differed in terms of test locations. In the Single condition, all test elements were chosen from the same set. In other words, they all had been assigned the same global velocity during adaptation. This method of testing the MAE has been shown to produce a "segregated" MAE direction, which is opposite to the tested set's adapting direction (Lee & Lu, 2012). In the Mixed condition, one-fifth of the elements from each set were presented during the test, so that the total number of test elements was equal in the two conditions. A total of 25 observers (single, $n = 13$; mixed, $n = 12$) participated in this experiment. Demonstration movies for the two conditions can be found in the Supplemental Materials.

Procedure

Each trial consisted of three phases—adaptation, test, and response—as outlined in Fig. 3. Across the three phases, observers were instructed to maintain fixation at a cross located at the center of the screen. During the adaptation phase, a five-direction adapting-motion pattern was presented.

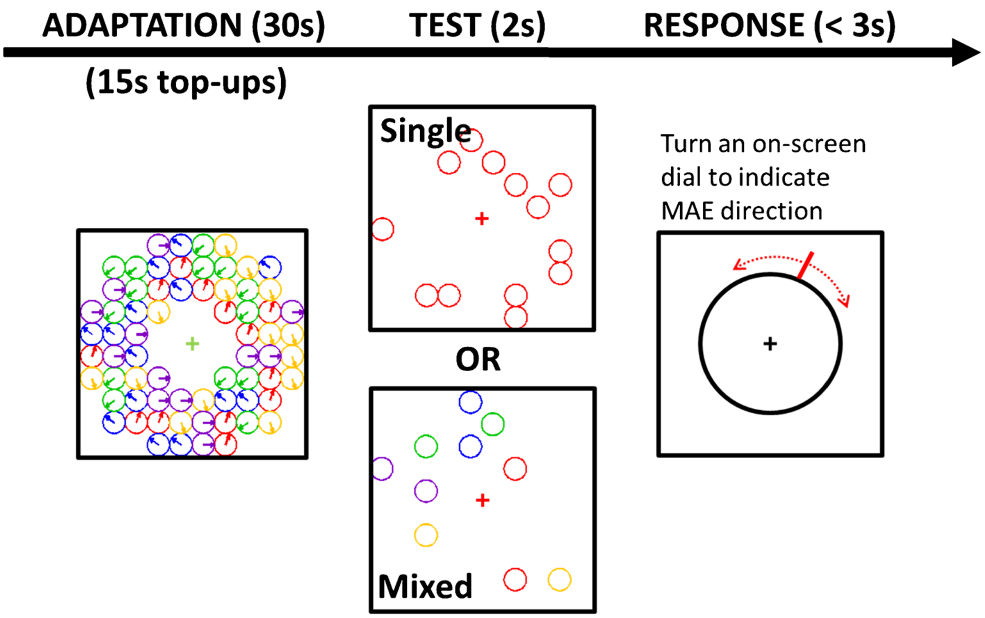

Fig. 3 Illustration of the procedure of Experiment 2. In both the adaptation and test phases, colors represent the assignment of elements to different sets. In the adaptation panel, arrows indicate assigned global-motion vectors. Both colors and arrows are for illustration purposes only and were absent in the stimulus

Before the adapting stimulus ended, three countdown beeps, 1 s apart, were presented to remind observers about the upcoming test phase.

Trials were presented in blocks, with the first trial having a longer adaptation duration (30 s), and the remaining top-up trials having a shorter adaptation duration (15 s). Each block included five trials (one initial + four top-ups). The adapting stimulus of each top-up trial was an excerpt (first frame randomly determined) of the one used in the initial trial within the same block, so that the orientations and local-motion velocities were identical across all trials in the same block. Each participant completed ten blocks, with a 30-s rest period inserted between blocks.

The test stimulus was presented right after the adapting stimulus disappeared. The test stimulus was a static pattern with elements chosen from different locations, depending on the condition, and was presented for 2 s. The static pattern in the test stimulus was generated from the last frame of the adapting movie to avoid abrupt changes from adaptation to test. The task was to report *one and only one* MAE direction perceived during the test phase. Responses were made by turning a simulated dial on the computer screen using the mouse.

In the Single condition, one of the five sets of elements was chosen to be the tested set in each trial. Within a block, each set was tested exactly once, so that the five trials in each block would cover all five sets. Test order of the sets was randomized within each block. In the Mixed condition, one-fifth of the elements were randomly chosen from each set to be the test elements. For both conditions, the test locations varied across trials within the same block, so that the same location would be tested exactly once in each block. In order to familiarize themselves with the procedure, observers completed two blocks of five practice trials (the durations of the initial adaptation, top-up adaptation, and rest period were 20, 10, and 20 s, respectively) before running the experiment session.

Results

We aligned the reported MAE directions according to global motion directions in the adapting stimuli using the following method. For the analysis in the Single condition, because all test locations were chosen according to the common global velocity shared during adaptation, we reported the difference between the adapting direction of the tested set and the MAE direction reported by observers. This procedure aligned the adapting direction of the tested set at 0º. If consistent adaptation were present, the expected aftereffect directions would be observed at 180º. In the Mixed condition, test elements were randomly selected from all five sets, which raised the possibility that observers might perceive five aftereffect directions opposite to the adapting directions. To be comparable with the alignment procedure in the Single condition, we first aligned all five of the adapting directions at 0º, regardless of test locations. For example, if the five evenly spaced adapting directions were 0º, 72º, 144º, 216º, and 288º, we scaled the adaptation directions by 5, and then performed integer division by 360. The resulting remainders were 0º for all five of the adapting directions. Applying the same transformation on the five expected global MAE directions (opposite to the five adapting directions—i.e., 180º, 252º, 324º, 36º, and 108º, respectively), the five transformed global MAE directions would be all aligned at 180º. If observers perceived MAE directions opposite to any of the five adapting directions, we would expect to observe a higher response frequency at 180º after this transformation.

Figure 4 depicts the distribution of the transformed MAE directions. As is shown in the left panel of Fig. 4, when test elements were taken from the same set in the Single condition, the distribution of the reported MAE directions was found to significantly deviate from a circular uniform distribution (Hodges–Ajne test, $p < .0001$). The distribution shows a clear peak at 180º, which is opposite to the global motion direction of the set during adaptation. However, in the Mixed condition, when test elements were taken randomly from all five sets (right panel of Fig. 4), the distribution of the transformed MAE directions was not different from a circular uniform distribution ($p = .229$). The same test was conducted on the raw data of the reported MAE directions for the Mixed condition. The analysis did not reveal any significant deviation from circular uniformity ($p = .687$).

The results from the first two experiments showed that, although observers were unaware of any global motion directions in the five-direction adapting stimulus, a clear aftereffect was observed in the opposite direction to the imperceptible global motion direction when this was tested at locations containing motion signals coherent with the global motion pattern. This result suggests that the generation of a directional global MAE does not require conscious perception of a global motion direction during adaptation. However, if test locations contained adapting-motion signals that were not coherent, no clear directional aftereffect was perceived. The dependency of aftereffect on test locations provides converging evidence that the visual system integrates local illusory signals at test locations across space in order to generate a global-motion aftereffect (Lee & Lu, 2012). The present studies further demonstrate that such an integration mechanism does not require conscious awareness of coherent motion directions during adaptation. Hence, spatial integration of local illusory signals per se is sufficient to produce a clear directional MAE.

In Experiment 2, the motion directions embedded in the adapting stimulus were all unidirectional with translational motion. To examine the generalization of such an effect, Experiment 3 was designed to test whether aftereffects would still be observed after adapting to imperceptible motion directions embedded in multiple radial and rotational motion patterns. If a similar pattern of result were observed, it would suggest that the higher-level processing on complex motion is involved in integrating local illusory signals to produce a global MAE.

Experiment 3: Adapting to imperceptible complex motion patterns yields MAE

Previous findings from neurophysiology (Duffy & Wurtz, 1991a; Tanaka & Saito, 1989), neuroimaging (Morrone et al., 2000), psychophysics (Lee & Lu, 2010; Morrone et al., 1995; Snowden & Milne, 1997), and computational models (Beardsley, Ward, & Vaina, 2003; Wu et al., 2009) suggest that there exist high-level computational processes that are specialized for analyzing complex motion patterns (e.g., optic flow and rotational patterns). They are complex because, unlike unidirectional motion flows, their flow fields contain different local velocities across locations. It is believed that these complex patterns are processed by neurons located in areas that are beyond MT and further downstream in the motion pathway, including MST (Duffy & Wurtz, 1991b;

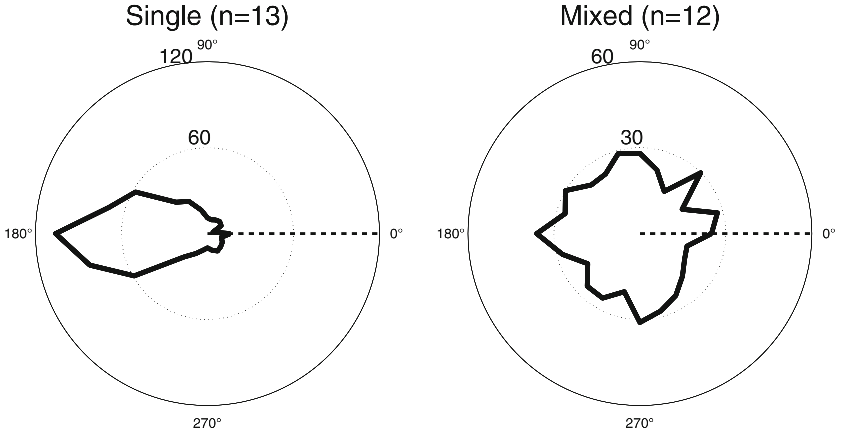

Fig. 4 Distributions of perceived MAE directions for the Single (left) and Mixed (right) conditions in Experiment 2. Responses are aligned as described in the text. The dashed lines indicate the adapting directions (aligned to be 0º), and solid lines indicate the frequencies of reported directions. Note that the scales of frequency are different between the two plots

Tanaka, Fukada, & Saito, 1989). Experiment 3 employed an adapting stimulus that was embedded with multiple complex motion directions (i.e., rotational and radial motion directions). Given that adaptation to the multiple-aperture stimulus yields local illusory signals, Experiment 3 aims to examine whether these local illusory signals can be integrated by units at the higher-level of motion processing in analyzing complex motion to generate a global circular/radial MAE.

Method

Stimulus

The adapting stimulus was the mixed pattern used in Experiment 1 for the complex-motion group. Elements in each of the four sets were assigned one of the four complex, global motion directions: clockwise, counterclockwise, expansion, and contraction. As shown in the results of Experiment 1, observers were not aware of any global motion directions in the adapting stimulus. We created five test conditions (Supplemental Movie 2 shows three of them). Four of the five test conditions were analogous to the Single condition in Experiment 1, in each of which all test elements were taken from the same set. In other words, on a particular trial of any of these four conditions, all test elements were assigned the same complex motion direction during the adaptation phase. We label each of these four Single conditions on the basis of the tested set's adapting direction: clockwise, counterclockwise, expansion, or contraction. The remaining condition was the Mixed condition, in which one-fourth of test elements from each set were presented simultaneously during the test phase.

Procedure

Adaptation and test durations were identical to those used in Experiment 2. The procedure was similar too, except that all five conditions (four Single and one Mixed conditions) were run within subjects. Each observer ran ten trials for each condition. Order of conditions was randomized across all 50 trials, which were blocked into ten blocks of five trials. In contrast to Experiment 2, in which participants were asked to rotate a dial to report one perceived MAE direction, Experiment 3 employed a forced-choice discrimination task, in which observers were instructed to report the perceived MAE direction by choosing one of the four complex motion directions: CCW (counterclockwise), CW (counterclockwise), Con (contraction), and Exp (expansion). Observers were provided a fifth option to choose "no motion" (labeled as "NoMAE" in the "Results") if no MAE was perceived during the test phase. Ten observers participated in this experiment.

Results

As is shown in Fig. 5, the perceived MAE direction was opposite to the tested set's adapting direction in the four Single conditions (the four groups on the left of Fig. 5). The response proportions of this opposite-MAE direction ranged from 85 % to 95 % for all four conditions, with each condition having a small proportion (4 % to 13 %) of trials in which the observer reported no MAE direction. By contrast, in the Mixed condition, the most frequently chosen option was NoMAE (36 %), and the directional responses were distributed (from 10 % to 24 %), suggesting that observers did not consistently perceive any specific MAE directions in this condition. These results reveal that spatial integration of local illusory signals is sufficient for generating a circular/radial MAE, despite the lack of conscious awareness of any complex motion patterns during adaptation.

Experiment 4: Dynamic MAE induced by adapting to imperceptible motion directions

The results from the previous experiments established the existence of an aftereffect induced by imperceptible global motion directions in translational and complex (circular/radial) motion patterns. However, these experiments only measured the perceived directions of global MAE and did not provide an objective measure of MAE strength. Experiment 4 employed the coherence nullification paradigm (Blake & Hiris, 1993) to quantitatively measure the strength of aftereffects. In addition, the previous two experiments used stationary images to measure static MAEs. Research has shown that static MAE and dynamic MAE reveal adaptation-induced changes at different levels of motion processing: MAEs tested with dynamic patterns are believed to probe adaptation-induced changes at higher-levels of motion processing, whereas static test patterns probe changes at a low level of motion processing (Ashida & Osaka, 1994; Culham et al., 1998; Mareschal, Ashida, Bex, Nishida, & Verstraten, 1997; Mather et al., 2008; Nishida, Ashida, & Sato, 1994, 1997; Nishida & Sato, 1995; Verstraten, Fredericksen, van Wezel, Lankheet, & van de Grind, 1996). If MAEs observed in Experiments 2 and 3 were based solely on the adaptation-induced changes at a low processing level, similar effects might not be observed using a dynamic test pattern. Experiment 4 was designed to test this possibility.

Experiment 4 tested whether dynamic MAE can still be induced after adapting to imperceptible motion directions. In contrast to the stationary images used in the previous two experiments, test stimuli in Experiment 4 were dynamic, with varying global-motion coherence levels. The strength of the MAE was measured using the coherence level at which the MAE percept was "nullified." In addition, because the MAE

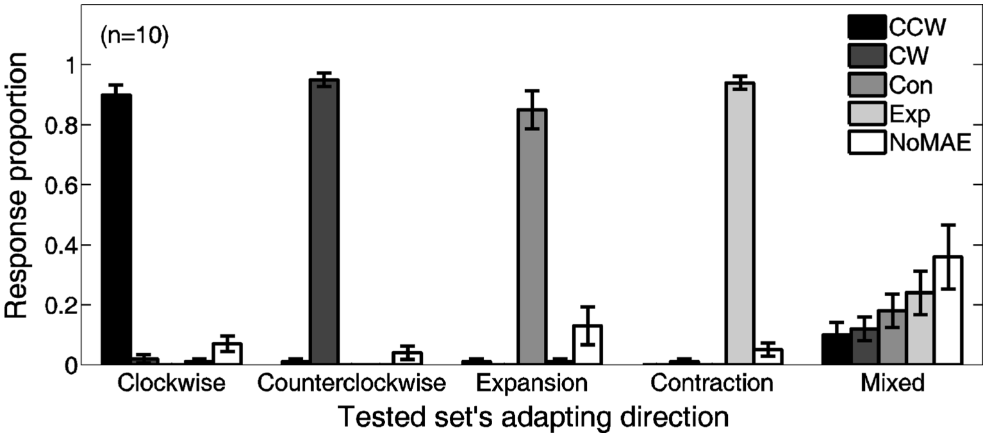

Fig. 5 Results of Experiment 3. Bar groups indicate conditions. Shades indicate different MAE directions reported by the human observers. Each error bar represents ±1 *SEM*

observed in the previous two experiments largely originated from the adaptation of local-motion detectors, it is important to compare its strength with other types of MAEs that involve different adaptation mechanisms. A number of psychophysical studies have reported a "phantom MAE" (e.g., Lee & Lu, 2012; Snowden & Milne, 1997; Weisstein, Maguire, & Berbaum, 1977), which refers to an MAE perceived when the test stimulus was presented at locations in the absence of adapting stimulus. Since low-level, local-motion detectors have small receptive fields, the generation of MAE at nonadapting locations is believed to result from the adaptation of high-level, global-motion detectors (Snowden & Milne, 1997). In Experiment 4, measures of phantom MAE served as a means to specifically probe the mechanism that generates MAE solely on the basis of global adaptation. Using the same method of measuring MAE strength, Experiment 4 was designed to allow comparison of the strengths of two types of global MAE: the aftereffect determined by spatial integration of local illusory signals (as observed in Exps. 2 and 3) versus the aftereffect of global adaptation generated by adaptation-induced changes in high-level, global-motion detectors (the phantom MAE).

Method

Design

Experiment 4 included two factors, number of adapting directions and test locations. The adapting stimulus contained either one global motion direction or five global directions. Test location was varied, with test elements being presented at either nonadapting or adapting locations. These conditions formed a 2 (global: adapt vs. not adapt) × 2 (local: adapt vs. not adapt) factorial design. The four conditions (illustrated in Fig. 6) were named by the level(s) of processing at which adaptation was introduced. With one adapting direction and test at adapting locations, the *Both* condition probed both local and global processing levels; with one adapting direction and test at nonadapting locations, the *Global* condition only probed the global motion-processing level; with five adapting directions and test at locations where motion signals were

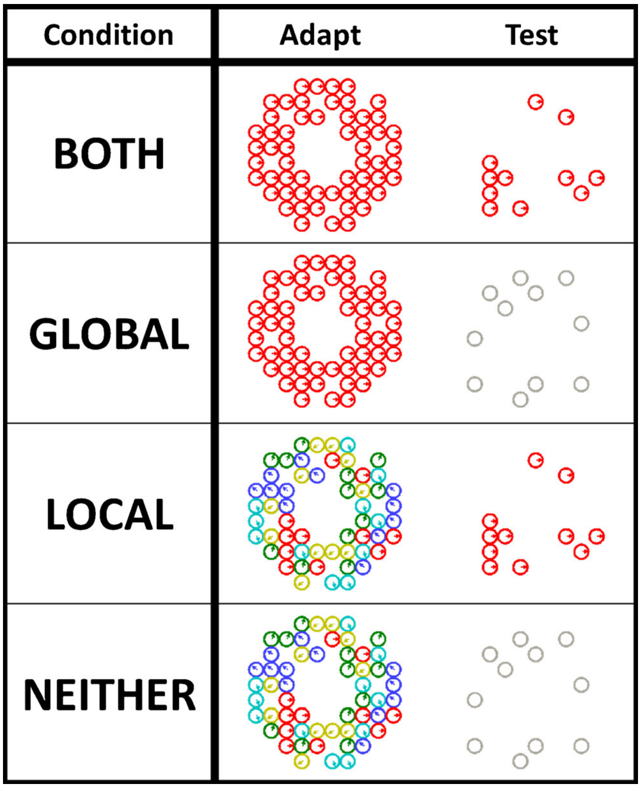

Fig. 6 Illustration of the design in Experiment 4. Colors and arrows represent the global adapting directions. Note that the elements in the test of the Both and Local conditions (right column, first and third rows) overlap with same-colored elements in the adapting stimulus (middle column), whereas the elements in the test of the Global and Neither conditions (right column, second and fourth rows) are at nonadapting locations that do not overlap with any of the adapting elements

coherent with one global motion direction during adaptation, the *Local* condition only probed the local motion-processing level; and with five adapting directions and test at nonadapting locations, the *Neither* condition served as a baseline control.

Stimulus

The stimulus parameters were identical to those used in Experiments 2 and 3, except for the following differences. We first randomly grouped elements into six sets. Then, one set was randomly chosen as the *reference* set, one as the *phantom* set, and the remaining four as *supporting* sets.

In the adapting stimulus, locations in the *phantom* set were always left blank in order to eliminate local adaptation at those locations. The global adapting direction assigned to the elements in the *reference* set was always horizontal (leftward or rightward, alternated across blocks). Across different conditions, we manipulated global adapting directions of elements in the *supporting* sets in order to control the number of adapting directions. In the Both and the Global conditions, in which we aimed to introduce global direction adaptation, the elements in all *supporting* sets were assigned the same global adapting direction as the *reference* set (i.e., leftward or rightward). This constraint resulted in a unidirectional adapting pattern with a 100 %-coherent global motion. In the Local and the Neither conditions, in which we aimed to minimize global direction adaptation, different global adapting directions were assigned to the four *supporting* sets, so that the five global directions (four *supporting* and one *reference*) were evenly spaced around 360º. This resulted in a multidirectional adapting pattern similar to that used in Experiment 2.

In the test stimulus, we manipulated the locations at which we presented Gabor elements. During the test phase in the Both and Local conditions, only elements in the *reference* set were presented, so that their global adapting direction had been either leftward or rightward during adaptation. During the test phases in the Global and Neither conditions, only elements in the *phantom* set were presented, so that no elements had been presented at these locations during the preceding adaptation phase.

In order to measure the strength of MAE using the nullification paradigm (see the “Procedure” section below for details), we varied the global-motion coherence in the test stimulus. We controlled the proportion of elements that signaled a globally coherent leftward or rightward direction (Amano et al., 2009; Lee & Lu, 2010). For example, in a test stimulus with +.70 coherence, 70 % of the Gabor elements were assigned the *same* global-motion vector (hence the positive sign) as that of the adapting stimulus (e.g., leftward), whereas the remaining elements were each assigned a random global direction, with a speed equal to that of the global adapting speed. In a test stimulus with –.40 coherence, 40 % of the elements were assigned a global-motion vector that was *opposite* to the adapting-motion vector (hence the negative sign; e.g., rightward), whereas each of the remaining 60 % was assigned a random global direction. Seven coherence values were tested for each condition. The coherence values for each condition were determined on the basis of the results of pilot experiments, as follows: –.95, –.70, –.30, 0, .30, .70, and .95, for the Neither condition; and –.50, –.10, .10, .30, .50, .70, and .95 for the other three conditions.

Procedure

As in previous experiments, observers were instructed to always maintain fixation at a cross located at the center of the stimulus area. On the first trial, the adapting stimulus was first presented for 60 s. Right after the adapting stimulus had disappeared, the test stimulus was presented for 280 ms. The response phase immediately followed and lasted for 2 s. Observers were instructed to perform a two-choice discrimination task, in which they determined whether the global motion direction of the test stimulus was leftward or rightward. We limited the time window of responses in order to minimize the fading of MAE through trials of top-up adaptation. Observers were encouraged to respond within 2 s, although response for a particular trial would still be recorded even if the following trial had begun. Almost all responses (about 99 %) were made within 2 s, and the longest response took only 3.6 s.

Similar to the procedure in Experiments 2 and 3, the following trials were “top-up” trials that had the same procedure as the initial trial, except that adaptation duration for the top-up trials was shortened to 6 s. For each condition, each observer ran ten blocks of 14 trials. Each block consisted of two trials for each of the seven coherence levels. Order of these 14 trials was randomized within each block. This resulted in 20 responses for each coherence level. Adapting direction of the *reference* set (i.e., left or right) alternated across blocks, and a rest period of 60 s was inserted between blocks. Observers ran all ten blocks of the same condition within the same experimental session. Order of conditions was counterbalanced across observers. Six observers, all naïve to the purpose of the experiment, participated in Experiment 4.

Results

At each coherence level, we computed the proportions of responses in which the observers reported that the test stimulus moved in the same direction. The strength of a dynamic MAE is measured as the shift of the point of subjective equality (PSE), which reveals the coherent-motion strength required in the test stimulus to nullify the MAE. For each observer in each condition, we fitted the data with the cumulative normal distribution function with two parameters, mean μ and standard deviation σ. The estimate of the μ parameter, corresponding to the coherence level at which the observer's response proportion was at 50 %, was taken to be the PSE estimate.

The data of one observer were removed from the analysis because the cumulative normal distribution function could not reliably fit the data ($R^2 < .50$ for one condition). For the remaining five observers, the function fitted their data well (R^2 from .82 to .99). The PSE shift away from the zero-coherence point, which is the null in motion coherence, was taken as the strength of the MAE.

Figure 7 shows response proportions as a function of the coherence ratio in test stimuli from a representative participant (left panel), and the strength of the MAE, measured as the shift of the PSE for each condition, averaged across all five observers (right panel). We analyzed the data using a 2 (global adaptation: presence or absence) × 2 (local adaptation: presence or absence) repeated measures analysis of variance. No significant interaction was found between the two factors [$F(1, 4) = 0.596$, $5p = .48$]. Both of the main effects were found to be significant [global adaptation, $F(1, 4) = 547.63$, $p < .0001$; local adaptation, $F(1, 4) = 14.876$, $p = .018$], implying that dynamic MAE can be generated by adaptation-induced changes at the local level, the global level, or both. As is shown in the right panel of Fig. 7, the strength of the MAE was strongest when adaptation was induced at both the global and local levels of motion processing (Both condition, $M = .77$). In contrast, aftereffects were absent when neither of the levels was adapted (Neither condition, $M = .01$). The "phantom" MAE observed in the Global condition ($M = .59$) and the strength of the MAE observed in the Local condition ($M = .31$) were both found to be significantly different from zero [Global vs. Neither, $F(1, 4) = 53.884$, $p = .002$; Local vs. Neither, $F(1, 4) = 23.539$, $p = .008$]. Interestingly, MAE was stronger when adaptation was induced at the global level only than when it was induced at the local level only [Global vs. Local, $F(1, 4) = 26.126$, $p = .007$]. Finally, the difference in MAE strength between the Both and Global conditions was not statistically significant [Both vs. Global, $F(1, 4) = 2.058$, $p = .225$], suggesting a strong contribution of adaption at high-level motion processing in determining the strength of MAE observed with the multiple-aperture display.

The results of Experiment 4 revealed two important findings about the MAE after adaptation to imperceptible motion directions. First, in the Local condition, dynamic MAEs were still observed, even when human observers were not aware any global motion directions during adaptation. This result suggests that the propagation of low-level adaptation effects per se is sufficient to produce not only a static MAE (as shown in Exps. 2 and 3), but also a dynamic MAE. Moreover, this integrative mechanism with local illusory signals is potent even in the absence of awareness of the underlying directions during adaptation. Second, the strength of the MAE observed in the Local condition was weaker than the aftereffect (i.e., phantom MAE) in the Global condition. Previous research has shown that the MAE tested at adapted locations or regions was usually stronger than the "phantom MAE" tested at nonadapted locations (e.g., Snowden & Milne, 1997). Our finding suggests that, by removing the adapting directions from awareness, it is possible to obtain a weaker aftereffect at adapted locations than the phantom MAE tested at nonadapted locations.

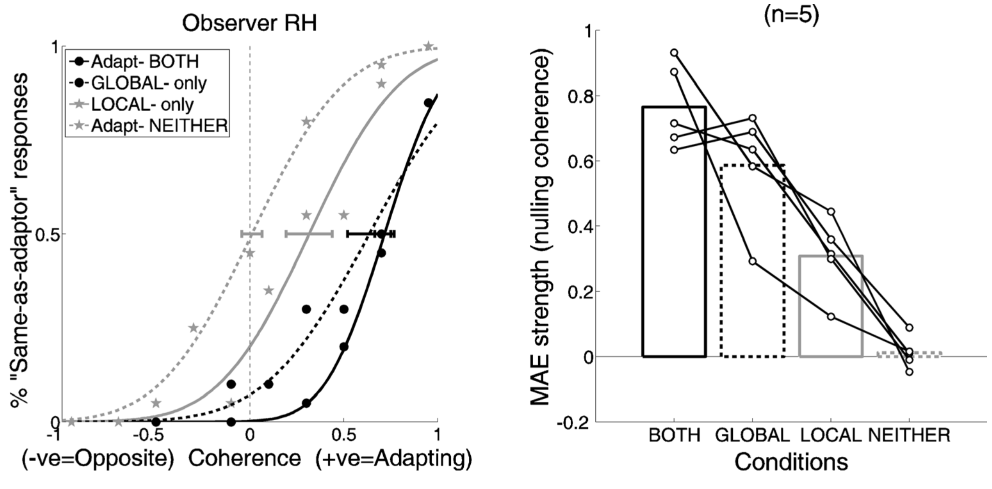

Fig. 7 Results of Experiment 4. (Left) Psychometric curves fitted for observer R.H. in the four conditions: Both (dark circles, solid line), Global (dark circles, dashed line), Local (light stars, solid line), and Neither (light stars, dashed line). Horizontal error bars indicate the 95 % confidence intervals of the points of subjective equality (PSE), the coherence level required in the test stimulus to nullify the MAE. (Right) Average MAE strengths (as shifts in the PSE from zero coherence) for the five observers. Each open circle marks the MAE strength for each observer in each condition. The results for each observer are connected with a thin solid line

General discussion

In our experiments, we found that adaptation of local-motion detectors per se is sufficient to produce a significant global MAE (translational, rotational, or radial). This MAE generation process did not require the conscious perception of any of the global motion directions during adaptation. Taken together, these results support the existence of a mechanism in the visual system that automatically integrates local illusory signals to produce a global MAE percept.

Relation to previous studies of awareness and adaptation

It is important to note the difference between the present study and previous ones in terms of the methods used to address the relationship between awareness and MAE. First, binocular-rivalry studies, in essence, render the adaptor invisible by presenting different stimuli to the two eyes. It has recently been shown that eye-of-origin information is preserved at the global, integrative stage of motion processing and contributes to computing motion in depth (Rokers, Czuba, Cormack, & Huk, 2011). Since the adaptation of this global processing stage can generate a global MAE percept (Snowden & Milne, 1997), disrupting the source of information feeding into this stage may affect its adaptation, and thus the subsequent MAE. When using binocular rivalry to study motion adaptation, researchers presented the motion adaptor to one eye and a rival stimulus to the other. Although any effect on the subsequently observed MAE may be due to awareness of the motion adaptor, it could also be due to weak adaptation effects caused by the ocularity of the motion adaptor. In the present study, we blocked the adapting direction(s) from observers' awareness while allowing observers to view the same motion adaptor with both eyes. This technique allows us to dissociate the effect of awareness from that of an eye-of-origin manipulation on the generation of MAE.

In addition to binocular rivalry, previous studies have used crowding as a technique to render the adapting-motion stimulus invisible (e.g., Aghdaee, 2005; Blake et al., 2006; Whitney & Bressler, 2007). These studies have shown that, when the motion adaptor was flanked by other stimuli, observers were unable to determine the direction of the adaptor but still perceived significant MAE at the adaptor location. Although these findings appear to be similar to the findings reported in the present study, it should be noted that all of these crowding studies tested the MAE without the involvement of motion integration over space. These studies measured MAE using a single grating, in which the motion signal was confined within a *local* region. Also, the adapting direction that was rendered invisible was confined by the *local* adapting direction, not the *global* motion that involves spatial integration of local signals. On the contrary, in the present study, we rendered the *global* adapting direction invisible and measured the *global* MAE after adaptation, to address a new issue that has not been studied in previous crowding research.

Our method is also different from that used by Nishida and Sato (1992, 1995), who created an adapting stimulus with both first-order (luminance-defined) and second-order (contrast-defined) motion signals using drifting gratings. By making the two types of motion drift in opposite directions, the investigators demonstrated that, under a certain condition, it is possible to observe significant MAE even when the adapting direction was ambiguous. In the critical condition in which the adapting stimulus was ambiguous, observers reported perceiving one adapting direction as often as perceiving the other, opposing one. Note that the adapting directions were not completely masked from visual awareness. This situation is different from what our observers reported in the present study, in which we used an adaptor with *imperceptible* directions. As is shown in Experiment 1, a multidirectional pattern was indistinguishable from a random pattern. In addition, in a pilot study, we found that observers were not even able to indicate the underlying directions or the number of directions present during adaptation when the number of directions was increased to five. Our findings, therefore, extend the hypothesis proposed by Nishida and Sato (1992, 1995), and show that the perceptibility of adapting directions is not necessary for the generation of MAE.

The rationale for our methods of "overloading" direction-selective mechanisms at the global level during adaptation is similar to the technique used by He and MacLeod (2001). Although they measured the tilt aftereffect (TAE) instead of the MAE after adapting to oriented gratings, the similarity between their study and the present study lies in the use of a "beyond-limit" adaptor. In their study, the perceptual dimension from which an aftereffect was tested was grating orientation. However, for the adaptor, they used gratings with a spatial frequency so high that observers' discriminability of orientation was at chance level. Analogously, in the present study, the perceptual dimension from which an aftereffect was tested was motion direction. We used motion patterns embedded with so many directions that observers' were unable to discriminate between a multidirectional pattern and a random pattern. To our knowledge, the present study was the first one to employ such a technique to render the adapting directions imperceptible and extract a significant directional MAE.

Propagation of low-level adaptation effects

In the multiple-aperture stimulus, the local MAE induced from an individual Gabor patch is orthogonal to its assigned orientation. Because each Gabor patch was assigned with a random orientation, using one or two local patches was unlikely to yield aftereffects consistently opposite to one of global motion directions in the adaptor. In addition, findings from our previous work using multiple-aperture motion patterns have provided strong evidence that a global, integrative mechanism is involved in generating the MAE percept by integrating local illusory signals at test locations (Lee & Lu, 2012). The findings in the present study provide converging evidence for the existence of a mechanism that integrates local illusory motion signals over space. Importantly, such an integrative mechanism does not rely on conscious awareness of adaptation motion directions.

This hypothesis has been supported by physiological studies of motion adaptation (Kohn & Movshon, 2003) and a psychophysical study of face adaptation (Xu, Dayan, Lipkin, & Qian, 2008), which showed that adaptation effects at a low level of processing can be propagated downstream to influence later stages of processing. This downstream propagation may be one important source of the perceived high-level aftereffects. In the present study, our results demonstrate how, in the case of motion adaptation, such propagation of low-level, local illusory signals can be accomplished via spatial integration of local illusory signals.

One might be concerned that observers could have just indicated the local percepts of MAEs at one or two locations in their responses and, thus, the present results do not necessarily imply the involvement of the spatial integration of local illusory signals. However, this strategy is unlikely to provide a parsimonious explanation to the experiments reported in the present study. First, if the perceived MAE did not involve the spatial integration of local illusory signals, the reported MAE direction should not be affected by the local MAE of the neighboring, nontested elements. Had that been the case, we would not have obtained the close-to-uniform distribution of MAE directions in the Mixed condition of Experiment 2, or the coherence-dependent psychometric curves in the Local condition in Experiment 4. Second, in similar experiments using multiple-aperture stimuli, we have shown that perceived MAE direction, after adapting to a bidirectional transparent pattern, is consistent with the integrated direction of local MAEs across space (Lee & Lu, 2012). Finally, instructions explicitly emphasized that the task was to indicate the “global, overall” perceived direction during the test phase. Observers had completed at least 20 practice trials and confirmed that they understood the instructions before proceeding with the actual experimental sessions. For all these reasons, it is unlikely that observers were merely reporting local MAE at one or two locations across all trials. Rather, the present findings support the existence of a mechanism in the visual system that integrates local illusory signals across space.

Our findings may also shed light on the functional goal of sensory adaptation in general. Most previous studies have used perceptible global motion directions as the adapting stimulus. Hence, the system “knows” the motion directions with which it is presented (e.g., leftward, expansion, or clockwise rotation), and it is, therefore, reasonable for the system to be adaptive to these perceptible directions. However, in the present study, often motion directions were imperceptible in the adapting period. Theoretically, the system could have avoided being adaptive to such apparently random motion, because it does not represent a meaningful motion environment. Nonetheless, our findings suggest that the visual system remains adaptive to the local motion signals, to the extent that adaptation-induced effects across locations can be subsequently integrated to generate a global MAE. In other words, when no specific global adapting directions are available, the visual system still retains local motion information, which is inherently ambiguous in signaling the global motion direction (Marr & Ullman, 1981). Such retention of local information is remarkably precise, given that the perceived global aftereffect direction can be determined by test locations. It has been proposed that sensory adaptation can be understood as a process by which the system, in response to changes in the environment, recalibrates its response characteristics and enhances its coding efficiency (Barlow, 1990; Clifford, Wenderoth, & Spehar, 2000). From a hierarchical-processing perspective, our findings suggest that the system can enhance its coding efficiency not only by recalibrating the response characteristics of high-level processing units, but also by temporarily altering the response characteristics of low-level detectors. It is possible that integration of the low-level readjustment effects via some high-level mechanisms is a means by which the hierarchical system improves its overall coding efficiency. It would be useful for future computational studies to investigate how this bottom-up, local-to-global, adaptation strategy may lead to more-efficient coding in representing the dynamic environment.

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