Research Article

A Motion Aftereffect From Still Photographs Depicting Motion

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ABSTRACT—*A photograph of an action can convey a vivid sense of motion. Does the inference of motion from viewing a photograph involve the same neural and psychological representations used when one views physical motion? In this study, we tested whether implied motion is represented by the same direction-selective signals involved in the perception of real motion. We made use of the motion aftereffect, a visual motion illusion. Three experiments showed that viewing a series of static photographs with implied motion in a particular direction produced motion aftereffects in the opposite direction, as assessed with real-motion test probes. The transfer of adaptation from motion depicted in photographs to real motion demonstrates that the perception of implied motion activates direction-selective circuits that are also involved in processing real motion.*

Humans quickly and efficiently extract motion information from a wide range of stimuli in the environment. Even visual stimuli that do not contain motion but only imply it, such as frozen-motion photographs, lead to the rapid and automatic extrapolation of motion paths (Freyd, 1983). For example, in the top photograph in Figure 1a, it is easy to see a sprinter running to the left. The sense of motion must be inferred from prior knowledge; there is, of course, no physical motion in the photograph. Such stimuli would appear to have little in common with the drifting dots and gratings commonly used to study neural mechanisms of motion processing, other than the fact that the observer knows that both types of stimuli depict motion in some sense. In the study reported here, we investigated how the sense of motion from static photographs is represented in the visual system.

The primate brain contains a number of visual areas involved in the analysis of moving objects and patterns (Maunsell & Newsome, 1987; Tootell et al., 1995). Such areas contain neurons that respond to moving images in a direction-selective manner (Dubner & Zeki, 1971; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Huk, Ress, & Heeger, 2001). The direction of motion, however, may be inferred not just from the analysis of visual motion, but also from low-level visual form cues, such as motion streaks (Burr & Ross, 2002; Geisler, 1999), or from higher-level cues, such as the posture of a person in motion (as in the photo of the sprinter in Fig. 1a). Is the sense of motion derived from such static cues instantiated by the same neural and psychological mechanisms that subserve the perception of physical motion? In particular, we sought to test whether viewing implied-motion images recruits the same direction-selective neural circuitry used for the perception of real visual motion. For example, does viewing the still photograph of the sprinter in Figure 1a elicit responses from the same leftward-selective neurons that would respond during the perception of real leftward motion?

Neuroimaging studies have shown that brain areas used to analyze physical motion are also activated by viewing implied-motion stimuli (Kourtzi & Kanwisher, 2000; Lorteije et al., 2006; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Senior et al., 2000). In these studies, visual motion areas, such as the human middle temporal/medial superior temporal complex (MT+), responded more strongly when subjects viewed photographs or silhouettes of animals, people, objects, or natural scenes containing implied motion than when they viewed similar images that did not imply motion (e.g., a cup falling off a table compared with a cup resting on a table, or a running athlete compared with an athlete at rest). These studies demonstrate that implied motion can activate brain areas also known to be engaged by real image motion.

However, one cannot infer from such studies whether viewing stimuli with implied motion elicits directional motion signals in the brain, nor whether the same subsets of neurons, with similar tunings, are activated for implied and physical visual motion. Functional magnetic resonance imaging measures net activity, and does not currently have the resolution to routinely resolve individual columns. Moreover, although area MT+ has been shown to carry direction-selective signals in response to visual motion (Huk & Heeger, 2002; Huk et al., 2001), it can also be

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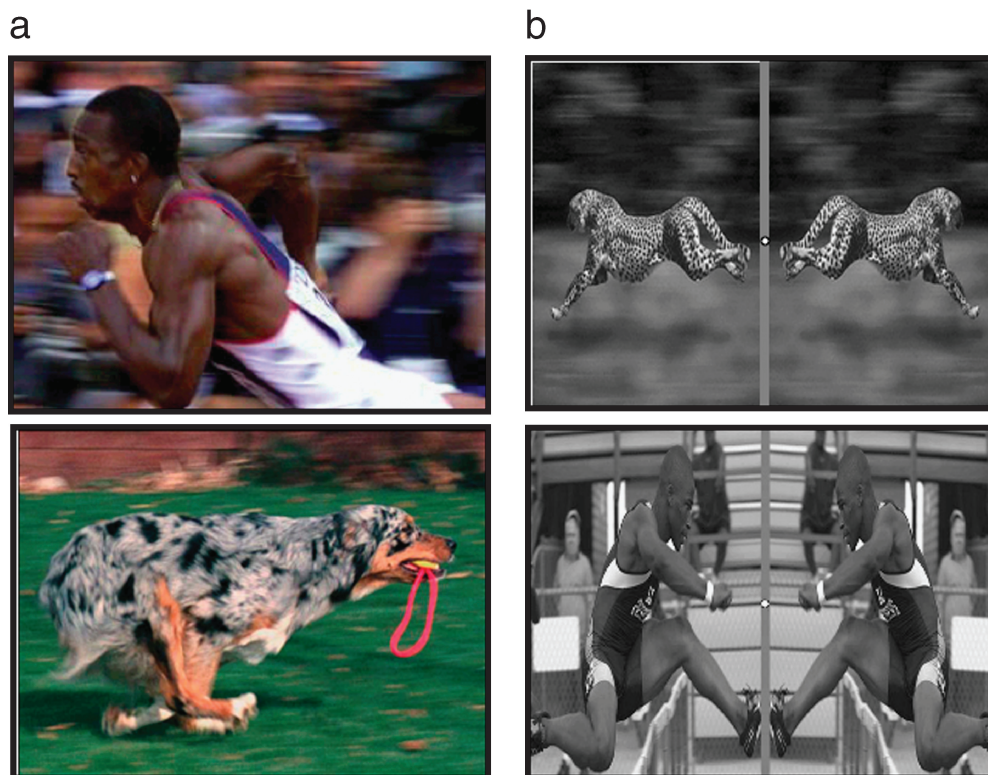
a

b

Fig. 1. Examples of test stimuli. In the first and second experiments, subjects viewed photographs with implied rightward or leftward motion (a), and in the third experiment, they viewed photographs with implied inward or outward motion (b).

activated by other factors, like attention and arousal (Beauchamp, Cox, & DeYoe, 1997; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Saenz, Buracas, & Boynton, 2002), that may not be directionally selective (Huk et al., 2001). Thus, a net increase in MT+ activation need not imply the existence of a direction-selective signal, nor do multiple instances of MT+ activation confirm that the same direction-selective neurons have been activated repeatedly (Grill-Spector & Malach, 2001; Huk & Heeger, 2002).

In order to infer whether the same neural circuits are employed by inference and perception in the domain of visual motion, we made use of a motion aftereffect (MAE) paradigm. The MAE is a well-studied psychophysical phenomenon (Mather, Verstraten, & Anstis, 1998; Wohlgemuth, 1911) used to infer and assess the properties of direction-selective neural mechanisms. Prolonged viewing of motion in one direction makes subsequently viewed stationary (or directionally ambiguous) patterns appear to move in the opposite direction. This illusion is believed to result from the adaptation-induced decrease in activity of directionally selective neurons that respond to the adapted-to direction of motion (Barlow & Hill, 1963; Mather et al., 1998; Sutherland, 1961). This direction-selective adaptation in turn causes an imbalance in the population activity of neurons that represent different directions of motion.

Because of this postadaptation imbalance, the neural population code will indicate a net direction of motion opposite the adapted-to direction when probed with stationary or directionally ambiguous stimuli. Thus, the presence of an MAE can be used as a psychophysical test for the involvement of direction-selective neural mechanisms.

We predicted that if viewing photographs of implied motion relies on the same direction-selective neurons that are involved in perception of physical motion, then viewing a series of such photos depicting motion in the same direction would adapt direction-selective neurons and produce an MAE. We tested this hypothesis in three experiments in which we measured whether viewing implied motion in one direction altered the perceived direction of subsequently presented real motion. In two experiments, the motion implied from the photographs was either leftward or rightward (Fig. 1a), and in the third experiment, the implied motion was inward or outward (Fig. 1b).

METHOD

Each experiment began with a baseline motion-sensitivity task using moving-dot test stimuli. Following the baseline task, subjects viewed a series of implied-motion photographs interleaved with test trials of moving-dot probes. The dot probes were used to assess whether or not an MAE resulted from viewing the

implied-motion photos. In the first experiment, subjects viewed pictures with implied motion to the left or to the right and were tested with dot displays containing leftward or rightward real motion, making two-alternative forced-choice judgments on the direction of dot motion (left or right). The second experiment was similar, except that after 50% of the picture sequences, selected at random, there was a 3-s delay between the offset of the last picture and the onset of the moving-dot test trial. This delay was introduced to test whether an MAE from implied motion, like MAEs from physical motion (Keck & Pentz, 1977), would decay during a brief period following adaptation. In the third experiment, mirror-reversed pairs of implied-motion photographs were shown simultaneously side by side to create implied motion either toward fixation ("inward") or away from fixation ("outward"). In all three experiments, subjects were instructed to attend to the pictures for a memory test following the experiment; there were no instructions to imagine or attend to the motion implied in the photographs. All subjects performed above chance levels on the old/new recognition memory test at the end of the experiment.

Participants and Equipment

All subjects (26, 19, and 32 for Experiments 1–3, respectively) were naive to the purpose of the experiments and were recruited from the Massachusetts Institute of Technology community. Subjects provided written consent and were paid for participation. They were seated approximately 40 cm away from the display, a CRT monitor with a resolution of 1024×768 pixels (26×19.5 cm) and a refresh rate of 75 Hz.

Moving-Dot Test Stimuli

We used a standard moving-dot direction-discrimination task (Newsome & Pare, 1988), which had previously been employed as a means to assess and quantify MAEs from adaptation to real motion (Blake & Hiris, 1993). Random dot displays such as those used in this task have been important for studying visual motion systems because they do not contain recognizable features that can be used to infer a change in location over time, and are thus thought to rely on primary motion-processing mechanisms.

In the first two experiments, each test stimulus consisted of 100 dots contained within a rectangular window whose length and width were 33% of the entire display (approximately $12° \times 9°$ of visual angle). We manipulated the proportion of dots moving coherently in a particular direction (motion coherence) from trial to trial, and subjects were instructed to indicate the direction of global motion using a key press (left or right). On each frame, a subset of the dots, equal to the percentage of dots moving coherently for that trial, was selected to move either left or right. All other dots disappeared and randomly reappeared at any other location within the test window. A new set of dots was reselected for coherent movement on each frame, so that the

trajectory of single dots could not be followed throughout a trial. Each 1-s test trial consisted of 25 frames displayed for 40 ms each. Dot displacement for coherent motion was approximately $0.05°$ per frame.

In the third experiment, the test stimuli were identical, except that they consisted of 200 dots, 100 on each side of fixation (instead of 100 total), and they moved horizontally toward or away from the vertical midline (instead of left or right). By a key-press response, subjects indicated whether the dots appeared to move inward or outward. The window of the test stimulus was the same size as in the first two experiments, so the dot density was double.

Baseline Motion Sensitivity

Prior to the adaptation phase of each experiment, subjects were tested on a baseline motion-calibration task, during which dot coherence ranged from 5% to 65% over 180 1-s trials consisting of 25 frames each; motion was either leftward or rightward in the first two experiments, and either inward or outward in the third experiment. A logistic function was fitted to the responses, with "leftward" or "outward" arbitrarily coded as negative coherence, and "rightward" or "inward" as positive coherence. For each subject, the amount of coherence corresponding to asymptotic performance (99% "rightward" or "inward" responses and 1% "rightward" or "inward" responses) was determined from the fitted logistic function. The average of the absolute value of these two values was considered the maximal dot coherence for each subject, and defined as 1 unit of normalized coherence. For each direction of motion, stimuli with 1 unit of normalized coherence and with 50% and 25% of this coherence value were used as test stimuli in the adaptation phase of the experiment. There were thus six different test stimuli per subject; within each block, the different stimuli were repeated an equal number of times, in random order. Across subjects, the mean for 1 unit of normalized coherence corresponded to 35% ($SD = 14\%$) actual dot coherence.

Adaptation to Implied Motion

The adaptation stimuli were 103 color photographs with either leftward or rightward implied motion. The photos, found from Internet searches, depicted people, animals, or vehicles in motion. No photos contained text, and all photos were mirror-reversed so that they could be used for both directions of adaptation. Each image was centered on the screen, and its size was scaled to a fixed area of 200,000 pixels (about $130°$ squared), with the original aspect ratio maintained.

In the first experiment, the direction of adaptation, left or right, was constant within a block, and there were 30 adaptation trials in each of six blocks. Each adaptation trial consisted of a sequence of pictures lasting either 60 s (1st trial in a block) or 6 s (other trials) and was followed by a moving-dot test trial (see Fig. 2). A sequence of pictures was generated by randomly sampling from the 103 photos without repeat until all photos
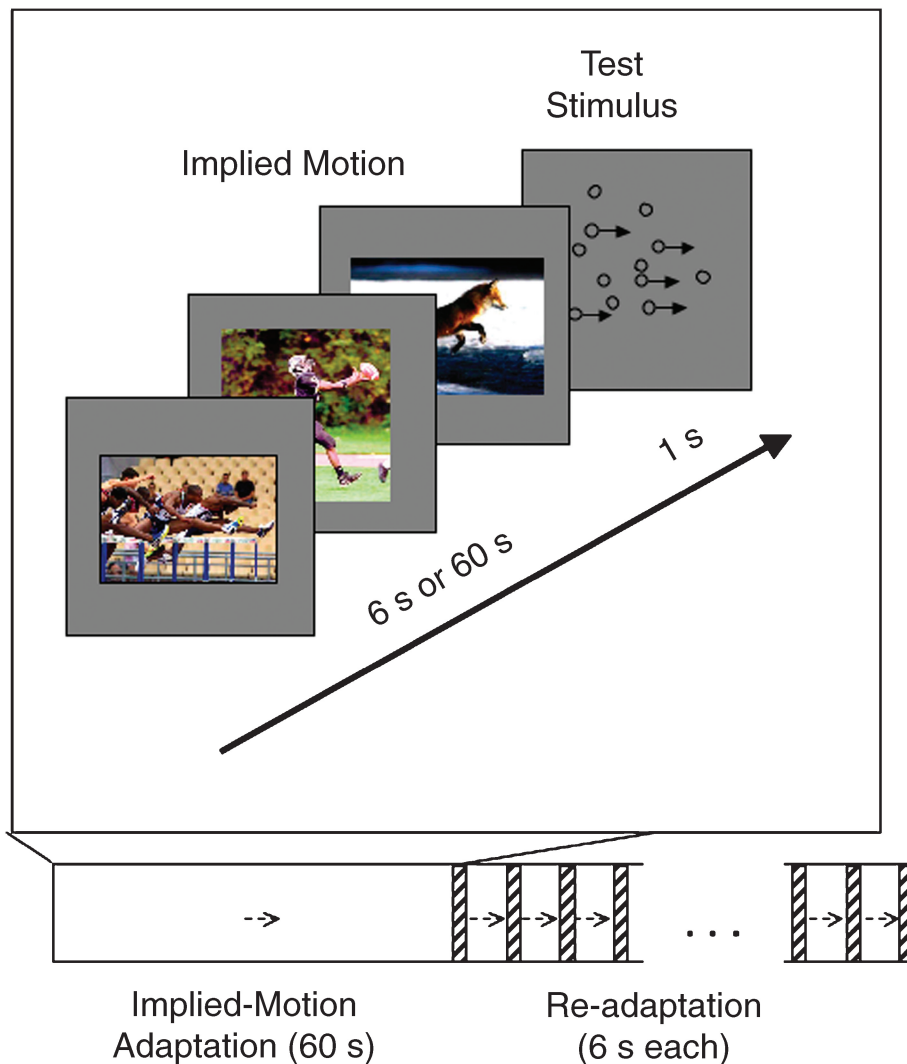
Fig. 2. Adaptation procedure. Adaptation consisted of viewing a succession of frozen-motion photographs with implied motion. Following 60 s of adaptation (the first trial per block), or 6 s of top-up adaptation, subjects made forced-choice judgments of the global direction of moving-dot test stimuli (25 frames presented over 1 s). The direction of adaptation varied randomly across six blocks. In the second experiment, there was a 3-s delay between the last picture shown on half the adaptation trials and the moving-dot test trial that came afterward.

were used, so that any picture was equally likely to follow every other picture. Pictures were shown every 545 ms, so that 110 photos were presented during the initial 60-s adaptation trial of each block, and 11 photos during each of the 6-s "top-up" adaptation trials. The initial adaptation trial and the 29 top-up trials in each block differed only in their duration.

The second experiment was identical to the first except for the following differences. There were 36 adaptation trials per block instead of 30, and on 50% of these trials, there was a 3-s delay with a blank screen between the last adapting photo and the onset of the test trial. Also, the presentation rate was 200 ms per picture, instead of 545 ms.

The adaptation procedure for the third experiment was the same as the procedure for the first experiment, except for the following differences. The 103 photos from the previous experiments were converted to gray scale and scaled to a fixed size of 512 by 768 pixels. Each picture and its mirror reversal were presented adjacently, such that the implied motion was either toward the center (inward) or away from the center (outward). Subjects were instructed to fixate a small spot (about 1°) at the border of the two images (see Fig. 1b). A pair of photos was shown every 427 ms, so that 140 pairs were seen during the initial 60-s adaptation trial and 14 were seen during the twenty-nine 6-s top-up trials.

Subject Exclusion

We excluded from analysis a small number of subjects who were likely to be guessing or otherwise unable to perform the direction-discrimination task. Two subjects from the first ex-

periment, 1 subject from the second experiment, and 3 subjects from the third experiment performed poorly on the baseline motion-sensitivity task, such that 1 unit of normalized motion coherence for these subjects would have exceeded 100% dot coherence. These subjects were excluded from analysis. In the first experiment, 5 subjects' performance on the dot-discrimination task did not exceed chance. That is, a logistic fit to the data for these subjects indicated that the likelihood of judging a test stimulus as moving in a particular direction (right or left) did not increase significantly with increased dot coherence in that direction. These subjects were also excluded from analysis.

RESULTS

We observed significant MAEs in all three experiments. After viewing implied motion in one direction, subjects were more likely to see the moving-dot test stimulus moving in the opposite direction. The population means, plotted in units of dot coherence normalized to each subject's motion sensitivity (see Method), showed that the direction of adaptation shifted the motion response function. This can be seen in Figures 3a through 3c by comparing for each pair of adapting conditions the point of perceived null motion, that is, the amount of motion coherence for which subjects were equally likely to respond "left" or "right" (the first two experiments) or "inward" or "outward" (the third experiment). For example, in Figure 3a, the point of perceived null motion contains more actual leftward motion coherence in the test stimulus following adaptation to leftward implied motion than following adaptation to rightward implied motion, a pattern consistent with an MAE in the direction opposite to the direction of implied-motion adaptation.

In Figures 3a through 3c, the size of the horizontal offset between paired functions reflects the amount of real motion needed to make a test stimulus presented following one direction of adaptation perceptually equivalent to a test stimulus presented following the opposite direction of adaptation. To quantify the MAEs across subjects, we fit separate motion response functions to each subject's data using logistic regression, and calculated the mean difference between the points of perceived null motion in paired adaptation conditions (see Fig. 3d).

In the first experiment, the point of perceived null motion differed by 0.22 ± 0.06 units of normalized motion coherence, $t(18) = 3.82, p = .001, p_{rep} = .99$ (unless otherwise noted, the significance of effects was assessed with two-tailed paired t tests comparing the location of the point of perceived null motion within pairs of adapting conditions). In terms of the actual (nonnormalized) test coherence, the shift in the null point was $8.7 \pm 2.5\%, t(18) = 3.48, p = .003, p_{rep} = .97$. If viewing implied motion did not lead to adaptation, the motion response functions would have overlapped, and hence there would have been no difference between the points of perceived null motion for rightward and leftward implied motion.

The results of the no-delay condition in the second experiment closely replicated the result of the first experiment: The null point shifted by 0.27 ± 0.09 units of normalized coherence, $t(17) = 6.47, p = .000, p_{rep} = .99$, or $8.9 \pm 1.9\%$ of actual test coherence, $t(17) = 4.74, p = .000, p_{rep} = .99$. However, with a 3-s delay between adaptation and test stimuli, the effect of adaptation was smaller: 0.10 ± 0.06 units of normalized coherence and $2.3 \pm 1.9\%$ of actual coherence. The difference between the no-delay and delay conditions was significant, $t(17) = 2.75, p = .013, p_{rep} = .94$, and $t(17) = 2.24, p = .038, p_{rep} = .90$, for normalized and nonnormalized test coherence, respectively.

Subjects in the third experiment showed significant adaptation to inward and outward implied motion. The point of perceived null motion shifted by 0.17 ± 0.04 units of normalized coherence, $t(28) = 4.98, p = .000, p_{rep} = .99$, or $5.7 \pm 1.0\%$ of actual coherence, $t(28) = 5.48, p = .000, p_{rep} = .99$.

DISCUSSION

In each of these three experiments, the viewing of photographs depicting movement led to systematic shifts in the responses to subsequent real-motion test probes. The test probes were more likely to be judged as moving in the direction opposite the direction depicted in the previous adapting photographs than to be moving in the same direction. The transfer of adaptation from implied motion to real motion provides evidence that still images depicting movement recruit direction-selective neurons, and demonstrates that processing implied motion can affect the subsequent perception of real motion.

Our results cannot be explained by low-level motion-energy biases in the image sequences, or by apparent motion between successive frames. The sequence of images was generated randomly on each adaptation trial. There was an equal likelihood that any particular pair of images would be seen in one order or the opposite order, and this rules out explanations based on spurious biases in motion energy or apparent motion. Further, it is unlikely that our results can be explained by systematic eye movements (e.g., Chaudhuri, 1991). Our use of inward and outward stimuli in the third experiment preclude explanations based on optokinetic nystagmus, and the fact that the pattern of results was the same as in the previous two experiments is evidence against explanations based on directional biases in eye movements during adaptation.

It also appears unlikely that the results obtained in these experiments were due to a strategic or cognitive bias, rather than a shift in the perception of the test stimuli. First, had the pattern of responses in the first experiment been driven by a nonperceptual bias, we would not have predicted the decline in the MAE after a brief delay, as observed in the second experiment. Second, a debriefing following the third experiment revealed that prior knowledge of the MAE did not explain the results: Of the 24 subjects who responded to a question asking whether or not they had heard of the MAE (5 subjects did not respond), 20
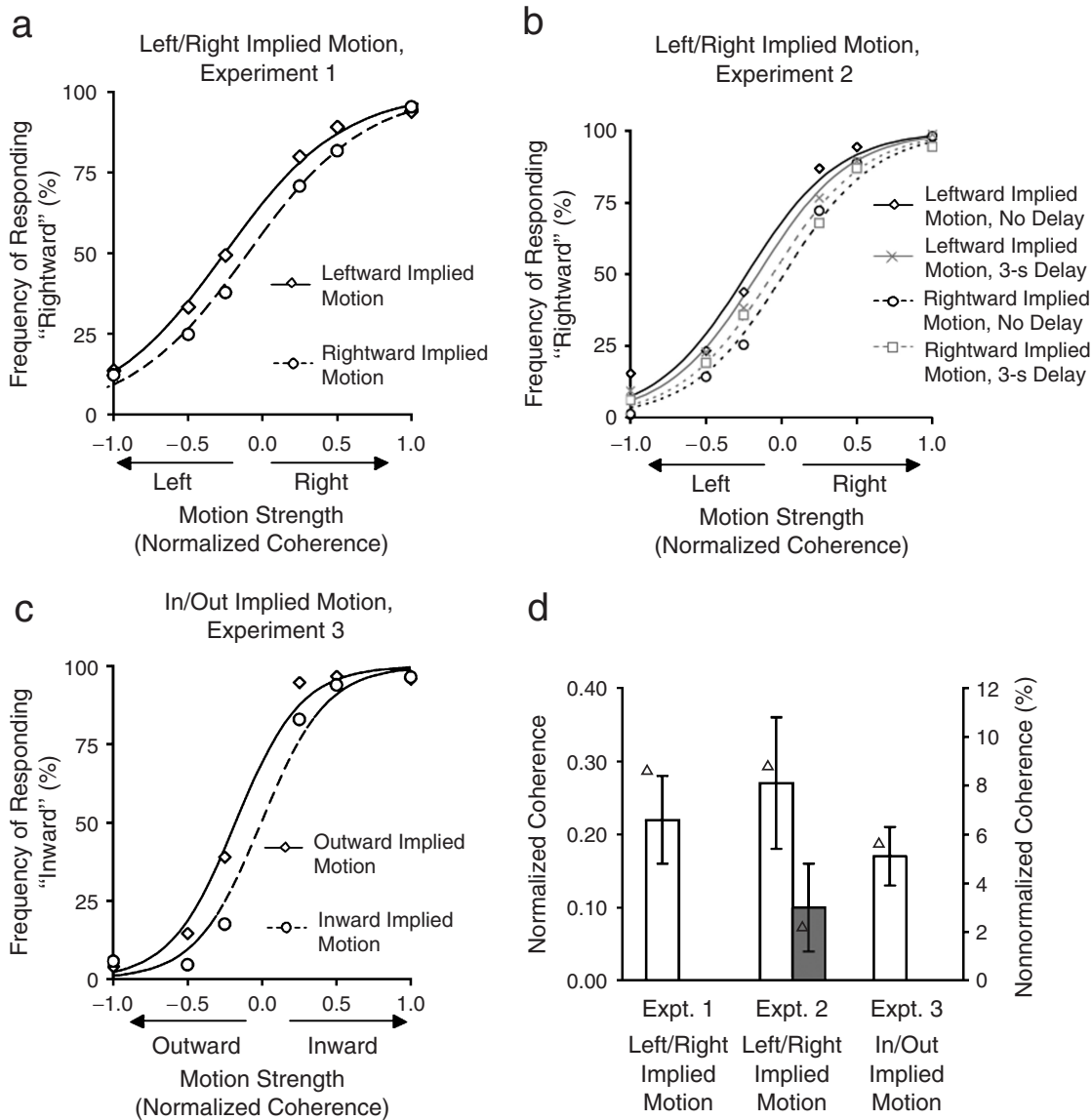
Fig. 3. Experimental results. For the first and second experiments (a and b), the frequency of responding ''rightward'' following adaptation to rightward and leftward implied motion is plotted as a function of motion coherence in the test stimulus. For the second experiment, results are shown separately for the delay and no-delay conditions. For the third experiment (c), the frequency of responding ''inward'' following adaptation to inward and outward implied motion is plotted as a function of motion coherence in the test stimulus. The graph in (d) summarizes the separation between the curves for each experiment. The bars show the mean separation across subjects in terms of normalized coherence; their shading indicates whether or not there was a delay between adaptation and test trials (white = no delay, gray = 3-s delay). The triangles indicate the separation in terms of actual (nonnormalized) coherence. Positive values indicate a separation in the direction predicted by adaptation. Error bars indicate standard errors.

said they had never heard of it. When forced to guess "whether prolonged viewing of upward motion would cause a subsequent static image to appear to move up or down," 14 of the 24 subjects responded "up," and 10 responded "down." The size of the observed MAE did not differ significantly depending on responses to these questions—"had heard" versus "had not heard" of the MAE (0.18 ± 0.03 vs. $0.28 \pm .015$ units of normalized coherence), $p = .552$ (two-tailed unpaired t test); answered "up" versus answered "down" (0.17 ± 0.05 vs. 0.23 ± 0.07 units of normalized coherence), $p = .438$.

Could our results be explained by aftereffects due to active visual imagery of motion? There is evidence that mental imagery of motion can activate motion-sensitive brain areas (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998; Grossman & Blake, 2001), and our own unpublished results suggest that imagery of motion can elicit an MAE. Nonetheless, although this explanation remains logically possible, it seems unlikely that subjects actively imagined motion in the experiments reported here. First, subjects were not instructed to imagine motion nor given any incentive to do so. Second, active imagery typically

requires from a few hundred milliseconds to several seconds (Cooper & Shepard, 1973; Kosslyn, 1976), and our stimulus presentation rates were relatively fast (2–5 Hz).

One might reasonably ask, nonetheless, whether viewing the photographs elicited direction-selective neural activity via automatic associative processes. We cannot rule this out, nor do we wish to. Such processes are compatible with Helmholtz's (1886/1924) notion of "unconscious inferences," which have been postulated to explain a wide range of perceptual phenomena (e.g., Barlow, 2001). In this view, pictorial cues to motion are learned from statistical regularities in the environment, such that static images containing familiar objects in motion can trigger motion responses via pattern-completion processes. Recently, by using explicit associative-learning paradigms, it has been shown that a previously meaningless static cue can, after training, bias the percept of an ambiguous-motion display (Qi, Saunders, Stone, & Backus, 2006) and can elicit directional signals in single neurons in macaque MT (Schlack & Albright, 2007). Moreover, when a moving stimulus repeatedly follows a predictable trajectory, direction-selective neurons in macaque parietal cortex signal the direction of that stimulus's motion when it is occluded (Assad & Maunsell, 1995).

Our results join a growing number of findings in the human and monkey literature showing interactions between form and motion processing (reviewed by Kourtzi, 2004). One important observation has been that a very simple type of form information, orientation, can strongly affect motion perception: Two types of stimuli that do not contain directional motion but do contain spatial orientation information, motion streaks (Burr & Ross, 2002; Geisler, 1999) and Glass patterns (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Ross, Badcock, & Hayes, 2000), have been shown to influence perceptual and neural visual motion processing. Because of sluggish temporal integration in the visual system, moving stimuli tend to create blur along the direction of motion, and the visual system may exploit this regularity to infer motion trajectories from orientation, including the orientation information in motion streaks and Glass patterns. We note, however, that the inference of motion from simple orientation cues and the inference of motion from high-level object and scene-related cues likely occur at different stages in the processing pathway. Motion streaks may be extracted quite early in processing (e.g., perhaps in primary visual cortex; Geisler, 1999). In contrast, inferring the direction of motion depicted in photographs likely occurs in higher-level object areas in visual cortex, as evidenced by electroencephalographic (EEG) studies showing a delayed response to implied-motion photographs (Lorteije et al., 2006), as well as by the sensitivity to the depiction of action in neurons in anterior regions of the temporal lobe in monkeys (Jellema & Perrett, 2003).

In summary, we found that direction-selective motion adaptation can result from viewing static images with implied motion. The direction-selective adaptation we report had an effect on subjects' perception of a real-motion stimulus immediately following adaptation. These findings demonstrate that inferring motion from purely form-based cues involves direction-selective motion mechanisms. Further, these mechanisms must rely on some of the same neurons used for motion perception because the adaptation transferred from implied motion to perception of real motion. That is, at least some neurons that are directionally selective for the perception of actual motion are also activated while observers view implied motion in that same direction. A very recent study has independently arrived at a related conclusion—that viewing real motion can affect the neural response to subsequent implied-motion photographs—using a physiological measure (EEG) instead of a perceptual measure (Lorteije et al., 2007). An exciting extension of the work reported here would be to directly investigate the neural signals involved in the perception of motion implied in static images.

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