

**Common mechanisms for the representation of
real, implied, and imagined visual motion**

by

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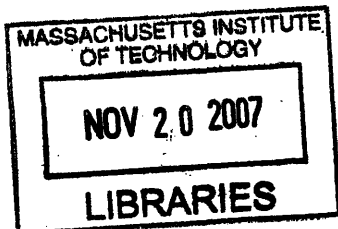
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COMMON MECHANISMS FOR THE REPRESENTATION OF REAL,
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Abstract

Perceptual systems are specialized for transducing and interpreting information from the environment. But perceptual systems can also be used for processing information that arises from other sources, such as mental imagery and cued associations. Here we ask how a particular sensory property, visual motion, is represented when it is not directly perceived but only imagined or inferred from other cues.

In a series of experiments, a motion adaptation paradigm is used to assess directional properties of the responses to mental imagery of motion and viewing photographs that depict motion. The results show that both imagining motion and inferring motion from pictures can cause direction-specific adaptation of perceptual motion mechanisms, thus producing a motion aftereffect when a subsequent real motion stimulus is viewed. The transfer of adaptation from implied and imagined motion to real motion indicates that shared mechanisms are used for the perception, inference and imagination of visual motion.

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It has been a great several years of graduate school, both at the Department of Brain and Cognitive Sciences at MIT, where I began graduate school and where I received my degree, and at the Psychology Department at Stanford, where I was a visiting scholar for the second half of my graduate career. I had the opportunity to learn from many people in these years, from Lera Boroditsky, my thesis advisor; from Alex Huk, who worked with me on all of the motion aftereffect studies; from Bart Anderson, my co-advisor for two years; from Nathan Witthoft, with whom I collaborated on much of my research as a graduate student; and from the many other faculty and graduate students both at MIT and at Stanford. The collaborative spirit fostered in Lera's lab and at both universities provided an environment that both made good ideas possible and made doing science fun. Many research assistants also provided help over the years, and a particular thanks is owed to Jesse Carton for his help in the implied motion studies.

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Chapter 1: Introduction

Mental representations of objects and scenes and their properties may arise through multiple processing routes. Bottom-up perceptual processing can bring a stimulus to mind (say, looking at a face). But thoughts of the same stimulus can also be triggered by an associated cue (hearing a voice or reading the person's name) or from volitional imagery in the absence of any relevant perceptual input. To what degree are common neural and psychological mechanisms used to represent such diverse thoughts?

In this thesis, I explore the nature of mental representations of one kind of property, visual motion, arising from multiple routes: the perception of physical motion, the inference of motion from action photographs, and mental imagery of motion. The goal is to assess whether the latter two more abstract senses of motion – from inference and imagery – are built upon mechanisms used to perceive real motion.

To address this question, I ask whether direction-selective motion responses are common to perceiving motion and to inferring or imagining motion: Does viewing a photograph of a gazelle running to the left recruit neural circuits that respond selectively to left physical motion? Does imagining an upward moving stimulus recruit neural circuits that respond to upward real motion?

Mental Imagery

Overview and behavioral evidence. When asked to make a judgment about objects or scenes in long-term memory, like whether a pea is darker than a Christmas tree, people often report that they form an image of the objects and inspect the image (1975). Similarly, imagery may be used to make decisions, such as whether a couch is

more likely to fit through a door if it is rotated on its side¹. People may also try to vividly imagine events in order to rehearse for the future or to recall details about the past, such as whether windows were left open before having left the house.

Taken at face value, these examples might seem to be acts of recapitulating perceptual processes, but many theorists have questioned the degree to which such an idea is sensible, necessary, or even possible (Fodor, 1981; O'regan & Noe, 2001; Pylyshyn, 2002). If the goal of perception is to arrive at an interpretation of sensory input (which is meaningless when uninterpreted), and the goal of imagery is to re-access the meaningful interpretation, why reproduce the whole process during imagery? This and related questions have spawned a tremendous amount of research into trying to determine experimentally precisely what properties and mechanisms constitute mental imagery, with a significant, ongoing debate between researchers with opposing views (e.g., Kosslyn, 1994; Pylyshyn, 2003).

An important study in 1910 demonstrated that mental imagery of a particular stimulus (e.g., a banana) and a dim and blurred visual presentation of the same stimulus were frequently confused by participants (Perky, 1910). Further explorations of the “Perky effect” have shown that even low-level visual tasks such as vernier acuity can be impaired during imagery of similar stimuli (Craverlemley & Reeves, 1987). Such results have been taken as evidence that “the materials of imagination are closely akin to those of perception” (Perky, 1910).

But what “materials” of perception? Information in the perceptual processing streams may be represented at various degrees of abstraction, from cells tuned to the

¹ Or, for me, since moving to the San Francisco Bay area, whether my car will roll into the street or onto the sidewalk if it falls out of gear and drifts while parked on a hill.

spatial location and orientation of luminance edges (Hubel & Wiesel, 1959) to cells that respond preferentially to a particular movie star, whether presented as a photograph or as a written name (Quiroga *et al.*, 2005), akin to the abstract “grandmother cells” hypothesized by Letvin (Gross, 2002). Thus another important question about imagery is not just whether it is similar to perception, but the extent to which mental images contain metric properties, as opposed to being fully abstracted representations.

Building on an observation of Ernst Mach in 1866, Roger Shepard and colleagues conducted an elegant set of studies to demonstrate quantitatively that mental images contain metric properties (Shepard & Cooper, 1982; Shepard & Metzler, 1971). In particular, Shepard and colleagues demonstrated that when trying to determine whether two objects are the same or different, subjects mentally align them, such that the time to make the determination is remarkably well described as a linear function of the angle of misalignment. Further studies have shown that the time it takes to shift one’s focus from one part of a mental image (e.g., the tail of a cat) to another part (its ear) is proportional to the distance of the parts (Kosslyn, 1973). Such results are part of a tradition of clever experiments which have sought to reveal the properties of mental images through indirect psychological tests. These experiments have demonstrated that mental images have a number of “image-like” properties typically associated with bottom-up perception, including size (Kosslyn, 1975), resolution (Finke & Kosslyn, 1980), visual angle (Farah *et al.*, 1992; Kosslyn, 1978), and even a contrast-sensitivity function that varies with dark-adapted and light-adapted states (D’Angiulli, 2002). The wide range of studies demonstrating shared, metric properties between imagery and perception, however, has left open the possibility that the similarity between the two types of processing is one of

analogy and not shared processing. This has led imagery researchers to consider additional evidence from cognitive neuroscience.

Neural evidence. One principal finding from the cognitive neuroscience literature is that visual mental imagery can activate visual cortical areas in a modality and a feature-specific manner. For example, imagining visual stimuli activates visual cortex and can suppress auditory cortex (Amedi *et al.*, 2005). Imagining visual motion activates the cortical area MT+ (Goebel *et al.*, 1998; Grossman & Blake, 2001) which processes real visual motion. Imagining faces or places activates brain regions that are more responsive to perception of the corresponding stimulus (O'Craven & Kanwisher, 2000). Moreover, visual imagery can activate early, retinotopically organized cortex (Kosslyn *et al.*, 1999; Kosslyn *et al.*, 1995; Slotnick *et al.*, 2005).

Other sources of evidence have added to the functional imaging literature to make the case that not only are perceptual brain areas activated during imagery, but the activation plays a functional role during imagery. For example, disruption to early occipital areas by transcranial magnetic stimulation interferes with imagery-based judgments of visual attributes (Kosslyn *et al.*, 1999). Furthermore perceptual deficits from focal brain damage are often accompanied by corresponding deficits in imagery, though there are also cases in which the deficits are dissociated (for review, see Farah, 1989).

However, the neuroimaging and neuropsychological evidence leaves many questions open regarding the perceptual mechanisms involved in mental imagery. For example, consider the topic of this thesis, visual motion: one cannot infer whether mental imagery of directional motion elicits directional motion signals in the brain, nor whether

the same subsets of neurons, with similar tunings, are activated for imagined motion and physical visual motion. fMRI 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 activated by other factors like attention and arousal (Beauchamp *et al.*, 1997; Corbetta *et al.*, 1991; O'Craven *et al.*, 1997; Saenz *et al.*, 2002) that may not be directionally-selective (Huk et al., 2001). Thus, a net increase in MT+ activation during imagery (Goebel et al., 1998) 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 repeatedly activated (Grill-Spector & Malach, 2001; Huk & Heeger, 2002). One of the two main aims of this thesis is to address these questions, and we return to them shortly.

Perceptual inferences

In addition to mental imagery, which is typically a purposeful, voluntary act, perceptual features can also be brought to mind in more automatic ways, even when not directly perceived. Perhaps the most famous example is that of Pavlov's dog, in which a sound was made to condition an anticipatory response in the expectation of food. Of course the conclusion that the dog actually thought of food or any of its sensory properties upon hearing the bell is antithetical to the basic approach of behaviorist science, in which the goal was, at least in part, to characterize the input-output relations without the need to make hypotheses about mental states. Nonetheless, such a possibility seems reasonable and the idea that associative learning can have effects on perception has been pursued more directly by cognitive and perceptual scientists. For example, Qi and

colleagues (2006) trained subjects to associate an arbitrary stimulus with a direction of rotational motion, and found that following training presentation of the cue biased the perception of an ambiguous motion stimulus. In what might be thought of a natural experiment in associative learning, Cox and colleagues (2004) showed that photographs of human bodies with a smudged oval above it (instead of a face) activated a region of visual cortex that responds selectively to faces, the fusiform face area (Figure 1). The body and the configural cues in the image may be a well-learned indicator to the likely presence of a face, just as a Pavlov's bell may have indicated the likely delivery of food.



Figure 1. An example of a stimulus reprinted from (Cox et al., 2004). The contextual information in the image provides information that a face is present. Stimuli such as these were shown to activate face-selective regions of visual cortex.

Representational momentum. An example in the domain of visual motion is the extrapolation of motion paths from images. Inferring motion trajectories is important for acting efficiently in dynamic environments. Even visual stimuli which 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). In Figure 1 one can see a person jumping. The sense of motion must be inferred from prior knowledge since 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. How is the sense of motion from photographs represented in the brain?

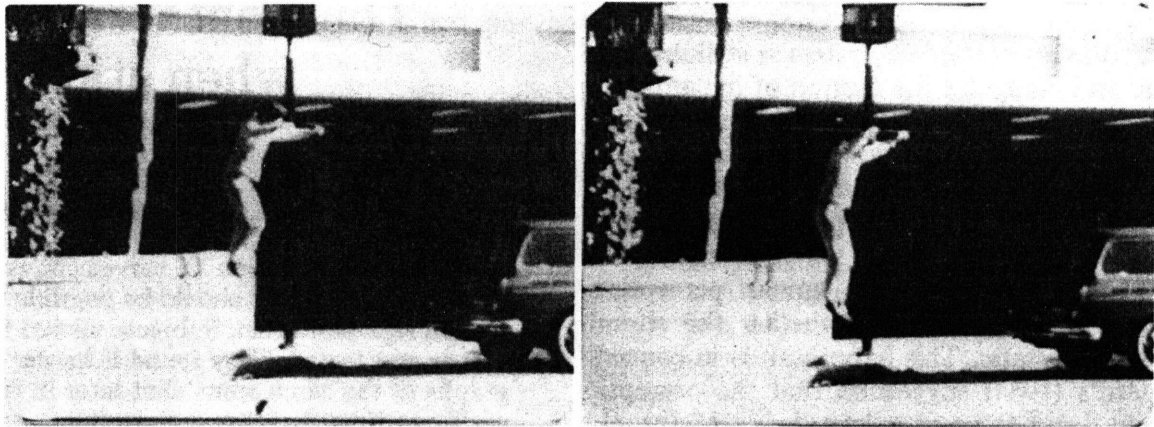


Figure 2. An example of a stimulus reprinted from (Freyd, 1983). When subjects briefly viewed an image like the one on the left, and then were tested with a similar image slightly later (like the one on the right) or slightly earlier from the same video clip, subjects were slower to say that the later picture was different from the original. This was taken as evidence that the later image was confused with the first image, presumably because subjects automatically extrapolated ahead upon seeing the first image. In later reports this and related phenomena became known as “representational momentum” (Freyd & Finke, 1984).

Form and motion. 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 powerfully in a direction-selective manner to moving images (Dubner & Zeki, 1971; Heeger *et al.*, 1999; Huk *et al.*, 2001). The direction of motion, however, may be inferred not just from analysis of visual motion but also from low-level visual form cues such as motion streaks (Burr & Ross, 2002; Geisler, 1999) or higher-level cues such as the posture of a person in motion (as in Figure

3). In the case of low-level form cues it is thought that early visual processing such as the orientation-tuned cells in primary visual cortex can extract the relevant information and contribute to downstream motion processing. How high level semantic cues from objects and scenes might contribute to motion processing is less well understood. Is the sense of motion derived from such static cues instantiated by the same neural and psychological mechanisms as those subserving 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 analyzing real visual motion. For example, does viewing the still photograph in Figure 3 elicit responses from the same leftward-selective neurons that would respond to real leftward motion?

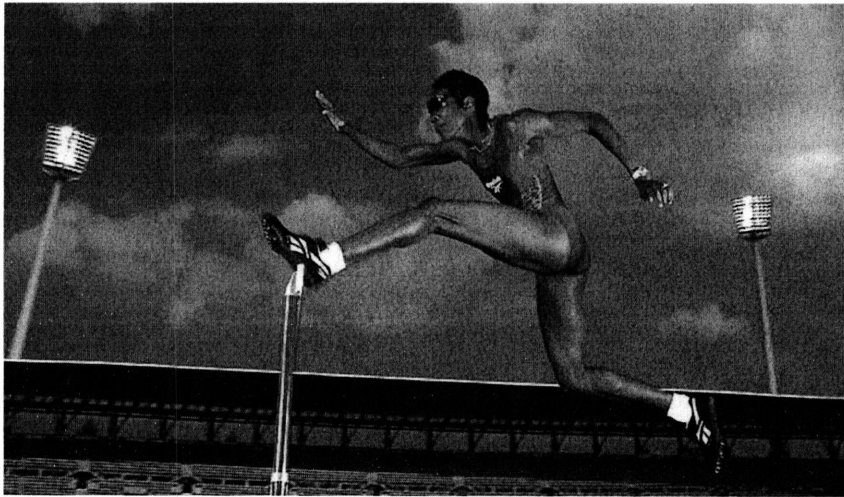


Figure 3. An example of an implied motion photograph used in the experiments in Chapter 4.

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 *et al.*, 2005; Senior *et al.*, 2000). In these studies, viewing photographs or silhouettes of animals, people, objects or natural scenes containing implied motion elicited greater activation in visual motion areas, most notably the MT/MST complex, than viewing similar images that did not imply motion (e.g., a cup

falling off a table compared to a cup resting on a table, or a running athlete compared to an athlete at rest). These studies demonstrate that implied motion, like imagery of motion, can activate brain areas also known to be engaged by real image motion. However, as in the case of mental imagery, one cannot infer from such studies whether viewing stimuli with implied motion elicits directional motion signals in the brain². In order to infer whether the same neural circuits are employed by imagery and perception in the domain of visual motion, we made use of a motion aftereffect paradigm.

Motion aftereffect

The motion aftereffect or the waterfall illusion is a striking and well-studied perceptual phenomenon. It occurs when prolonged viewing of motion in one direction affects the perception of motion in subsequently seen stimuli. In particular, a static object or directionally ambiguous motion appears to move in the direction opposite to the previously seen motion. Motion aftereffects have been observed at least as far back as Aristotle, although not until Lucretius in the first century B.C. was the direction of the aftereffect unambiguously described as being *opposite* to the prior motion (see (Wade & Verstraten, 1998)). Both descriptions were of aftereffects from water flowing in a stream. The phenomenon was rediscovered a number of times in the 19th century, most famously by Robert Addams whose observation of the Fall of Foyers in Scotland led to the name “Waterfall Illusion”; shifting his gaze from prolonged viewing of the falling water to the nearby rocks led to an illusory upward motion “equal in velocity to the falling water”. A

² Very recently, while in the late stages of editing this thesis, a study using EEG has shown direction-selective responses to implied motion (Lorteije *et al.*). This study provides independent, convergent evidence (though using very different methods) that implied motion and real motion processing share some direction-selective mechanisms. It is discussed further in Chapter 4.

comprehensive review of 19th century studies, as well as 34 original studies, was later published in 1911 by Wohlgemuth for his doctoral dissertation.

Many explanations for the illusion have been offered, but an important component of many of the explanations, including that hypothesized by Wohlgemuth (1911) and measured by Barlow and Hill (1963), is the activity-related change in responsiveness of motion sensitive neurons. In this view the aftereffect results from the adaptation-induced decrease in activity of directionally selective neurons that respond to the adapted direction of motion. This direction-selective adaptation in turn causes an imbalance in the population activity of neurons that represent different directions of motion. Because of this post-adaptation imbalance, the neural population code will indicate a net direction of motion opposite to the adapted direction when probed with stationary or directionally-ambiguous stimuli. Thus, the presence of a motion aftereffect can be used as a test for the involvement of direction-selective neural mechanisms (Kohn & Movshon, 2003; Petersen et al., 1985; Van Wezel & Britten, 2002).³

Moreover, one can vary properties between the adapting stimulus and the test stimulus in order to make inferences about the representation of motion. For example, if a motion stimulus is viewed through only the left eye and a static test stimulus is subsequently viewed only through the right eye, one will experience a motion aftereffect. This interocular transfer demonstrates through a simple behavioral observation that at

³ It is worth noting that an understanding of the neural and psychophysical basis of the motion aftereffect remains far from complete. For example it has recently been demonstrated that shifts in the directional tuning of motion sensitive neurons may be at least as critical for explaining the aftereffect as reductions in the magnitude of responses (Kohn & Movshon, 2004). Perhaps because of the difficulty in achieving a single, unified explanation of the phenomenon, Edward Adelson described the motion aftereffect to me as “A quagmire, a miasma, and a morass” (personal communication). It is not the purpose of this thesis to arrive at a mechanistic explanation of the motion aftereffect, nor do the experiments rest on the assumptions of any particular model of the effect. Instead, the transfer of the aftereffect from one condition to another is used to infer the existence of shared representations between the conditions, without regard to exactly how adaptation occurs, or how motion is processed.

least some motion processing must take place centrally (not in each eye separately). More generally, one can make inferences about the properties of neural circuits by measuring whether adaptation transfers from one stimulus to another. Because of this, aftereffects have been an important tool for studying perception (e.g., Gibson, 1933; Gibson, 1937; Held, 1980)) and have famously been described as the psychologist's microelectrode (Frisby, 1980).

Hypotheses

We predicted that if visual imagery of motion is subserved by the same direction-selective neural mechanisms that are involved in the perception of physical motion, then actively imagining motion should adapt these neurons and produce a motion aftereffect. Similarly, if viewing photographs of implied motion also uses the same direction-selective neurons that are involved in perception, then viewing a series of such photos depicting motion in the same direction would likewise adapt direction-selective neurons and produce a motion aftereffect. We tested these hypotheses in a series of experiments where we measured whether imagining continuous motion in one direction, either with the eyes open or closed, altered the perceived direction of subsequently presented real motion (Chapter 3); and in a series of experiments in which we measured whether viewing implied motion in one direction altered the perceived direction of subsequently presented real motion (Chapter 4). We also compared these results to baseline experiments with adaptation to real motion.

Chapter 2: General Methods

Adaptation with interleaved test stimuli

The procedure for all the experiments had the same basic structure: prolonged adaptation with interleaved test stimuli. Adaptation, depending on the experiment and condition, could consist of mental imagery, viewing partially occluded motion, viewing photographs with implied motion, or viewing real visual motion.¹ In order to maximize the effect of adaptation, the direction of motion adaptation was always constant within a block of trials. The first trial in each block contained a long period of adaptation (60 s) and subsequent trials contained “top-up” adaptation periods of 6 s each. The logic is that the initial adaptation trial in each block builds up an adapted state and counters any residual adaptation from previous blocks of trials, and the subsequent trials maintain the adapted state. The direction of adaptation changed between blocks. Between periods of adaptation, brief test stimuli consisting of moving dots were presented to the subject, and a forced choice judgment on the direction of dot motion was made (e.g., left or right). By maintaining adaptation for a long period in one direction, a range of different test stimuli can be presented to the subject and repeatedly tested. This procedure – a long initial period of adaptation, followed by shorter top-up periods with interleaved test stimuli – has been widely used to assess adaptation to a variety of stimulus types, including spatial frequency (Blakemore & Sutton, 1969), motion (Hiris & Blake, 1992), tilt (Wolfe, 1984), and, more recently, the gender or race of faces (Webster *et al.*, 2004).

¹ Note that for consistency and simplicity, the word “adaptation” is used in reference to each of these experimental conditions; in fact, whether direction-selective motion mechanisms are indeed adapted by a particular task, such as imagery, is the hypothesis being tested, and not an assumption.

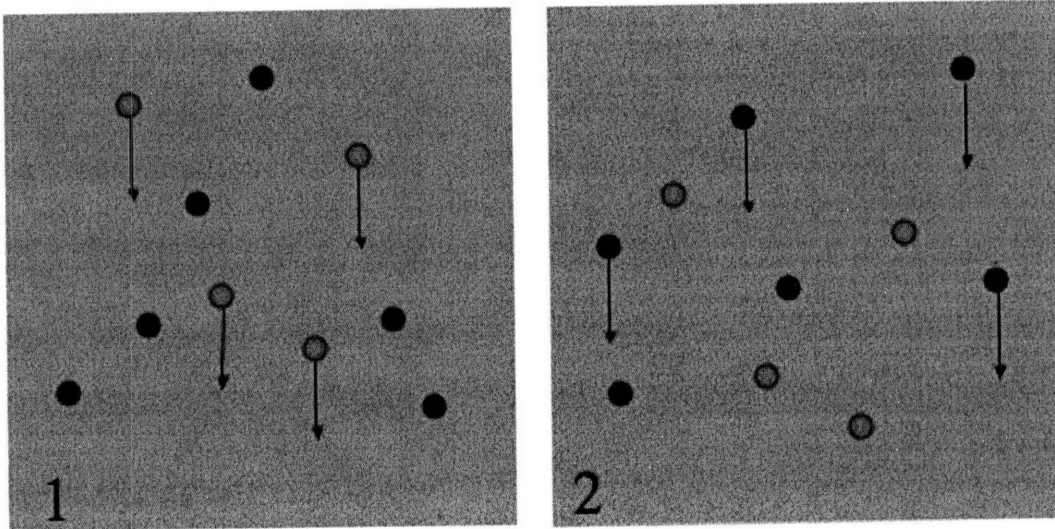


Figure 1. A two-frame schematic depiction of a random dot test stimulus. In this example 4 of 10 dots (indicated in red) move coherently downward from frame 1 to 2. The other 6 dots disappear and are randomly repositioned. In frame 2, 4 new dots are selected at random to move downward. This “limited lifetime procedure”, in which new dots are selected randomly in each frame, prevents subjects from tracking individual dots to make a judgment on the direction of motion. Instead, subjects rely on a global sense of motion. The size, number, and luminance of dots and the frame-to-frame step-size are purely schematic. Detailed descriptions of the stimulus properties are in the methods section of each experiment.

Random dot test stimuli

The effect of adaptation on motion perception was assessed in all experiments (except experiment 6 in Chapter 4²) with a standard moving-dot direction-discrimination task (Newsome *et al.*, 1989; Newsome & Pare, 1988). Random dot displays such as those used in this task (Figure 1) 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, as distinct from processing of shapes or spatial positions (Anstis, 1970; Braddick, 1974; Nakayama & Tyler, 1981). In our versions of these displays, most of the dots served as noise, disappearing and then reappearing in a new location from frame to

² For this experiment, a directionally ambiguous flickering stripe pattern was used as the test stimulus. These methods are detailed in Chapter 4.

frame. A proportion of the dots, however, moved coherently in a particular direction. This proportion, or “motion coherence”, varied from trial to trial, as did the direction of coherent motion. The direction of coherent motion was always either the same as or opposite to the direction of adaptation. Subjects were thus forced to choose one of two directions in their judgments. The task is easy when the coherence is high and hard when the coherence is low.

Predicted shift due to motion adaptation

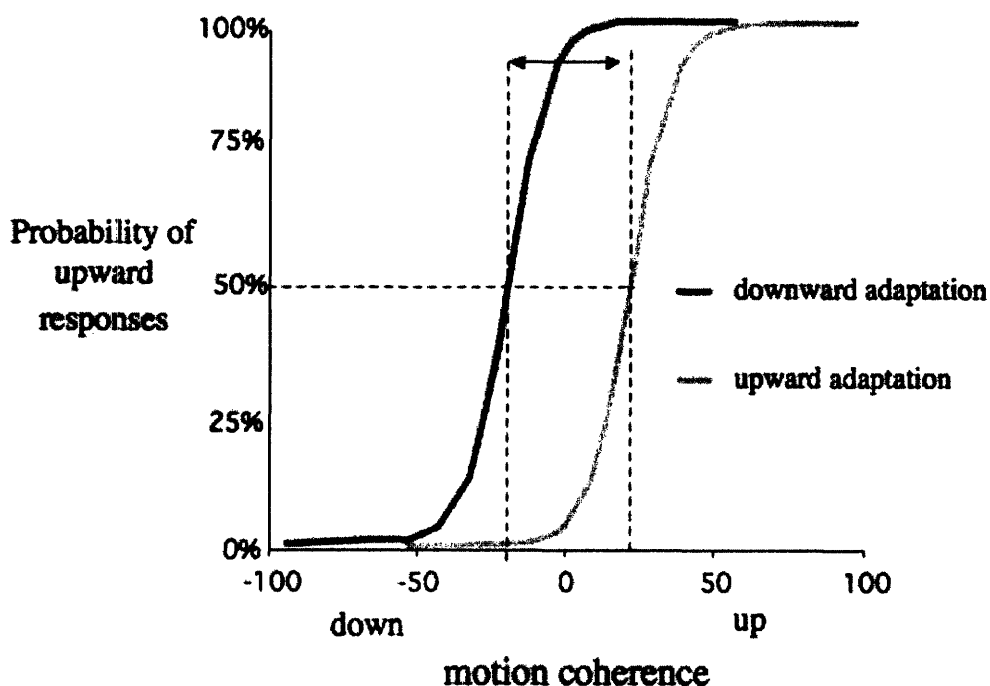


Figure 2. Hypothetical motion sensitivity functions following adaptation. The null points (dashed vertical lines) are shifted to reflect motion aftereffects: following upward motion adaptation, a downward aftereffect is nulled by upward coherence in the test stimulus, and *vice versa* following downward motion adaptation. The separation between the null points (double-headed arrow) is a convenient measure of the aftereffect.

Nulling the motion aftereffect

This type of stimulus has been previously employed as a means to assess and quantify motion aftereffects from adaptation to real motion (Blake & Hiris, 1993; Hiris &

Blake, 1992). By varying the level of coherence from trial to trial as well as the direction of coherence (same as or opposite to adaptation), a motion sensitivity function can be extracted (Figure 2). From this function, one can easily find the point of perceived null motion, that is the amount of motion coherence for which the subject is equally likely to judge the dots as moving in the two opposite directions. The logic is that motion adaptation (say to upward motion) produces an aftereffect in the opposite direction (downward). The aftereffect can be nulled by a fraction of dots moving coherently in the direction opposite the aftereffect. Thus adaptation can then be assessed as the difference in the null points between paired conditions, such as adapting to upward motion and to downward motion.

Using dynamic dot test probes as a method for assessing motion aftereffects has several advantages. First, by testing a range of coherence values and measuring the shift in the motion sensitivity function, the aftereffect is measured in units of the stimulus and not behavior (a “stimulus-referred” method): The size of a motion aftereffect can be expressed as the amount of dot coherence that must be added to a test stimulus following one kind of adaptation to make it perceptually equivalent to the same stimulus following another kind of adaptation. This contrasts with the kind of measure one gets if only the neutral point is tested, e.g., by making a judgment on a static stimulus or a fully ambiguous stimulus after adaptation. The units in the latter kind of measure are the increased (or decreased) likelihood of making a particular response, a measure in units of human behavior and not stimulus dimensions.

Additionally, dot probes are useful because they give subjects an objective task: there is in fact more motion in one direction than another on any given trial. All subjects

who participated in these experiments were naïve to the purpose of the experiment. The wide range of coherence values tested allowed us to validate that subjects were in fact doing the task, in that their responses were predicted (in part) by the actual motion of the test stimulus. In the occasional case in which this was not true, subjects were excluded from analysis (see below).

Finally, dynamic dots are an advantageous stimulus because, at least according to some reports (Blake & Hiris, 1993; Hiris & Blake, 1992), they can perceptually null a motion aftereffect. If one adapts to motion (saw downward) and experiences a motion aftereffect (upward), then a dot stimulus with partially coherent motion in the opposite direction (downward) can counter the aftereffect such that it appears to have no coherent motion. In other words, illusory motion can be perceptually neutralized with actual motion coherence in the opposite direction. In contrast, a test object that has illusory motion due to a motion aftereffect cannot be made to look static by adding motion in the opposite direction. One possible explanation for this is that when motion is added to a test object, the observer can still tell that the *position* changes, even if the motion is nulled, creating a cue conflict. Because there are no stable edges or object parts in the dot stimulus, there may be no cue conflict between the motion system and a system tracking object location.

Fitting of curves with logistics

The responses to random dot test stimuli were modeled as a logistic regression fitted with a maximum likelihood algorithm (Cox, 1970; Palmer *et al.*):

$$P(x) = 1 / (1 + \exp(Y)),$$

$$\text{where } Y = -(\alpha + \beta * x + \gamma * A).$$

In this equation, x is the motion signal in units of coherence, with positive values arbitrarily assigned to a particular direction, such as upward, and negative values assigned to the opposite direction. $P(x)$ is the probability that the subject judges the dots as moving in the positive direction (e.g., upward). A is the direction of adaptation (+1 or -1) and α , β , and γ are free parameters.

The free parameters correspond to an overall bias to respond in a particular direction (α), the steepness of the psychometric functions with respect to motion coherence (β), and the effect of adaptation (γ). Dividing 2γ by β yields a measure of the separation between the paired curves in units of coherence (e.g., the length of the double-headed arrow in Figure 2). The same bias (α) and slope (β) were assumed for all conditions for each subject to reduce the number of free parameters in the model.

In some experiments subjects adapted to multiple types of stimuli, not just multiple directions. For example, in Chapter 3, Experiment 1 had occluded motion and motion imagery, and Experiments 2 and 3 had imagery with eyes open and with eyes closed. For these experiments, an additional pair of terms, γ_2 and A_2 , were added inside the exponential corresponding to the additional adaptation condition:

$$P(x) = 1 / (1 + \exp(Y)),$$

$$\text{where } Y = -(\alpha + \beta * x + \gamma * A + \gamma_2 * A_2)$$

In the first experiment, for example, A corresponded to imagery adaptation (-1 or +1 for downward or upward imagery, respectively) and A_2 corresponded to occluded motion adaptation (-1 or +1 for downward or upward occluded motion, respectively). During imagery A_2 was 0 and during occluded motion blocks A was 0.

Subjects and equipment

Equipment and displays. All experiments were conducted in a quiet, dark room. Subjects were seated approximately 40 cm away from the display, an Apple iMac with a built-in CRT monitor, with a resolution of 1024 x 768 pixels (26 x 19.5 cm) and a refresh rate of 75 Hz. All experiments were programmed using Vision Shell stimulus presentation software, a package developed at the Harvard Vision Lab that uses C libraries and runs on the Macintosh OS 9 operating system.

Participants. All subjects were recruited from either the MIT or the Stanford community. Subjects at MIT were paid for participation (\$5 for 30 minutes or \$10 for 60 minutes). Subjects at Stanford were either paid the same amount or received course credit. All subjects gave informed, written consent, and all experiments conformed to the university guidelines for human subjects testing, either at MIT (Committee on the Use of Humans as Experimental Subjects) or at Stanford (Human Research Protection Program).

Exclusion criteria. A small number of subjects in each experiment did not show a significant effect of motion coherence. For these subjects, irrespective of the direction or type of adaptation, the likelihood of judging a test stimulus as moving in a particular direction (say, up) did not significantly increase with increased dot coherence in that direction. Specifically, the parameter estimated for motion coherence in the logistic fit (β) was less than two standard errors of the same parameter estimate. Additionally, a small number of subjects performed poorly in a baseline motion discrimination task prior to adaptation. For these subjects, curve fits showed that asymptotic performance (99% accuracy on the direction judgments of the dots) required more than 100% coherence in the test stimuli. These subjects were also excluded from analysis.

Chapter 3: Motion Aftereffects from Imagined and Real Visual Motion

The experiments in this chapter comprise a manuscript in preparation by Jonathan Winawer, Alex Huk, and Lera Boroditsky.

Abstract

Mental imagery, like perception, has distinct modalities. For example, one can imagine visual properties of an object such as color or acoustic properties such as pitch. Does the experience of these properties during imagery reflect underlying computations similar to, and shared with, those used during sensory processing? Or is the connection more abstract, with little shared between imagery and perception other than the fact that they sometimes both concern the same thing? The studies in this chapter take advantage of a well-studied feature of perceptual processing, directional responses to visual motion. A series of experiments addresses whether imagining a moving pattern, like viewing real motion, can elicit a motion aftereffect assessed with real motion test stimuli.

In the first study, subjects either imagined a pattern move up or down with their eyes open, or passively viewed a large occluding rectangle around the periphery of which a moving pattern could be seen. Both imagery and viewing occluded motion led to a motion aftereffect, such that dynamic dot test probes were more likely to be seen moving in the direction opposite of adaptation. A second study demonstrated that aftereffects could be obtained from motion imagery whether the eyes were open or closed during imagery. This finding was replicated and extended in a third study in which subjects imagined horizontal motion either inward or outward, ruling out the possibility that aftereffects from imagery were coupled to eye movements. To investigate whether these effects were restricted to imagery of items in short-term perceptual memory, a fourth

experiment was conducted in which subjects had only limited exposure to the real motion patterns to be imagined. A motion aftereffect was observed in this experiment as well, suggesting that imagery of motion can engage perceptual motion mechanisms without relying on short-term stored representations. Finally, motion aftereffects from real visual motion were assessed using similar methods to quantify the magnitude relative to imagery.

The transfer of adaptation from imagined motion to perception of real motion demonstrates that at least some of the same direction-selective neural mechanisms are involved in both imagination and perception of the same kind of stimuli.

Experiment 1: Can mental imagery of a moving stimulus produce a motion aftereffect?

In the first experiment, our primary question was whether imagining a moving grating, either upward or downward, could elicit a motion aftereffect. In the imagery condition of the experiment, subjects actively imagined a moving grating while fixating a central fixation square. Motion aftereffects were assessed with random dot test probes presented between periods of imagery.

In a second condition, we asked whether a motion aftereffect could be elicited by having subjects fixate a central occluder around which a moving grating could be seen. This condition was not directly relevant to the hypothesis that mental imagery recruits direction selective motion mechanisms because subjects were not instructed to imagine. But because the dynamic dot test stimuli appeared in a small region in the center of the large occluded region where there was no motion, a motion aftereffect in this condition would indicate a non-retinotopic motion aftereffect. This condition served as an

intermediate between perception of motion and imagery of motion, and also as a way to re-familiarize subjects with the appearance of the grating to be imagined. It is also served as a partial replication of prior findings of non-retinotopic motion aftereffects (Bex *et al.*, 1999; Snowden & Milne, 1997; Weisstein *et al.*, 1977).

A pilot study was conducted on 6 subjects, and then a follow-up study with 32 new subjects. The follow-up was identical to the pilot in every respect except for slight differences in the baseline motion sensitivity test and the selection of coherence values of the test stimuli.

Methods

Subjects and equipment. 38 subjects, naïve to the purpose of the experiment, were recruited from the MIT community. Subjects provided written consent and were paid for participation.

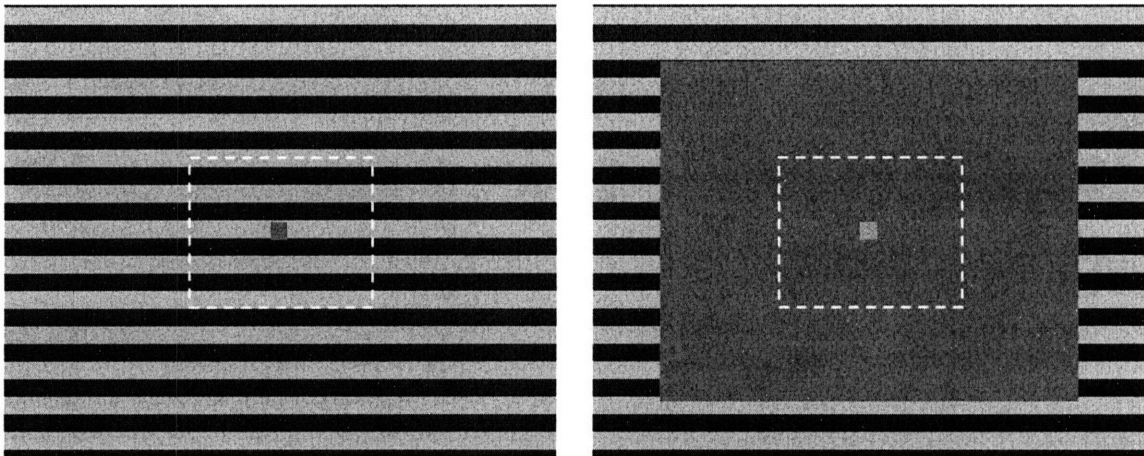


Figure 1. Adapting stimuli for Experiment 1. Each stimulus filled the screen. The stimulus on the left, which could move either upward or downward, was shown to subjects prior to the adaptation blocks. The “timing guide”, or central fixation square pulsated with the average luminance of the stimulus passing behind it. On occluded motion trials, a large gray rectangle filled 75% of the screen (right). On imagery trials, the occluder filled 100% of the screen, such that there was no visible motion. The dashed white lines indicate the size of the test area with random dots. The figures are drawn to scale.

Adapting stimuli. In the beginning of the experiment, subjects were shown examples of the moving stimulus that they were later to imagine (Figure 1). The stimulus was a square wave horizontal luminance grating with a spatial frequency of about .5 cycles per degree. The grating moved either upward or downward at a speed of 2° per second. Subjects were instructed to attend carefully to the appearance and speed of the grating (while fixating a central square, approximately 1°) so that they could later imagine the grating as accurately and vividly as possible. In order to facilitate continuous motion imagery, the intensity of the fixation square was modulated, matching the average luminance of the grating passing behind it. The pulsating square, which contained no net directional motion, had the same temporal frequency as the grating. After this familiarization stage, the pulsating square, shown alone on an otherwise blank screen, was used as a visual timing guide for motion imagery with eyes open.

In the occluded motion condition, a gray rectangle, 75% of the width and 75% of the length of the display occluded the grating, such that the moving grating was visible in the periphery (upper, lower, left, and right 12.5% of the screen).

Dynamic dot test stimuli. Test stimuli consisted of 100 dots contained within a rectangular window, centered on the screen, whose length and width were 33% of the entire display (approximately 12 by 9 degrees of visual angle). On each frame a subset of the dots, equal to the percentage of dots moving coherently for that trial, were selected to move up or down. All other dots disappeared and randomly reappeared at any other location within the test window. A new set of dots was re-selected for coherent movement on each frame. This “limited lifetime” procedure was used so that the trajectory of single dots could not be followed throughout a trial. Each test trial consisted

of 25 frames displayed for 40 ms each (1 s total). Dot displacement for coherent motion was approximately 0.07 degrees per frame.

Baseline motion sensitivity. The experiment began with a baseline motion calibration task. For the 6 pilot subjects the dot coherence in the baseline task was $\pm 6\%$, $\pm 12\%$, or $\pm 24\%$ over 48 trials, where positive numbers are arbitrarily assigned to upward motion and negative numbers to downward motion. These same 6 coherence values (3 up and 3 down) were used for test stimuli during the adaptation blocks. These values were chosen because pilot testing on the author showed that accuracy asymptoted at or below about 24% coherence.

Because performance on the baseline task was highly variable among the pilot subjects, a wider range of coherence values was used for the remaining subjects. For these subjects the test values for the experimental conditions were chosen according to performance on the baseline task, such that test stimuli were approximately perceptually matched across subjects. The baseline task consisted of 180 trials, during which dot coherence ranged from 5% to 65%, either upward or downward. A logistic function was fitted to the responses, with downward coherent motion coded as negative and upward coherence coded as positive.¹ Based on the fitted logistic function, the amount of coherence corresponding to 99% accuracy in each of the two directions was determined for each subject (Figure 2). The average of these two unsigned values was considered the maximal dot coherence for each subject, and defined as one unit of “normalized coherence”. The test stimuli presented during the adaptation phase of the experiment

¹ For simplicity of programming, the logistic function for the baseline task was fit using a least squares method, and not the more typical maximum likelihood procedure. Specifically, the logistic was transformed into a line, in which the x variable was the motion coherence and the y variable was the log odds of the responses (0 for “down” responses and 1 for “up” responses). These fits yield slightly different parameters than the estimation by maximum likelihood, but they are quite close.

contained ± 0.25 , ± 0.5 , or ± 1 units of normalized coherence. Note that while the amount of coherence producing 99% upward responses and the amount producing 99% downward responses was not necessarily symmetric (as in the example in Figure 2), the actual test values used in the experiment were always symmetric, in order to avoid the possibility of the test stimuli themselves inducing a motion aftereffect.

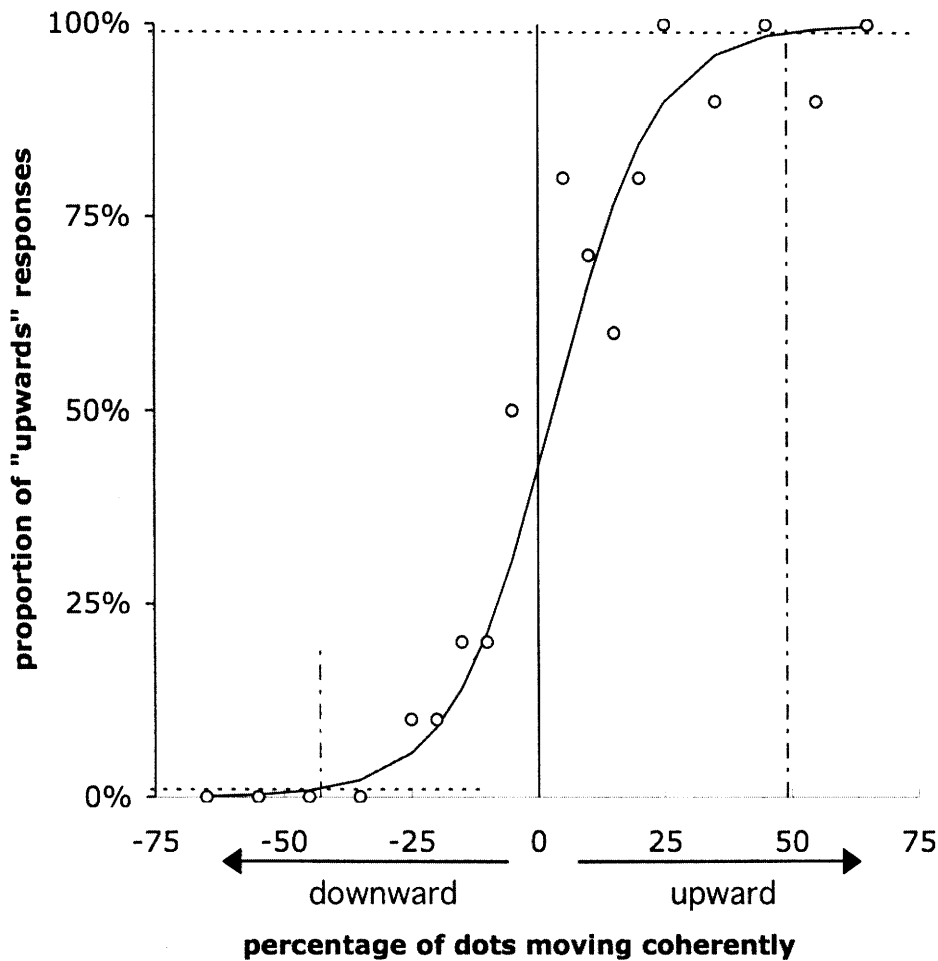


Figure 2. Baseline motion discrimination task for a single representative subject. The task consisted of up/down judgments on dot stimuli (x-axis, downward dots arbitrarily assigned to negative coherence values). The coherence values producing 99% responses based on the logistic fit (smooth curve) in each direction are indicated by dashed vertical lines. For this subject the values are 49% upward coherence and 43% downward coherence, averaged to 46%. For this subject, 46% upward coherence was defined as one unit of normalized coherence, and was the maximally coherent test stimulus seen during the subsequent experiment. The 6 test stimuli viewed by this subject, ± 1 , ± 0.5 , and ± 0.25 “normalized” coherence, correspond to $\pm 46\%$, $\pm 23\%$, and $\pm 12\%$ actual coherence.

Procedure. The instructions were programmed as part of the experiment to ensure that all participants received the identical instructions, and to minimize the possibility of experimenter bias. Subjects first viewed 6 examples of high coherence dot displays to familiarize them with the kind of judgments to be made (3 up and 3 down). This was followed by the baseline motion discrimination task. Subjects then viewed the full-screen moving grating twice in each direction (up and down) in order to familiarize them with its appearance.

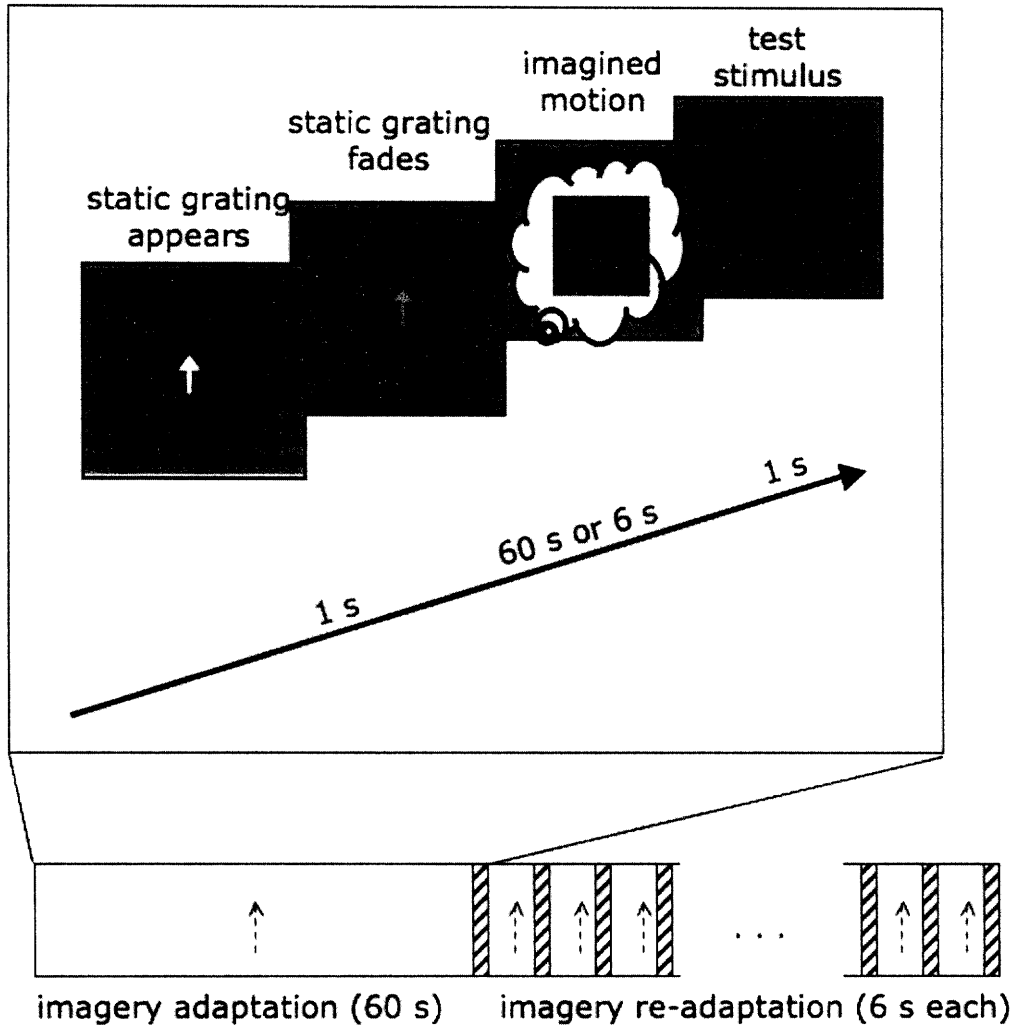


Figure 3. Experimental procedure. Subjects imagined a moving grating pattern while fixating a small pulsing square. The direction of adaptation and whether the block contained imagery or occluded motion was constant within a block and randomized across 8 blocks of 24 trials. The first trial in each block consisted of 60 s of imagery or occluded motion adaptation, and subsequent trials had 6-s top-up adaptation. Moving dot test stimuli were presented after each period of adaptation, and subjects made a two alternative forced choice decision as to the direction of the dot motion (up/down).

The adaptation phase consisted of 4 imagery and 4 occluded motion blocks, with two upward and two downward blocks of trials for each type of adaptation. There were 24 trials per block with each of the 6 coherent values being presented 4 times. Each block began with a 60-s adaptation trial followed by 6-s top-up adaptation trials (Figure 3).

Imagery trials began with the appearance of a static grating and a small arrow indicating the direction of subsequent motion imagery. The grating and arrow

immediately began to fade into gray, taking 1 second to disappear. The subject then imagined motion on a screen that was blank except for a fixation square. On alternate blocks, subjects either imagined motion or fixated a central occluder around which the moving grating could be seen.

At the end of the experiment, subjects were given a brief questionnaire adapted from the Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973). The questionnaire is a self-reported assessment of the vividness of mental imagery. Subjects are given a series of verbal descriptions of scenes, faces, and objects, and asked to vividly imagine each of them with their eyes open and then again with their eyes closed. After imagining each scene, subjects choose a 1-7 score corresponding to their self-assessed vividness of imagery. We also asked subjects two additional questions: *Have you ever heard of the 'Motion Aftereffect' or 'Waterfall Illusion' before, and After viewing upward motion, would you expect a static image to appear to move up or down.*

Results and Discussion

Pilot subjects. In the pilot study we found that both imagining motion and viewing occluded motion produced significant motion aftereffects. Imagination of upward motion led to a greater likelihood of seeing the dynamic dot test stimulus moving down compared to imagination of downward motion. The same pattern was observed for viewing occluded motion. These patterns can be clearly seen in the population motion sensitivity curves, which show the mean results for the 6 pilot subjects (Figure 4). Had there been no effect of imagery or viewing occluded motion, each pair of curves would overlap. If subjects had answered based on an association (e.g., with a bias to respond upwards following upwards imagery) then the difference between the curves would have

been in the opposite direction than what was actually observed. These results are consistent with the hypothesis that imagery of visual motion involves some of the same directional-selective motion processing circuits also used for perception of motion.

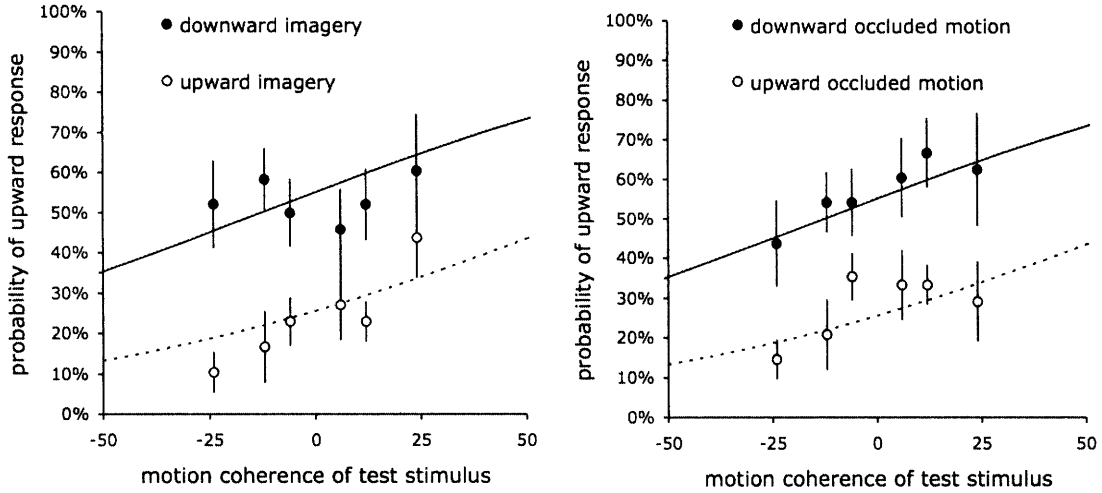
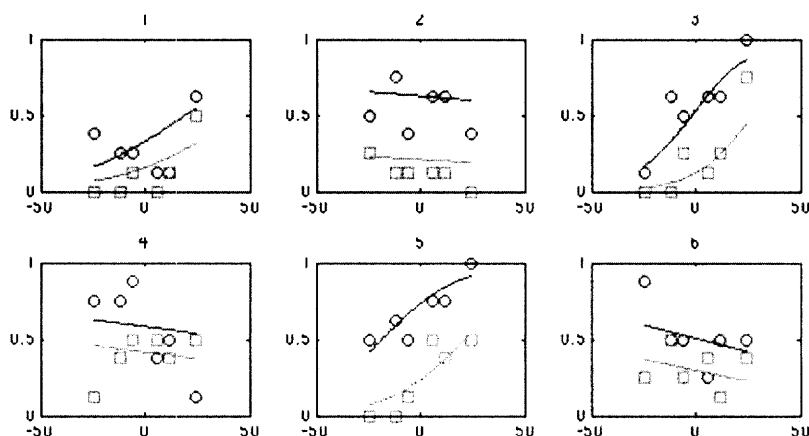


Figure 4. Population motion response functions for 6 pilot subjects following upward or downward imagery (left), or viewing upward or downward occluded motion (right). Subjects were more likely to perceive upward motion in the test stimulus following downward imagery adaptation or viewing downward occluded motion. Data points represent the mean likelihood of responding upward \pm 1 standard error of the mean. The x-axis is the motion coherence. Positive numbers are arbitrarily assigned to upward motion. Curve fits are logistic regressions, with the slope constrained to be the same in each fit.

However, it is also evident from the data shown in Figure 4 that the subjects' responses were not greatly affected by the coherence in the test stimuli, that is the slopes are quite shallow. This means that the range of coherence in the test stimuli was not well matched to the range of the subjects' motion sensitivity, making it difficult to accurately estimate each subject's sensitivity function. In fact, an analysis of the individual subjects shows a split: collapsing across the imagery and occluded motion conditions, 3 subjects show significant sensitivity to motion coherence (subjects 1, 3, and 5) and 3 do not (Figure 5). A significant effect of motion sensitivity was defined as a z-score of at least 2 for the motion coherence parameter on the logistic fit. (See General Methods.)

Imagery Pilot



Occlusion Pilot

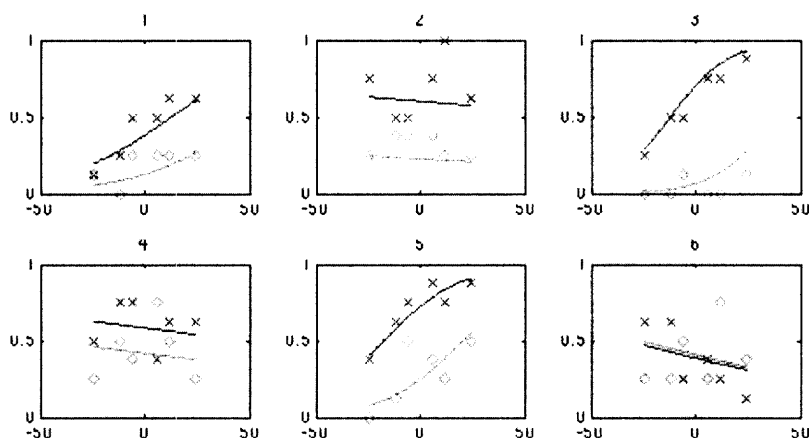


Figure 5. Individual motion response functions for 6 pilot subjects following imagery (top), or viewing occluded motion (bottom). Red indicates downward imagery or occluded motion, and green upwards. Each subject showed an effect in the predicted direction, being more likely to see the dots as moving upward following downward adaptation compared to upward adaptation, as predicted by a motion aftereffect. However, there is high variability between subjects in their motion sensitivity, with some subjects showing flat slopes (poor sensitivity to motion coherence) and some showing steep slopes (good sensitivity).

Normalized coherence. These results suggest that the range of coherence values in the test stimuli was far too restricted for some subjects, but reasonably good for others. For the remaining 32 subjects (as well as all subjects in subsequent experiments), the coherence values used during adaptation were chosen to be equivalent with respect to subjects' motion sensitivity as determined in the baseline (see General Methods). Once

the sensitivity was determined from the baseline, the maximal coherence used during adaptation was considered one unit of “normalized coherence”. Comparing the size of a normalized unit of coherence in the main experiment and the maximum values tested in the pilot experiment, it is clear that the pilot study was biased towards low coherence values.

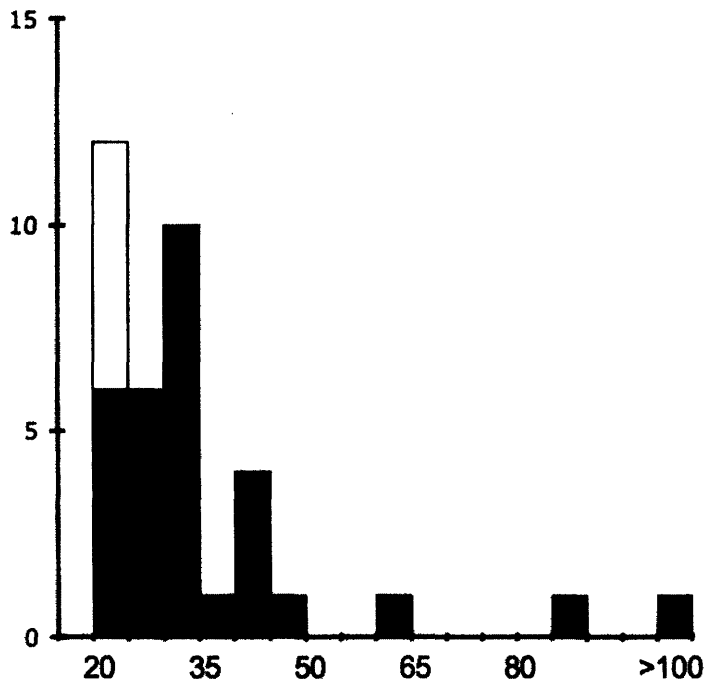


Figure 6. Frequency histogram of the maximal coherence value of test stimuli during adaptation. The y-axis is the number of subjects. For the 6 pilot subjects (white), this value was arbitrarily chosen to be 24% coherence. For the remaining subjects (black), this value, considered 1 “standardized unit” of coherence, was chosen based on performance on the baseline task, and ranged from 22 to over 100% actual coherence. (Greater than 100% is possible because the value was extrapolated from a fitted curve.)

Out of 32 subjects in the main experiment, one was excluded from analysis due to poor baseline performance (a normalized coherence of more than 100%), and one was excluded for lack of sensitivity to motion coherence during the experiment (a z-score of less than 2 for the motion coherence parameter estimate). (See General Methods for details.)

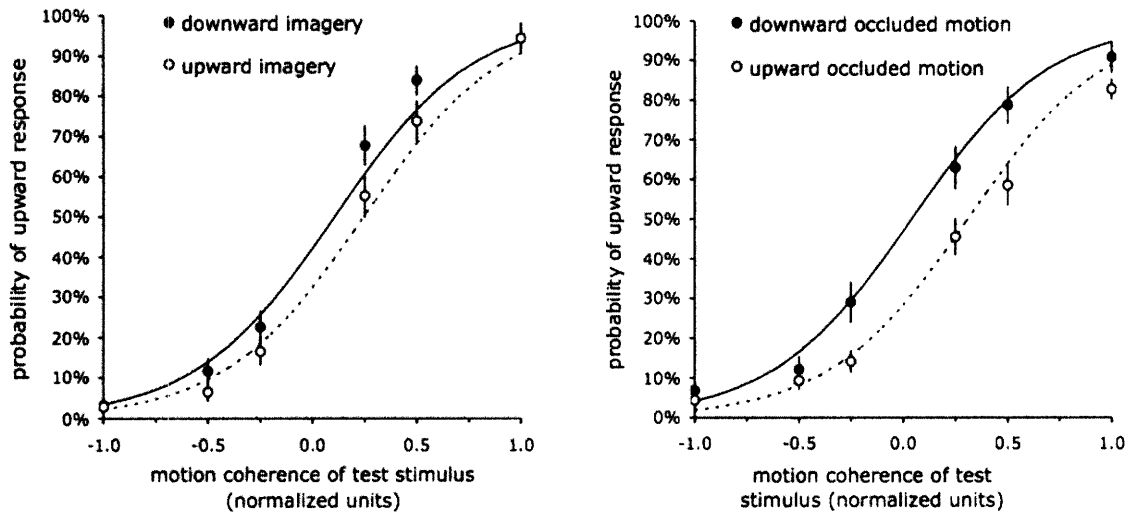


Figure 7. Mean motion response functions during imagery adaptation (left) and viewing occluded motion (right). Both conditions produced motion aftereffects, as evident by the separation between the curves in each panel. Negative numbers on the x-axis mean downward coherence. Individual points are subject means \pm 1 sem.

Motion aftereffects from mental imagery in the main experiment. When tested with a range of motion stimuli calibrated to each subject's baseline performance, mental imagery of motion again produced a motion aftereffect, as indicated by the difference in the point of perceived null motion (Figure 7, left). These results support the finding from the pilot study. Moreover performance with respect to the dot coherence (irrespective of adaptation) was clearly much better than in the pilot experiment, as can be seen both in the population responses (Figure 7) and in the individual subject plots for the imagery condition (Figure 8) meaning that the slopes of the motion responses are steeper and look more like typical sigmoidal psychometric functions.

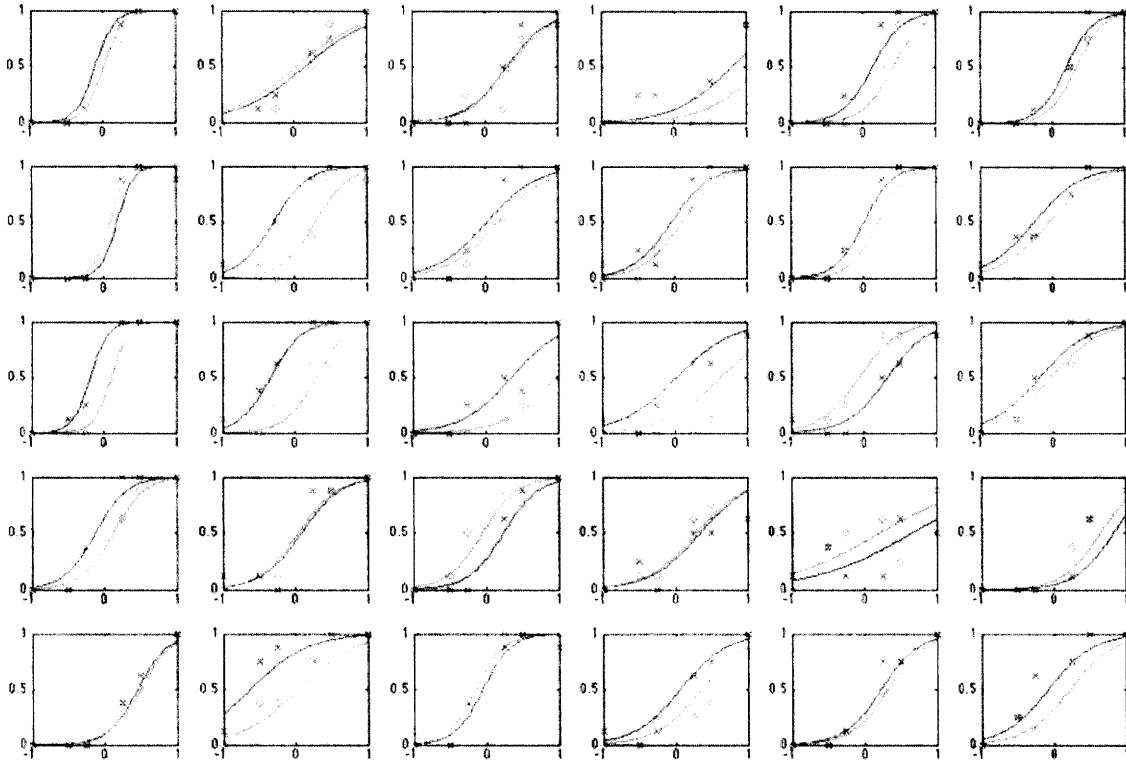


Figure 8. Individual motion response functions from the imagery condition. Red indicates downward imagery and green indicates upward imagery. The y-axis is the probability of an upward response, and positive values on the x-axis indicate upward coherence. Red curves to the left of green are consistent with motion aftereffects and scored as positive separations. When the green curve is to the left it is scored as negative.

To quantify the size of the motion aftereffects, we measured the difference in the point of perceived null motion for each individual subject as a function of upward versus downward imagery (Figure 8). We counted this value as positive if the separation between the null points was in the direction predicted by an aftereffect and negative if it was in the opposite direction. For the imagery condition, the mean separation between the curves for upward versus downward imagery was 0.15 ± 0.05 units of normalized motion coherence ($t(29) = 2.79$; $P = .009$, two-tailed paired t-test; Figure 9). Note that if the curves for individual subjects are replotted with the actual, un-normalized coherence values of the test stimuli instead of with normalized units, then the shapes of the curves are exactly the same; only the scale of the x-axis changes. In terms of the un-normalized

coherence, the separation between the curves was $5.5\% \pm 2.3\%$ ($t(29) = 2.43$; $P = .021$).

Note also that the effect can be measured without the assumptions of curve fitting by comparing the likelihood of responding “upward” at each coherence value using paired t-tests. This comparison shows significant effects of imagery at 0.25 and 0.5 units of normalized coherence ($t(29) = 2.44$, $P = 0.02$; $t(29) = 3.03$, $P = 0.005$, 2-tailed t-tests).

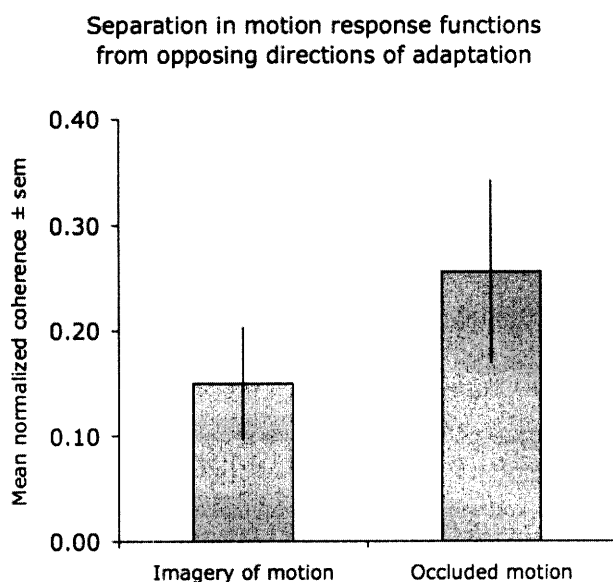


Figure 9. A summary of the mean separation between the motion response functions following upward and downward imagery, and upward and downward occluded motion. Positive numbers indicate a separation between curves that is consistent with a motion aftereffect.

Vividness of imagery and knowledge of the motion aftereffect. The motion aftereffects reported above were not modulated by subject’s reported knowledge of the motion aftereffect: the amount of adaptation from imagery in terms of normalized coherence was 0.12 versus 0.17 for 12 subjects familiar with the motion aftereffect versus 18 subjects not familiar with the motion aftereffect ($t(19) = 0.36$, $P = .72$, 2-tailed, unpaired t-test). There was also no correlation between self-reported vividness of imagery and the magnitude of the motion aftereffect for motion imagery ($r^2 = 0.01$, $P = .92$).

Motion aftereffects from occluded motion in the main experiment. Viewing occluded motion also led to a significant aftereffect, slightly larger than that found for imagery (Figure 7). The mean shift was of 0.26 ± 0.09 units normalized motion coherence ($t(29) = 2.95$; $P = .006$) and in terms of raw coherence, $7.7\% \pm 3.4\%$ ($t(29) = 2.60$; $P = .014$; Figure 9). These results are consistent with past reports of non-retinotopic motion aftereffects from “phantom gratings” (Snowden & Milne, 1997; Weisstein et al., 1977). Phantom gratings perceptually complete across uniform regions, giving rise to the illusion of stripes in the occluded region. Subjective reports from a few subjects indicate that our occluded motion condition did not in fact give rise to a strong phantom percept across the whole occluder, probably because of the large size of the occluder and the fact that it was intermediate in luminance between the dark and light bars, thus not being consistent with the presence of “camouflaged” stripes (Anderson *et al.*, 2002). Nonetheless we did not systematically study the subjective appearance of the grating and cannot say conclusively whether the motion aftereffect in this condition is the same phenomenon as that previously reported for phantom gratings, or is instead due to a high level inference that there was movement behind the occluder. Such high level inferences of motion were studied more directly in a series of experiments on implied motion, reported in Chapter 4, in which there was no visual motion at all during adaptation.

Occluded motion and fixation. For the occluded motion condition, we note that there was in fact a small amount of visual motion on the screen outside the occluded region. Although subjects were instructed to carefully fixate the flickering central square, it is possible that subjects ignored the instructions. If they indeed broke fixation and looked

directly at the moving grating in the periphery, then that motion aftereffect would be due to real visual motion and not occluded motion. Subsequent to the experiment, 4 new subjects were tested on the occluded motion task while their eyes were tracked, to determine whether they could maintain fixation and whether a similar aftereffect would be observed. We found that none of the 4 subjects looked away from fixation during the task (Figure 10), and that the size of the motion aftereffect was comparable to that found without eye tracking ($0.24 \pm .15$ units of normalized coherence versus 0.26 ± 0.09 , eye track versus non-eye track).

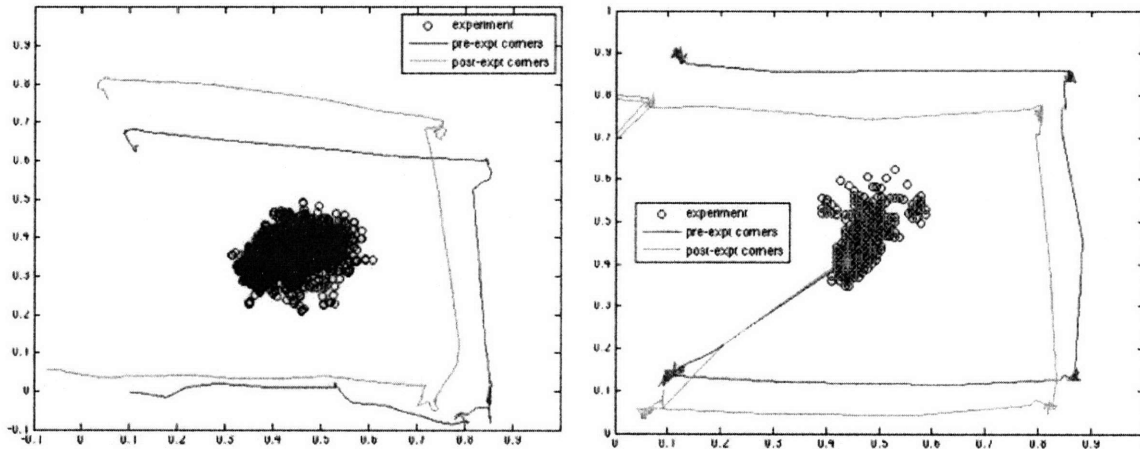


Figure 10. Two representative eye traces of subjects tested in the occluded motion experiment with eye tracking. The blue circles are gaze locations during a block of 24 trials of occluded motion adaptation. At the start (red line) and end (green line) of each block, subjects briefly fixated targets at the four corners of the occluder. The difference between the two paths indicates a slow drift in the calibration during the block. The tight clustering of the blue dots shows that subjects held fixation and did not look near or outside the border of the occluder; in fact the spread of the dots is an upper limit on the spatial spread of fixation, as the tracker added a small amount of measurement jitter due to imperfect tracking. Tracking was done with a ViewPoint eye tracker recording the eye position at 33 Hz, tracking gaze based on a calibrated map of the pupil location.

Model fits. To keep the number of free parameters in the model fits low, all data from each subject was fit by a single logistic function. Thus there was a single slope and single bias term for each subject, as well as one term for the effect of imagery adaptation and one term for the effect of occluded motion adaptation. (See General Methods.) The

same results are obtained however, if the occluded motion and imagery conditions are modeled separately; each condition shows a significant motion aftereffect of about the same magnitude (a mean shift of 0.150 vs. 0.145 normalized units for imagery, single fit versus separate fits; and a mean shift of 0.256 vs. 0.265 normalized units for occluded motion).

Subject variability. Not every subject showed motion aftereffects, both in the imagery condition and the occluded motion condition (Figure 8). Some variability, as in all measurements, presumably reflects sampling error. Given modest effect sizes, a greater number of trials might be required to have sufficient sensitivity to measure the motion aftereffect with certainty in each subject. Generally subjects found that 30-60 minutes of mental imagery was quite demanding and many more trials was not feasible. (There were 192 trials of imagery or occluded motion in Experiment 1.) The effect may also vary because subjects differed in their ability or their effort to vividly imagine motion, and such individual differences might not be captured by the self-report survey. Recent studies have highlighted the fact that individual differ not just in an overall ability to form mental images, but in the particular types of imagery they are good at (Kozhevnikov *et al.*, 2005), and further that only a subset of imagery tests may be predictive of performance on particular tasks (Mast & Kosslyn, 2002). However, we note that the motion aftereffects in each condition of the main experiment were also confirmed by two-tailed sign-tests, demonstrating that the results were not primarily driven by large effects in a few subjects (median separation between the motion response functions different from 0: imagery, $P = 0.043$; occluded motion, $P = 0.002$).

Summary and Conclusions.

Together, the set of results in the first experiment demonstrate that mental imagery of motion, as well as viewing occluded motion, can elicit a motion aftereffect as assessed with real-motion dynamic test probes. The transfer of adaptation from imagery suggests that mental imagery of motion can engage direction-selective perceptual motion mechanisms, demonstrating a high level of specificity in the activation of sensory mechanisms under volitional control.

Experiment 2: Does the motion aftereffect from mental imagery depend on the eyes being open during imagery?

In the first experiment, a motion aftereffect was observed from mental imagery of motion and from viewing occluded motion. In both conditions, subjects had their eyes open while fixating a pulsating square. Although the fixation square did not contain any directional motion, luminance flicker can strongly engage motion-processing mechanisms (Adelson & Bergen; Qian & Andersen, 1994). It is possible that some visual input may have been necessary to produce the motion aftereffect. Alternatively, bottom-up visual input can also compete with mental imagery, as in the Perky effect (Perky, 1910), and hence having one's eyes open in the absence of perceptual motion might be expected to interfere with imagery. We were thus interested in evaluating the effect of keeping the eyes closed versus open while imagining visual motion. In this experiment, subjects imagined motion, upward or downward, either with eyes open or closed.

Methods

Subjects and equipment. 33 naïve subjects were recruited from the MIT community. Subjects provided written consent and were paid for participation. One subject was excluded from analysis due to poor baseline performance and three were excluded for lack of sensitivity to motion coherence during the experiment.

Adapting stimuli. The moving grating that subjects were instructed to imagine was the same as that in Experiment 1. As with the first experiment, subjects were instructed to attend carefully to the appearance and speed of the grating so that they could later imagine it as accurately and vividly as possible. In order to facilitate continuous motion imagery, the pulsating fixation square again served as a timing guide during imagery with the eyes open. In addition to the square guide, subjects also heard a tone that cycled in pitch (spanning one-half octave, starting from middle C). During the “eyes closed” blocks, subjects were instructed to close their eyes each time the static grating faded, and to use the cycling tone as a timing guide for imagery. At the end of each imagery period, the tone stopped cycling, and was followed by a brief pause and then a single beep, cueing subjects to open their eyes and attend to the test stimulus.

Test stimuli. The same random dot test stimuli were used as in Experiment 1. Six coherence values, 3 up and 3 down, were again chosen according to performance during a baseline task of 180 trials.

Procedure. The procedure was nearly identical to that of Experiment 1, with a few exceptions. There were again 8 blocks of 24 trials, but instead of 4 imagery blocks and 4 occluded motion blocks, there were 4 eyes-open and 4 eyes-closed imagery blocks. For this experiment, in addition to seeing 4 examples of the moving grating during the

instruction phase of the experiment, subjects also viewed the grating 4 times for 6 s each before each block to re-familiarize them with its appearance. The direction of the grating alternated up and down during these 4 re-familiarization examples. After these examples, instructions were provided as to the direction of imagery and whether the eyes were open or closed for the upcoming block. Because these instructions came after viewing the example gratings, subjects could not selectively attend to the gratings moving in the direction of subsequent imagery, and hence selective attention to real motion preceding the imagery blocks could not explain any adaptation effects.

Results and Discussion

Both conditions yielded significant motion aftereffects (Fig. 11), similar in magnitude to that measured in the first experiment. The mean separation between the curves for upward and downward imagery was 0.19 ± 0.06 units of normalized motion coherence (mean \pm SEM; $t(28) = 2.99$, $P = .006$, 2-tailed t-test) in the eyes closed imagery condition, and 0.11 ± 0.05 in the eyes open imagery condition ($t(28) = 2.32$, $P = .028$). In terms of the actual (un-normalized) dot coherence, these separations were $5.8\% \pm 1.8\%$ ($t(28) = 3.25$, $P = 0.003$) with eyes closed, and $3.7\% \pm 1.2$ ($t(28) = 2.27$, $P = .031$) with eyes open.

Thus the presence of visual input such as flicker is not necessary for imagery to produce adaptation, and hence an aftereffect. In fact, there is a hint that the eyes closed condition led to a stronger aftereffect, but there was not a significant difference between conditions ($t(28) = 1.58$, $P = .12$, within subjects paired t-test). As with the first experiment, the motion aftereffects in each condition were confirmed with a sign test ($P = 0.015$, eyes open imagery; $P = .0041$, eyes closed imagery).

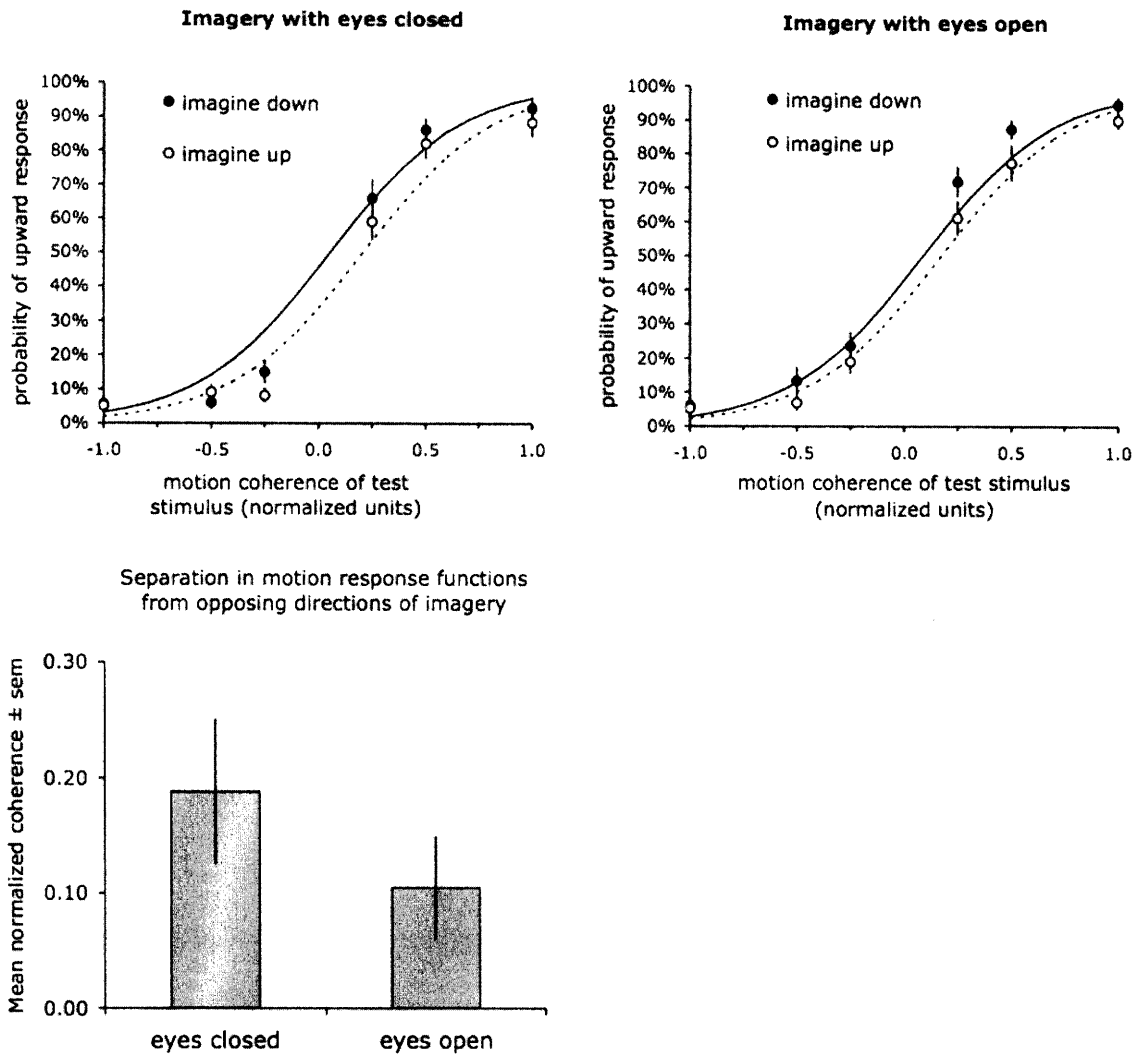


Figure 11. Motion aftereffects following upward and downward imagery, both with the eyes closed and the eyes open. The upper plots show the population motion sensitivity functions. Positive numbers indicate a separation between curves that is consistent with a motion aftereffect

Experiment 2 thus serves as a replication of the imagery condition in Experiment 1, and also extends these results by demonstrating that the motion aftereffect does not depend on visual input during imagery: imagining a moving stimulus in a dark room with closed eyes engaged direction-selective perceptual motion mechanisms sufficiently to cause a small but reliable aftereffect.

Experiment 3: Can a motion aftereffect be obtained with inward / outward motion?

The purpose of the third experiment was to address the possibility that eye movements during imagery contributed to the motion aftereffects measured in the first two experiments. In this experiment, subjects imagined horizontal motion either inward (toward fixation) or outward (away from fixation), either with their eyes open or closed. The effect of motion imagery on subsequent motion perception was assessed with dynamic dot test probes that moved inward or outward.

Methods

Subjects and equipment. 31 naïve volunteers were recruited from the Stanford community. One subject was excluded from analysis due to poor baseline performance and two were excluded for lack of sensitivity to motion coherence during the adaptation experiment.

Adapting stimuli. The in-out adapting stimulus consisted of two vertical square-wave gratings which abutted at the midline of the screen. The gratings moved horizontally either towards the center (“inward”) or away from the center (“outward”). All other details were as for the up-down imagery in Experiment 2.

Test stimuli for in/out imagery. The test stimulus consisted of 200 dots, 100 on each side of fixation. The dot density was thus twice that of the first two experiments. The coherent dot motion was horizontal inward or horizontal outward on a given trial. The stimulus was otherwise identical to the test stimulus used for up/down imagery experiments.

Baseline motion task. The baseline task differed slightly from the task in the second experiment. There were 192 trials instead of 180 trials, covering a wider range of coherence values (up to 100%, instead of up to 65%, as a few subjects in the prior experiments had motion thresholds above 65%). Performance on the baseline task again determined the coherence values used during the experiment. However, the range of coherence values used was slightly different; instead of three values of normalized coherence four times per block in each of two directions, subjects were tested with a greater number of values once each per block ($\pm 100\%$, $\pm 66\%$, $\pm 44\%$, $\pm 29\%$, $\pm 19\%$, $\pm 13\%$, $\pm 8\%$, $\pm 5\%$, $\pm 3\%$, $\pm 2\%$, $\pm 1\%$, and 0% of one normalized unit of coherence.)

Procedure. The procedure was identical to that used in Experiment 2.

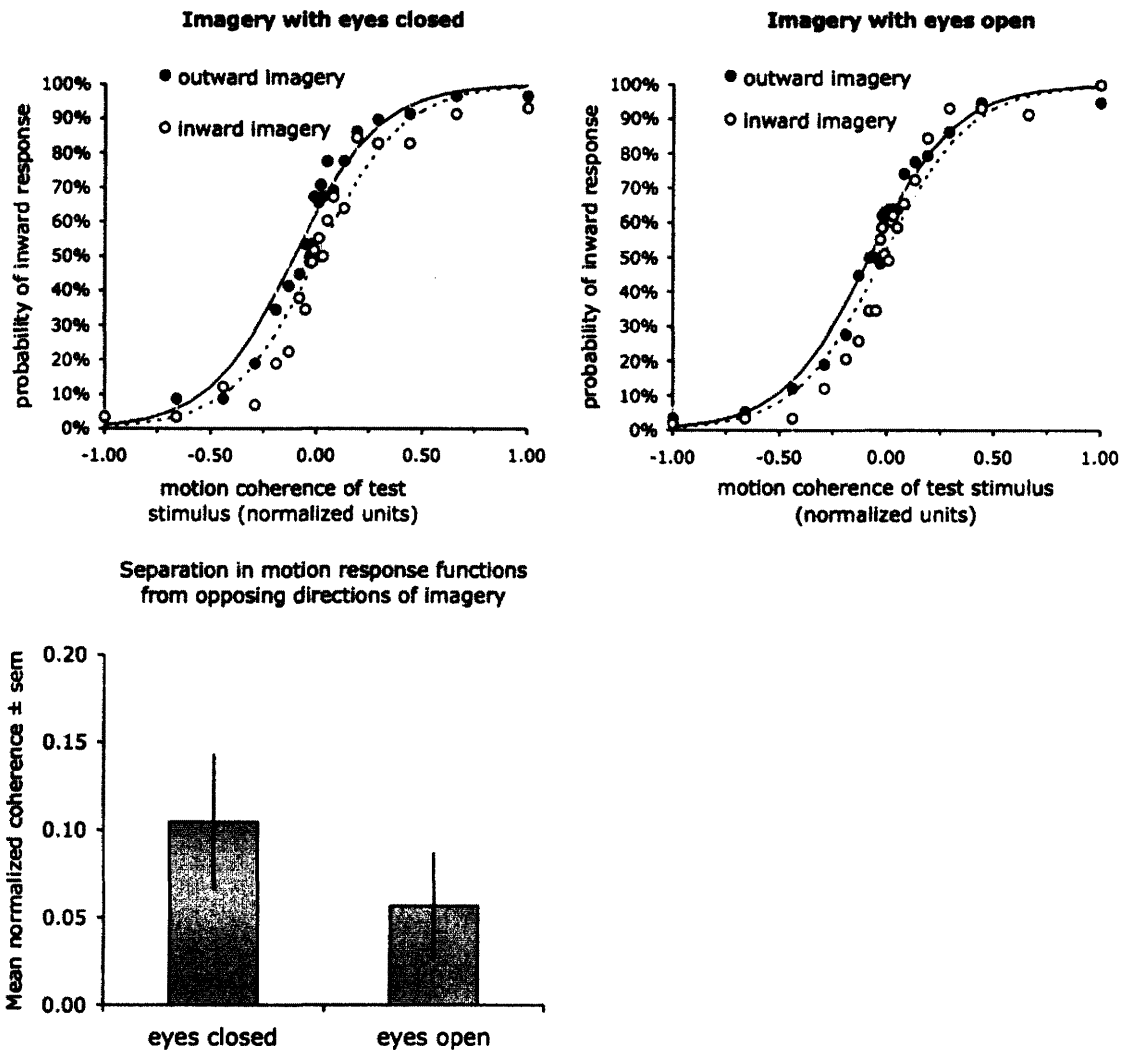


Figure 12. Motion aftereffects following inward and outward imagery, both with the eyes closed and the eyes open. The upper plots show the population motion sensitivity functions. The bottom plot shows the mean separation between the curves for individual subjects. Positive numbers indicate a separation between curves that is consistent with a motion aftereffect.

Results and Discussion

Mental imagery of inward or outward motion, like upward and downward imagery, elicited a motion aftereffect, as seen in the shifts in the motion sensitivity plots (Figure 12), though the effects were about half the size as that found for upward and downward imagery, and significant only for the eyes closed condition. The separation between the curves for inward and outward imagery was 0.10 ± 0.04 units of normalized motion coherence ($t(27) = 2.72, P = .011$, 2-tailed t-test) in the eyes closed imagery

condition, and 0.06 ± 0.03 in the eyes open imagery condition ($t(27) = 1.84, P = .08$, 2-tailed t-test). In terms of the un-normalized dot coherence, these separations were $3.8\% \pm 1.7\%$ ($t(27) = 2.32, P = 0.028$) with eyes closed, and $1.9\% \pm 1.4$ ($t(27) = 1.38, P = .18$) with eyes open. Sign tests revealed significant motion aftereffects in both conditions ($P = 0.0094$, eyes open imagery; $P = 0.0015$, eyes closed imagery).

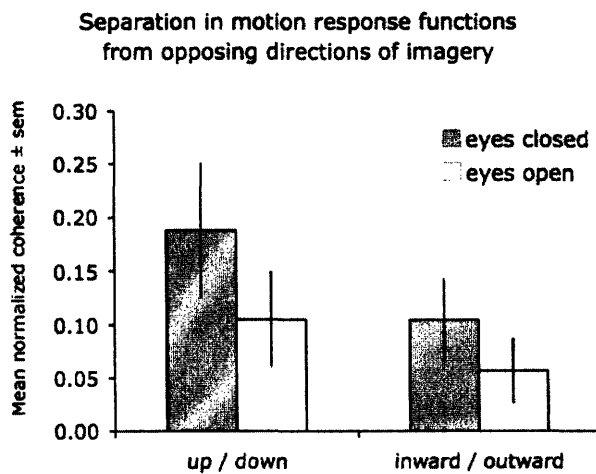


Figure 13. A comparison of experiments 2 and 3 Overall imagery shifted the motion response functions in the direction predicted by adaptation (hence the positive bars). The shift was bigger during imagery with eyes closed than with eyes open.

Experiments 2 and 3 together. In both the second experiment with upward and downward imagery and the third experiment with inward and outward imagery, there was a trend towards a bigger effect of imagery when subjects had their eyes closed. This observation was tested in a 2 x 2 mixed design ANOVA, with eye condition (open vs. closed) as a within-subjects repeated measures factor, and the type of imagery (up/down vs. in/out) as a between-subjects factor. The size of the separation between motion response functions from opposing directions of imagery was used as the dependant measure. The ANOVA confirmed that imagery was more effective with the eyes closed than open across the two experiments (a separation of 0.14 versus 0.08 units of

normalized coherence, eyes closed versus open; $F(1, 55) = 4.49, P = 0.039$). The size of the aftereffect did not significantly differ based on the type of adaptation (0.15 versus 0.08, up/down imagery versus in/out imagery, $F(1, 55) = 1.31, P = 0.257$).

The fact that imagery of inward or outward motion led to a motion aftereffect provides a replication of the first two experiments, and also extends the results to a condition in which the direction of imagery was not confounded with possible eye movements. In the first two experiments, subjects were instructed to fixate during conditions in which their eyes were open, and they presumably had no visual input during conditions in which their eyes were closed; however, it is nonetheless possible that they could have made eye movements during the imagery period in the direction of imagery. Motion aftereffects have been observed from eye movements in the absence of directional visual motion (Chaudhuri, 1991). Had subjects made pursuit eye movements during imagery (with saccades back to fixation), the eye movements themselves, and not mental imagery, might have caused the aftereffect. Were this the case we would have predicted there to be no effect for inward or outward adaptation, contrary to what we observed.

An interesting question that arises from adaptation to inward or outward imagery is whether two local, retinotopic populations of neurons, each tuned to either leftward or rightward motion simultaneously adapted; or whether higher level motion systems tuned to more complex motion (i.e., inward or outward motion (Huk *et al.*; Saito *et al.*; Tanaka *et al.*)) adapted. These possibilities cannot be directly distinguished from the results of these experiments. Other research on adaptation to high-level motion systems, such as attentional tracking (Culham *et al.*, 2000), has provided evidence for sites of adaptation

that are tuned to more complex motion and that have less retinotopic specificity than bottom-up stimulus adaptation. If that were true of mental imagery as well, it would imply that inward or outward imagery adapts circuits tuned to inward or outward motion, though further experiments are needed to confirm this.

Experiment 4: Does imagery-induced adaptation depend on reactivation from short-term memory?

In each of the first three experiments, we observed significant motion aftereffects resulting from mental imagery of motion. For some types of visual imagery, such as imagery of oriented Gabor patches, there is evidence that the effect of imagery on subsequent perception of visual stimuli depends on having recently seen the stimulus to be imagined. In this sense, Ishai and Sagi (Ishai & Sagi, 1995, 1997a) have argued that imagery may work, in part, by accessing a short-term, iconic memory buffer. In the second and third experiments, subjects saw 4 examples of the moving gratings during the instruction phase and again at the start of each of the 8 imagery blocks. In the first experiment, subjects saw full examples of the moving grating only at the beginning of the experiment and not at the beginning of each block; however, blocks of occluded motion, in which there was real visual motion in the periphery, were interspersed with blocks of imagery. These interspersed occlusion blocks may have served to refresh the perceptual memory of the motion stimulus. In the current experiment, we asked whether imagery of motion, inward or outward, could produce a motion aftereffect if subjects were not given examples of the motion to be imagined before each block of imagery.

Methods

Subjects and equipment. 28 naïve volunteers were recruited from the Stanford community. Two were excluded for lack of sensitivity to motion coherence during the experiment.

Stimuli. The adapting and test stimuli were identical to those in Experiment 3.

Procedure. The procedure was identical to that of Experiment 3 except in two ways. First, subjects did not see examples of the moving gratings at the beginning of each block of trials. They were shown 4 examples of the gratings, two up and two down, for 6 s each during the instructions (as in the previous two experiments), but they did not see further examples during the remainder of the experiment, which took about 25-30 minutes. Secondly, there were four blocks of imagery, all with eyes closed, instead of 4 blocks with eyes closed and 4 with eyes open. Thus the experiment was half as long.

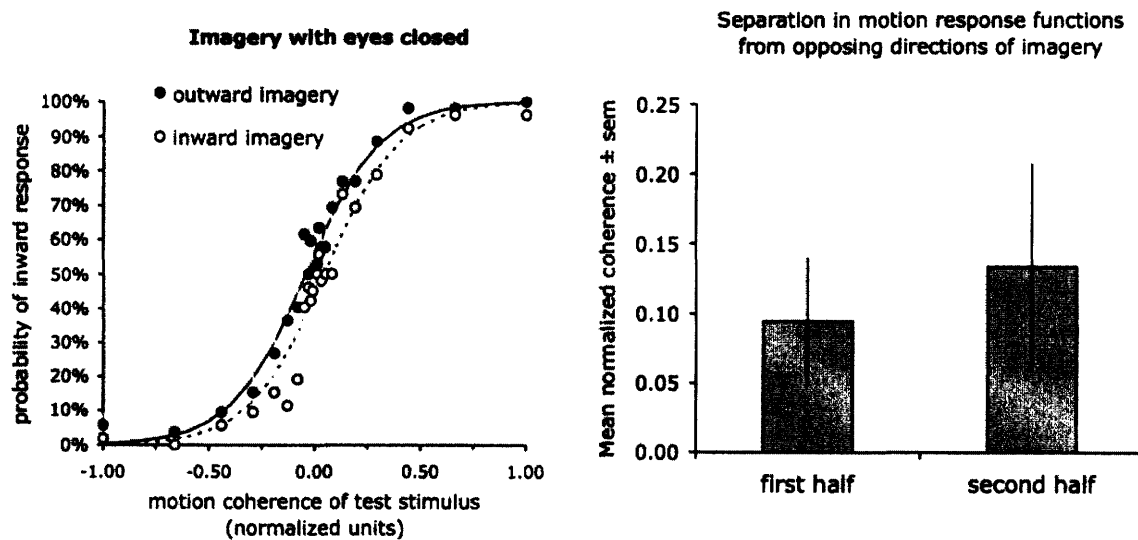


Figure 14. Motion aftereffects following inward and outward imagery with the eyes closed. In this experiment, subjects did not see examples of the moving grating before imagery blocks. On the right, the average separation between the individual subjects' curves for inward and outward imagery are split into halves: the first inward versus first outward imagery blocks ("first half") and the second inward versus second outward blocks. The size of the separation between curves did not differ by half.

Results

The effect of inward and outward motion imagery in this experiment was similar to that found in Experiment 3, despite the fact that subjects did not see examples of the stimulus-to-be imagined at the start of each block (Figure 14). Overall, the separation between motion sensitivity functions was 0.11 ± 0.05 units of normalized coherence ($t(25) = 2.07, P = 0.049$), comparable to that found in Experiment 3 for the eyes closed condition (0.10 ± 0.04).

A further analysis of this experiment was conducted by separating the four blocks into two pairs: the first block of inward imagery and the first block of outward imagery (“First half”) and the second block of inward imagery and the second block of outward imagery (“Second half”). Since there were two blocks of each direction of imagery arranged in random order, the “first half” blocks included the first block and either the second (if the direction of imagery changed between the first and second blocks) or the third (if it did not). The second half included the last block and either the second or third. As each block took about 6 minutes, the second half blocks included one block that started at least 18 minutes after the four examples were seen during the instructions, and one block that started at least 6 or 12 minutes after the last grating was viewed. Note also that the real grating was viewed for a total of only 24 seconds, at the very beginning of the experiment. The size of the aftereffect did not differ significantly between the two blocks (Figure 14), with a separation of 0.09 ± 0.05 versus 0.13 ± 0.07 units of normalized coherence (first half versus second half, $P = 0.47$, 2-tailed paired t-test).

These results contrast with those of prior studies investigating the effects of short-term memory on the effectiveness of imagining oriented Gabor patches: In a series of

experiments, Ishai and Sagi (Ishai & Sagi, 1995, 1997a) found remarkably specific effects of imagery on subsequent visual perception, but the effects were restricted to cases in which the stimulus to be imagined had been viewed repeatedly just prior to imagery. Specifically, imagery of oriented “flanker” Gabor patches, like visual perception of flanker Gabor patches, was shown to increase the sensitivity to detect a low contrast, central Gabor patch of the same orientation between the two flankers. Imagery of the flankers only improved detection of the real, low-contrast central target if the subjects had previously completed a series of trials in which the flankers were actually present (with no imagery required). The effects were quite specific in that imagery of the flankers did not facilitate detection of the central target if the target was not viewed through the same eye that the previous, real flankers had been seen; and imagery of the flankers was only facilitatory if the imagined flankers were of the same orientation as the previously viewed flankers. Furthermore, the perceptual experience had to be recent and unobstructed by intervening noise: if there was a gap of 5 min separating the perception trials and the imagery trials, or if visual noise patterns were shown after each perception trial, or if there were only 10 (instead of 50) preceding perception trials, then imagery of the flankers had no benefit. Their interpretation was that volitional imagery could reactivate in a highly specific manner those representations that had been recently driven by bottom-up perceptual processing channels, but that it could not create such specific representations from long term memory.

It appears that such a mechanism does not play a critical role in our experiments on imagery of motion; we observed an effect of imagery even when the stimulus to be

imagined was presented briefly (a total of 24 s), non-specifically (equally often in both directions), and with a long gap prior to imagery.

Experiment 5: Adaptation to real visual motion

As a basis of comparison to the imagery experiments, adaptation to real motion was measured using the same stimuli and procedures.

Methods

Subjects and equipment. 31 naïve subjects were recruited from the MIT community for adaptation on upward or downward real motion. Three subjects were excluded from analysis due to poor baseline motion discrimination and three were excluded for lack of sensitivity to motion coherence during the experiment. Four additional subjects were run in a pilot study of adaptation to inward or outward real motion.

Stimuli. The adapting grating and the test dots for upward and downward real motion adaptation were identical to those used in Experiment 2 for upward and downward imagery, except that the grating was actually shown during all trials. Similarly, the adapting grating and test stimuli for inward and outward real motion adaptation were identical to those used in Experiment 3, except that the grating was actually shown.

Procedure. For upward and downward real motion, the procedure was identical to that used in Experiment 2 except for the following differences. There were only four blocks of trials instead of 8 (because there were no eyes closed trials). Hence there was also no auditory timing guide. Examples of the grating were not shown at the beginning

of each block because subjects did not need to imagine the grating. Finally, the instructions were to fixate and not to imagine motion. Note that the fixation square pulsed in luminance, just as it did during the eyes open condition of Experiment 2.

For adaptation to inward and outward motion all details were the same except that the range of coherence values in the test stimuli were the same as those used for inward and outward imagery in Experiment 3, and not the same as those used for upward and downward imagery in Experiments 1 and 2.

Results and Discussion.

As expected, viewing real visual motion led to a robust motion aftereffect (Figure 15). Viewing downward motion led to a greater likelihood of seeing the dots move upwards, and *vice versa*, and viewing outward motion led to a greater likelihood of seeing the dots move inward. For upward and downward motion, the separation between the two functions following opposite directions of adaptation was 0.73 ± 0.25 units of normalized coherence ($t(23) = 2.92, P = 0.008$), or $21\% \pm 6.4\%$ in terms of the actual, un-normalized coherence ($t(23) = 3.44, P = 0.002$). Adaptation to inward or outward motion also led to a large motion aftereffect: a separation between curves of 0.31 ± 0.02 units of normalized coherence. These effects were about 3 – 6 times bigger than those found from imagery.

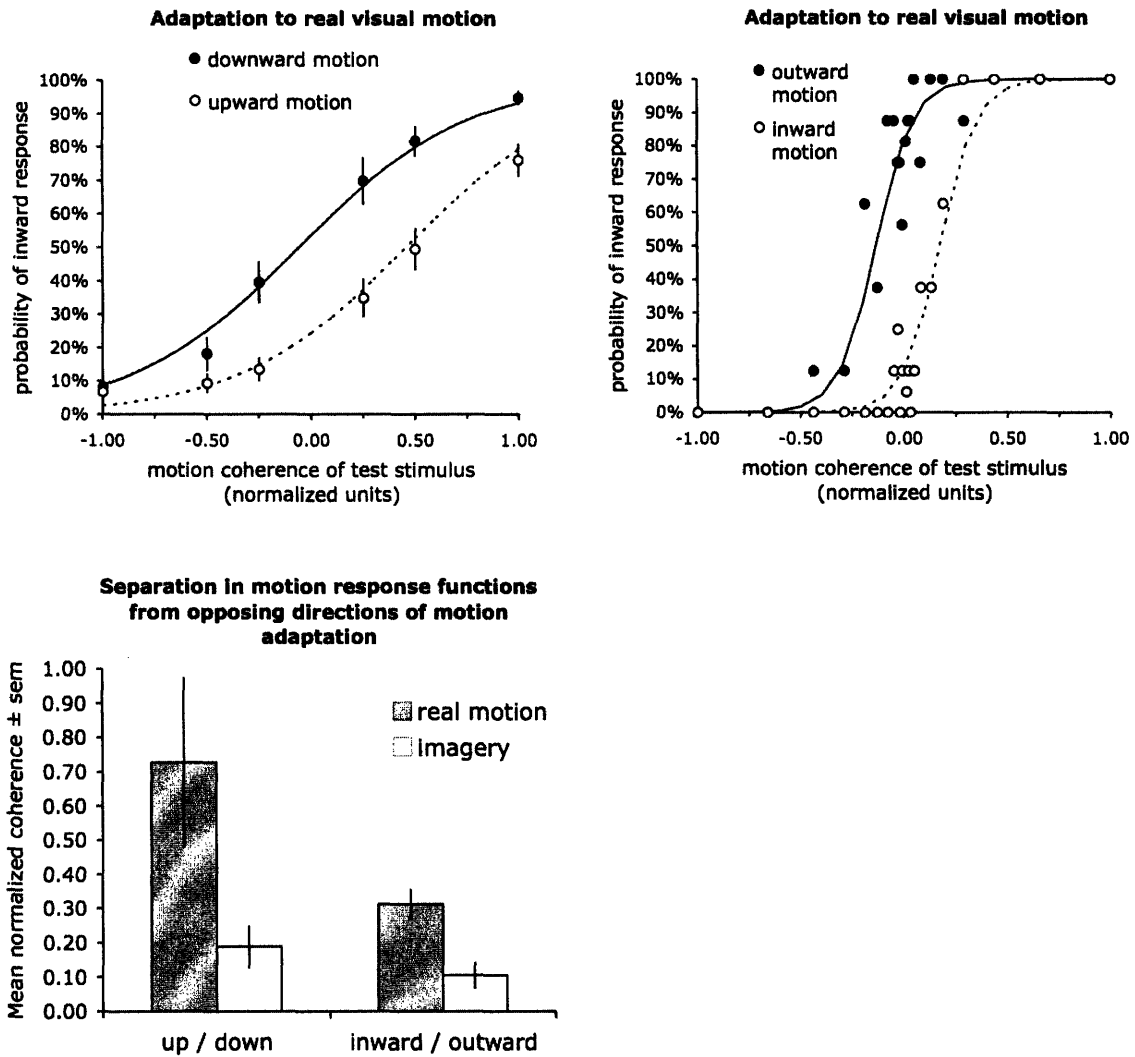


Figure 15. Motion aftereffects following adaptation to real visual motion, either upward and downward (top left, 26 subjects) or inward and outward (top right, 4 subjects) Positive values on the x-axis indicate upward motion or inward motion. The aftereffect is similar to that seen from imagery of motion, but about 3-4 times larger (bottom). The imagery results in the bars chart are replotted from the eyes closed condition of Experiment 2 (up / down) and 3 (in / out).

General Discussion

Across 5 experiments we have observed motion aftereffects from imagining motion, viewing occluded motion, and viewing real motion. We quantified the effect as the difference in dot coherence between the null points following one direction of adaptation versus the opposite direction. All experiments showed significant shifts in the null point in the direction consistent with a motion aftereffect, demonstrating for the first

time that imagery of motion recruits direction-selective neural mechanisms also used for perceiving real motion. We also extended prior results demonstrating that motion completed across an occluder can cause a motion aftereffect in the location of the occluder.

The motion aftereffects from imagery that we find were smaller than the motion aftereffects from real motion. This is consistent with findings showing that imagery leads to less activation of sensory cortical areas than perception of the same stimuli (e.g., (Goebel *et al.*, 1998; Grossman & Blake, 2001))(Kosslyn *et al.*, 1997), and consistent with the notion that mental images tend to be less detailed than perceptual representations.

Relation to other work

The prior work most directly connected to our principle conclusion – that motion imagery can engage and adapt direction-selective motion neurons – is a study by Gildea and colleagues (Gidea *et al.*, 1995). That study demonstrated that real motion adaptation affected imagery of motion, the converse of our experiments. The two sets of studies are convergent in showing a transfer of adaptation between real and imagined motion, but nonetheless the conclusions drawn are quite different. Gildea and colleagues considered two possible explanations for their effect: that adaptation affected the *speed* of an imagined, moving stimulus, and that adaptation affected the *location* of an imagined, static stimulus. Based on an analysis of the stimulus properties used in their experiments and a review of the prior literature on velocity aftereffects, they concluded that the second explanation is consistent with their effects and that the first is not. They thus interpret their results as evidence that motion imagery consists of picturing a static

stimulus at a series of locations and inferring motion by the change in location. (The explanation for their effect according to this view was that each successive static frame during the attempted motion imagery was displaced by the motion aftereffect.) If their interpretation is correct and it applied in our experiment, we would have expected there to be no transfer of adaptation from motion imagery to motion perception, contrary to what we observed. Instead we believe our results provide positive evidence that imagery of motion involves and adapts direction-selective motion mechanisms.

Our results are also consistent with a prior finding that imagining motion can lead to the illusion of roll vection (Mast *et al.*, 2001). In this study, imagining rotating motion around the line of sight in an environment without visual cues to the direction of gravity led to the illusion that horizontally arranged dots were tilted relative to the ground, an effect known to occur with real rotational motion. This study demonstrated an effect of motion imagery on a spatial judgment that depends on the integration of non-visual gravity signals with visual motion signals. Our studies add to this by showing that motion imagery recruits and adapts directional motion mechanisms.

Another novel aspect of these findings is that they are unlikely to be explained by reactivation during imagery using a short-term sensory memory system, as has been hypothesized to explain stimulus specific effects of imagery on perception (Ishai & Sagi, 1995, 1997b). We infer this because, first, in all the studies there was only minimal viewing of actual motion stimuli; second, in all the studies there was an equal exposure to real motion stimuli in both directions prior to imagery, such that any attempt to recall retrieve short-term memories would also require the subject to be able to select one among competing memories; and third, in study 4 the real motion stimuli were seen only

at the beginning of the experiment, without a decline in effect over the course of the experiment. Our interpretation is that top-down processes are able to selectively activate populations of neurons tuned to the direction chosen for that task. In the case of imagery driven facilitation of Gabor detection, it is possible that the top-down signals are non-specific, and that the specificity in the effects fall out of the specificity of what happens to be in short-term perceptual memory. Nonetheless, we did not conduct experiments in which we asked subjects to imagine a motion stimulus having given them no examples at all of real motion stimuli; the experiments in the next chapter on implied motion more directly test the role of pure long-term memory on activation of motion signals.

Eye movements

Could the aftereffects we observed be due to systematic eye movements? This is an important consideration since visual imagery can lead to a pattern of eye movements similar to visually inspecting a scene (Brandt & Stark, 1997), and eye movements in the absence of retinal motion can lead to a motion aftereffect (Chaudhuri, 1990, 1991; Freeman *et al.*, 2003). Although we did not track eye movements during adaptation (except for a few subjects in the occluded motion condition of Experiment 1), the results from the experiments with inward/outward imagery (experiments 3 and 4) discount the possibility that the motion aftereffects we report arise from pursuit eye movements during adaptation.

Attention to motion

Another possible explanation for our results is that the aftereffects we measure are due to attentional processes. It has been suggested that imagery, including spatial imagery

and motion imagery, may rely on the same processes as spatial attention (Pylyshyn, 2002). Furthermore, both attending to a direction of motion (Alais & Blake, 1999) and attentionally tracking a moving stimulus (Culham *et al.*, 2000) have been shown to modulate or induce motion aftereffects, and attending to motion stimuli can increase the neural response to motion (Beauchamp *et al.*, 1997; Corbetta *et al.*, 1991; O'Craven *et al.*, 1997; Saenz *et al.*, 2002; Watanabe *et al.*, 1998). In our experiments where subjects imagined motion with their eyes open, they fixated a flickering fixation square which, although containing no net direction of motion, contained equal motion energy in opposite directions. Thus if subjects were able to isolate and preferentially attend to or track the direction of motion in which they were instructed to imagine, then the motion aftereffect might be thought of as an attentional modulation of adaptation to real motion. If this were the case, however, one would predict no aftereffect when subjects were imagining with the eyes closed. Instead, we find that imagery in the eyes closed condition led to a motion aftereffect slightly larger than the motion aftereffect with eyes open, thus ruling out selective attention to real visual motion as the source of the motion aftereffects we measured.

A related interpretation would be that subjects imagined motion by moving spatial attention using a process independent of visual stimuli. However, the possibility of inducing a motion aftereffect by attending to a direction of motion below the threshold of detection using low coherence dot stimuli has been tested and rejected, leading the authors to conclude that feature-based attention cannot amplify a signal that is not present (Alais & Blake, 1999). Moreover, even if imagining a moving stimulus did recruit attentional processes, our effects could only be explained if these attentional processes

resulted in direction-specific adaptation of motion neurons in the absence of detectable real motion. This would thus not alter our principal claim, that imagining motion relies on direction-specific neural mechanisms also used for processing real visual motion.

Whether attention serves as a mediating factor in our experiments, and more generally whether it is even possible to imagine a stimulus without attending to it, cannot be resolved with the results we report.

Level of adaptation

As highlighted by the attentional literature on motion processing, it is important to note that there are many motion systems potentially subject to adaptation. For example, though both attentional tracking of moving stimuli and bottom-up processing of moving stimuli lead to motion aftereffects, the aftereffects have been shown to have different properties (Culham et al., 2000), leading the authors to conclude that tracking adapts a relatively high level motion system compared to adaptation from bottom-up motion signals. Moreover, top-down attentional influences on motion processing can occur at various stages of the visual processing stream dependent on the task and the type of motion attended (Watanabe et al., 1998). From the experiments reported here, we can conclude that whatever motion mechanisms are adapted via imagery must contribute to judgments of the direction of perceptual motion stimuli. But we cannot as yet say precisely what the properties of the adapted system are. Potentially this can be understood by methods that more directly measure the neural substrates of the motion systems undergoing adaptation.

Generality of effects of imagery

Finally, we ask how general these findings are: Does mental imagery always rely on low-level sensory mechanisms? Does imagery of all stimulus classes engage the corresponding perceptual networks? There is a growing neuroimaging literature indicating that imagery can activate brain areas that normally respond preferentially to the perceptual or motor attribute being imaged, including area MT for motion (Goebel et al., 1998), the fusiform face area for faces and the parahippocampal place area for houses (O'Craven & Kanwisher), as well as auditory areas (Halpern & Zatorre, 1999; Zatorre & Halpern, 2005), motor areas (Porro *et al.*, 1996), and somatosensory areas (Yoo *et al.*, 2003) for the corresponding imagery task. These results suggest that sensorimotor reactivation from top-down signals may be a quite general property of imagery.

The degree to which early sensory mechanisms are recruited, however, is probably variable, depending on the task and perhaps on the individual. Kosslyn and colleagues (Kosslyn & Thompson, 2003) reviewed the neuroimaging literature to ask what factors predicted the activation of V1 in mental imagery experiments. In addition to one methodological factor (the use of fMRI as opposed to PET), they found that two factors, whether participants had to note high resolution details and whether they had to attend to visual shapes (as opposed to spatial locations) predicted systematic differences in whether or not V1 was activated by imagery. Moreover, as discussed earlier, Ishai and Sagi have reported on differences in the effects of imagery dependent on whether the stimuli were imagined from long-term or short-term memory, with greater involvement of early sensory mechanisms for imagery mediated by short-term memory (Ishai & Sagi,

1995, 1997b). One of these authors also reported neuroimaging results demonstrating differences between imagery from short-term and long-term memory (Ishai *et al.*, 2002).

It seems reasonable to assume that volitional imagery is flexible, drawing on the whole range of perceptual representations, from those that are close to the initial sensory encoding to the fully abstracted, depending on the nature of the task and the specificity of the stored information (a prediction noted by Hebb (1968)). The experiments presented here provide novel evidence for the involvement of a particular kind of sensory representation, directional motion signals, in an imagery task, demonstrating one case in which top-down signals exert a highly specific effect on sensory representations.

Chapter 4: Motion Aftereffects from Viewing Photographs that Depict Motion

Experiments 1, 2, and 4 have been accepted for publication in Psychological Science as “A motion aftereffect from still photographs depicting motion” by Jonathan Winawer, Alex Huk, and Lera Boroditsky.

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 viewing physical motion? A series of studies is presented testing whether implied motion is represented by the same direction-selective signals involved in the analysis of real motion.

In the first experiment, subjects viewed a series of static photographs depicting people, animals, or vehicles moving in a particular direction, either left or right. This led to a motion aftereffect in the opposite direction as assessed with real motion dot test probes. To evaluate the temporal properties of the aftereffect, in a second study a brief delay (3 s) was sometimes inserted between viewing implied motion photographs and viewing the subsequent real motion test probe. On trials with delays the motion aftereffect was reduced by more than half, similar to what is found with delays during adaptation to real motion, suggesting that the aftereffect from implied motion and from real motion decay at a similar rate. In a third experiment, subjects viewed either pictures with implied motion or similar pictures of oriented scenes with no implied motion. A motion aftereffect was found only after viewing pictures with implied motion, indicating that the depiction of motion, and not just orientation, is critical to produce motion adaptation from viewing photographs. In a fourth experiment, subjects viewed mirrored

pairs of images, with implied motion either inward toward fixation or outward away from fixation. This too led to a motion aftereffect in the opposite direction. The interaction between real motion and implied motion was tested in a fifth experiment in which subjects viewed mirrored photographs of implied motion that actually moved slowly within a fixed aperture. When the real motion and the implied motion were in the opposite direction, the two tended to cancel, causing a reduced motion aftereffect or no aftereffect. Finally, the aftereffect from viewing implied motion as well as from real patterned motion was assessed by a different means in a sixth experiment in which the test stimulus was a counterphase grating instead of dynamic dot displays.

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. These results provide a concrete example of how a sensory processing mechanism, such as the direction-selective circuits involved in the analysis of visual motion, can be re-employed to instantiate abstract representations.

Experiment 1: Does viewing photographs that depict motion cause a motion aftereffect?

In this study we asked whether viewing images of people, animals, and vehicles with a common direction of implied motion would cause a motion aftereffect as measured with partially coherent, moving dot probe stimuli. The experimental design was analogous to that used for the mental imagery and real motion adaptation studies of Chapter 3, consisting of prolonged adaptation to one direction of implied motion with interleaved test stimuli.

Methods

Subjects and equipment. 26 naïve subjects were recruited from the MIT community. Subjects provided written consent and were paid for participation. Equipment and testing environment were the same as for the studies in Chapter 3. (See Chapter 2, General Methods.)

The performance of 5 subjects did not significantly exceed chance in terms of the dot discrimination task during the experiment and were excluded from analysis. In addition, two subjects performed poorly on the baseline motion sensitivity task. These subjects were also excluded from analysis. (See Chapter 2, General Methods.)

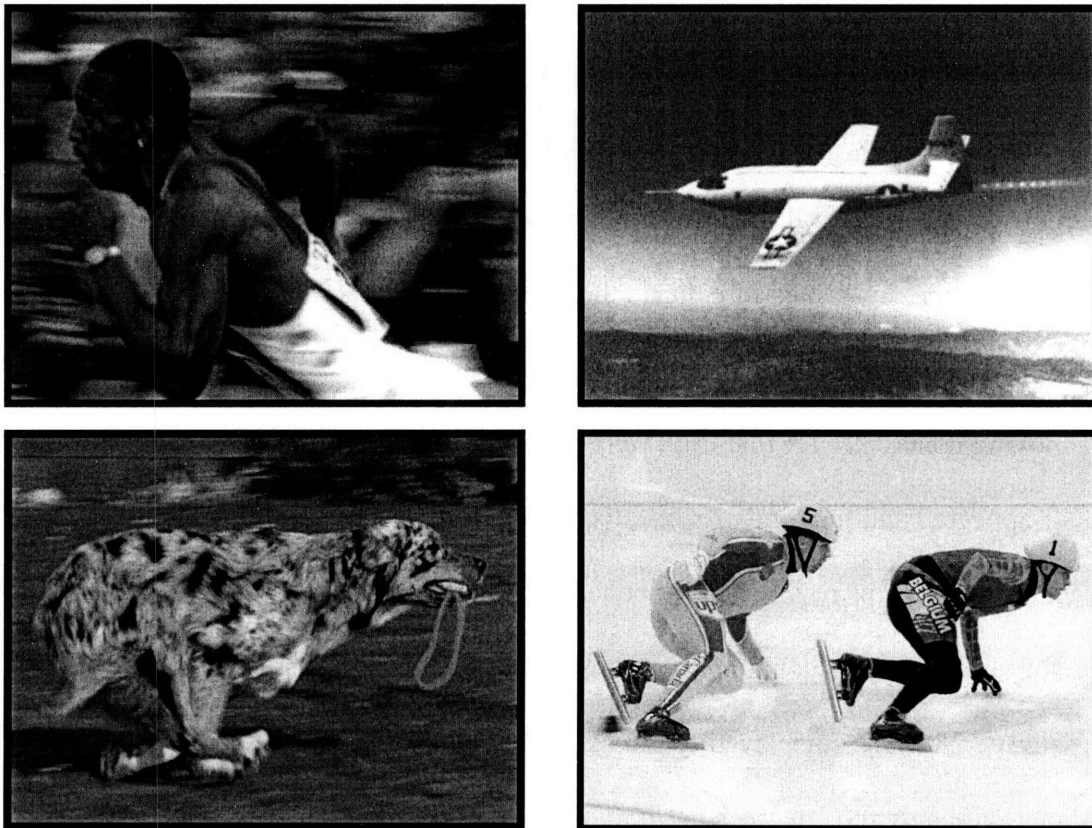


Figure 1. Examples of implied motion stimuli used in Experiment 1. There were 103 different photographs, each of which could appear facing the right or the left.

Adapting stimuli. 103 photographs with either leftward or rightward implied motion were found from Internet searches (e.g., Figure 1). Photographs depicted people, animals, or vehicles (or combinations of these) in motion. All photographs (or their mirror reversals) were used for both leftward and rightward adaptation. Images were centered on the screen and the size was scaled to a fixed area of 200,000 square pixels, keeping the original aspect ratio of each picture.

Dynamic dot test stimuli. As with the mental imagery and real motion adaptation experiments in Chapter 3, we used a standard moving-dot direction-discrimination task (Blake & Hiris, 1993; Hiris & Blake, 1992; Newsome *et al.*, 1989; Newsome & Pare, 1988) to assess the state of adaptation. Test stimuli consisted of 100 dots contained within a rectangular window whose length and width were 33% of the entire display (approximately 12 by 9 degrees of visual angle). The proportion of dots moving coherently in a particular direction (“motion coherence”) was varied from trial to trial, and subjects were instructed to indicate the direction of global motion as either “leftward” or “rightward”. On each frame a subset of the dots, equal to the percentage of dots moving coherently for that trial, were 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 re-selected for coherent movement on each frame, so that the trajectory of single dots could not be followed throughout a trial. Each 1-second test trial consisted of 25 frames displayed for 40 ms each. Dot displacement for coherent motion was approximately 0.07 degrees per frame, or 2 degrees per second.

Baseline motion sensitivity

As with the experiments in Chapter 3, subjects were tested on a baseline motion calibration task prior to the adaptation phase of the experiment. Dot coherence ranged from 5% to 65% over 180 trials in random order, either left or right. Performance on the baseline task was used to determine motion coherence thresholds, and thresholds were used to determine dot coherence for the subsequent adaptation phase. Specifically, the amount of dot coherence needed for asymptotic performance (99% accuracy based on fitted data) was considered one unit of “normalized coherence”, and subjects were tested on $\pm 100\%$, $\pm 50\%$, and $\pm 25\%$ of this value during adaptation. Across subjects, one unit of normalized coherence corresponded to $35\% \pm 14\%$ of actual dot coherence (mean \pm SD). Thus while the actual dot coherence values varied across subjects, the coherence values were equal relative to baseline motion sensitivity, and hence presumably perceptually similar across subjects.

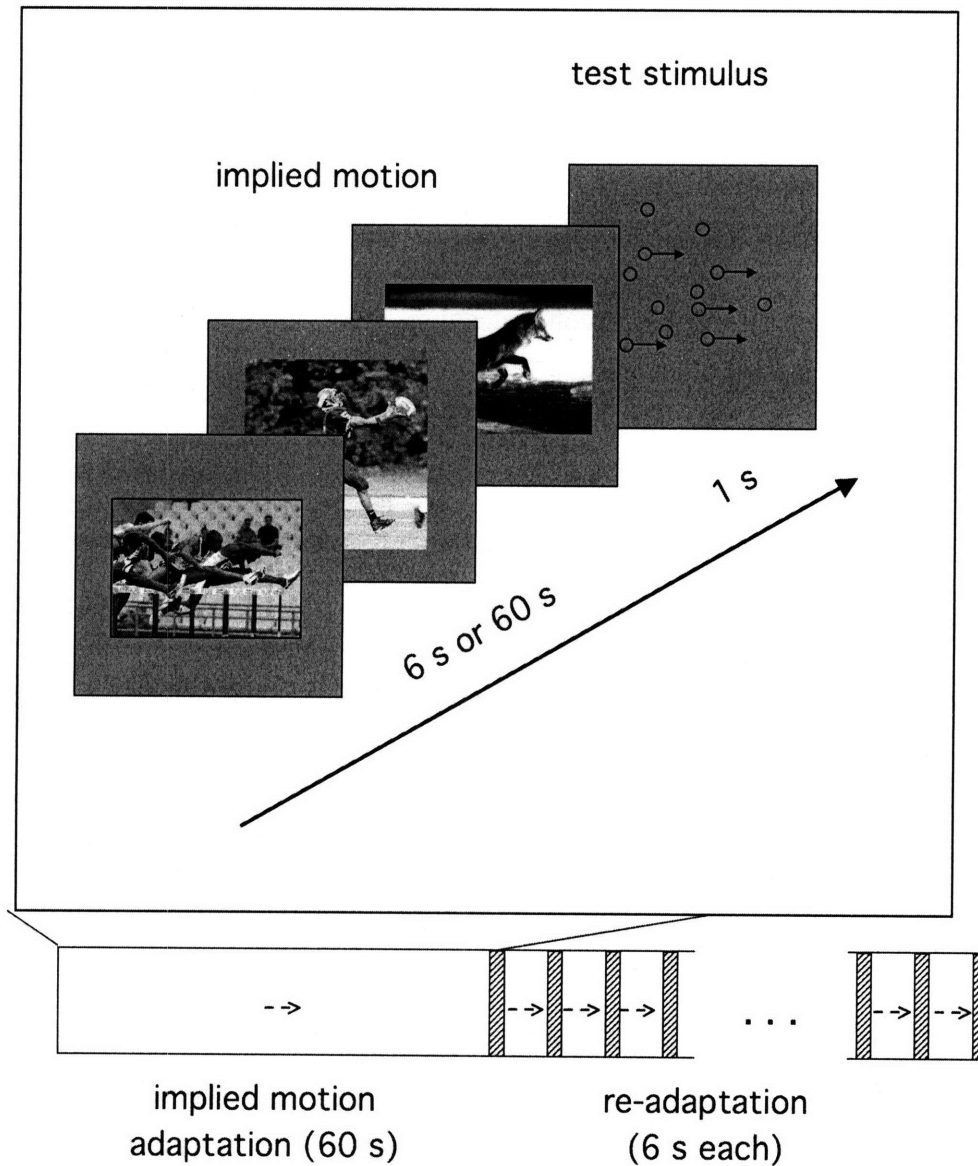


Figure 2. Adaptation consisted of viewing a succession of frozen motion photographs with implied motion. Following 60 s of adaptation (1st trial per block), or 6 s of top-up adaptation, subjects made judgments of the global direction of dynamic dot test stimuli. The direction of adaptation varied randomly across 6 blocks.

Procedure. Following the baseline task, subjects completed 6 blocks of trials in which they viewed implied motion photographs interleaved with tests of dynamic dot probes (Figure 2). The direction of adaptation, left or right, was constant within a block of trials, with 30 trials per block. Each of the 6 test stimuli was presented an equal number of times per block in random order. A sequence of pictures was generated by

randomly sampling from the 103 photographs without repeat until all photographs were used, such that any picture was equally likely to follow every other picture. The first trial in each block contained a 60-s adaptation period, and each of the subsequent 29 trials contained 6-s of “top-up” adaptation. Pictures were shown every 545 ms, so that 110 photographs were presented during the initial 60-s adaptation trial of each block, and 11 photographs during each of the 6-s “top-up” adaptation trials.

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. A brief recognition memory test was given after the 6 adaptation blocks, consisting of 20 photographs viewed during the experiment and 20 similar lures that were not seen.

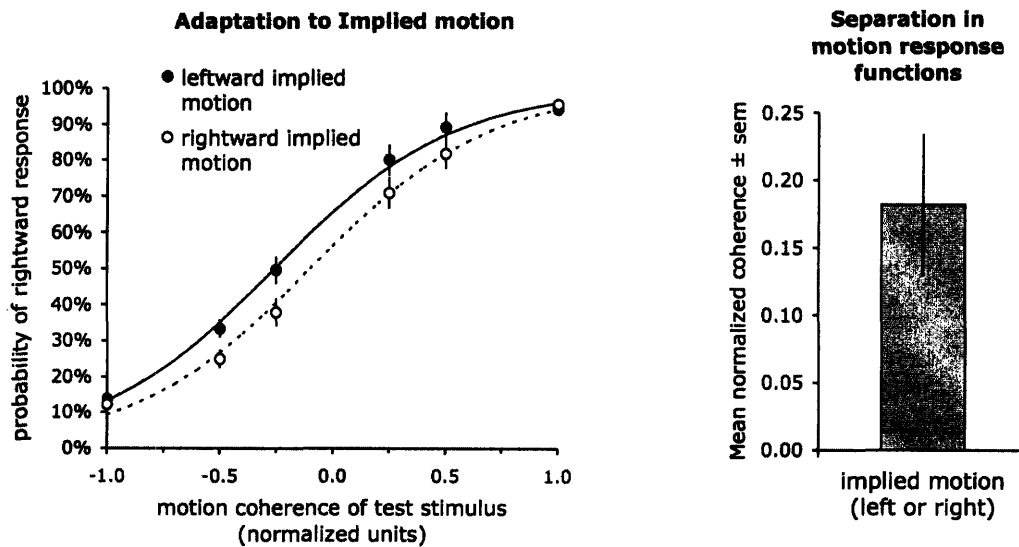


Figure 3. Adaptation from viewing photographs depicting motion. The population motion response function (left) shows that viewing leftward implied motion increased the likelihood of responding “rightward” to the test stimulus, and *vice versa*. The x-axis is the normalized motion coherence with positive numbers arbitrarily assigned to rightward motion. Data points represent the mean likelihood of responding rightward. Error bars represent ± 1 standard error of the within subjects difference at each coherence value (viewing rightward implied motion versus viewing leftward implied motion). Curve fits are logistic regressions. Bar plot (right) shows the average separation between the motion response functions across individual subjects.

Results and Discussion

All subjects performed above chance at the old/new recognition memory test given after the adaptation phase.

Viewing implied motion led to a significant motion aftereffect. After viewing implied motion to the right or left, subjects were more likely to see the dynamic dot test stimulus moving in the opposite direction. The population means, plotted in units of dot coherence normalized to each subject's motion sensitivity, show that the direction of the implied motion in the photographs shifted the motion response function in the direction predicted by a motion aftereffect (Figure 3). This can be seen by comparing the point of perceived null motion in each of the paired adapting conditions, that is the amount of coherence in the dot displays for which subjects were equally likely to respond left or right.

The point of perceived null motion point differed by $0.18 \pm .05$ units of normalized motion coherence ($t(18) = 2.35$; $P = 0.003$, 2-tailed paired t-test). In terms of the actual (un-normalized) test coherence, the separation between the null points was $6.1 \pm 1.9\%$ ($t(18) = 3.32$, $P = .004$). These results were also confirmed by a two-tailed paired sign test ($P = 0.019$), indicating that the median shift in functions was in the direction predicted by a motion aftereffect. 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 opposite adapting directions.

Experiment 2: Does adaptation to implied motion, like adaptation to real motion, decline with a brief delay between and test?

The second experiment was similar to the first, except that on 50% of trials, selected at random, there was a 3-second delay between the offset of the last picture viewed and the onset of the test stimulus. This delay was introduced to test whether a motion aftereffect from implied motion, like motion aftereffects from physical motion (Keck & Pentz, 1977), would decay during a brief period following adaptation.

Methods

Subjects and equipment. 22 new subjects were recruited for the second experiment, either from the MIT or the Stanford community. Other details were as for Experiment 1. One subject performed poorly on the baseline motion sensitivity task and one subject showed a lack of sensitivity to the coherence of the test stimulus during the experiment. Each was excluded from analysis.

Adapting stimuli. Adapting stimuli were identical to those in Experiment 1, except that photographs were also shown at a rate of 200 ms per picture instead of 545 ms per picture. There were thus 30 images shown per 6-s “top-up” adaptation trial.

Procedure. The procedure was identical to that of Experiment 1 except for two differences. First, there were 36 trials per block instead of 30. Second, on 50% of trials selected at random within each block, there was a 3-second delay between the last adapting photo and the onset of the test stimulus. During the delay the screen was gray and subjects were instructed to keep their eyes open.

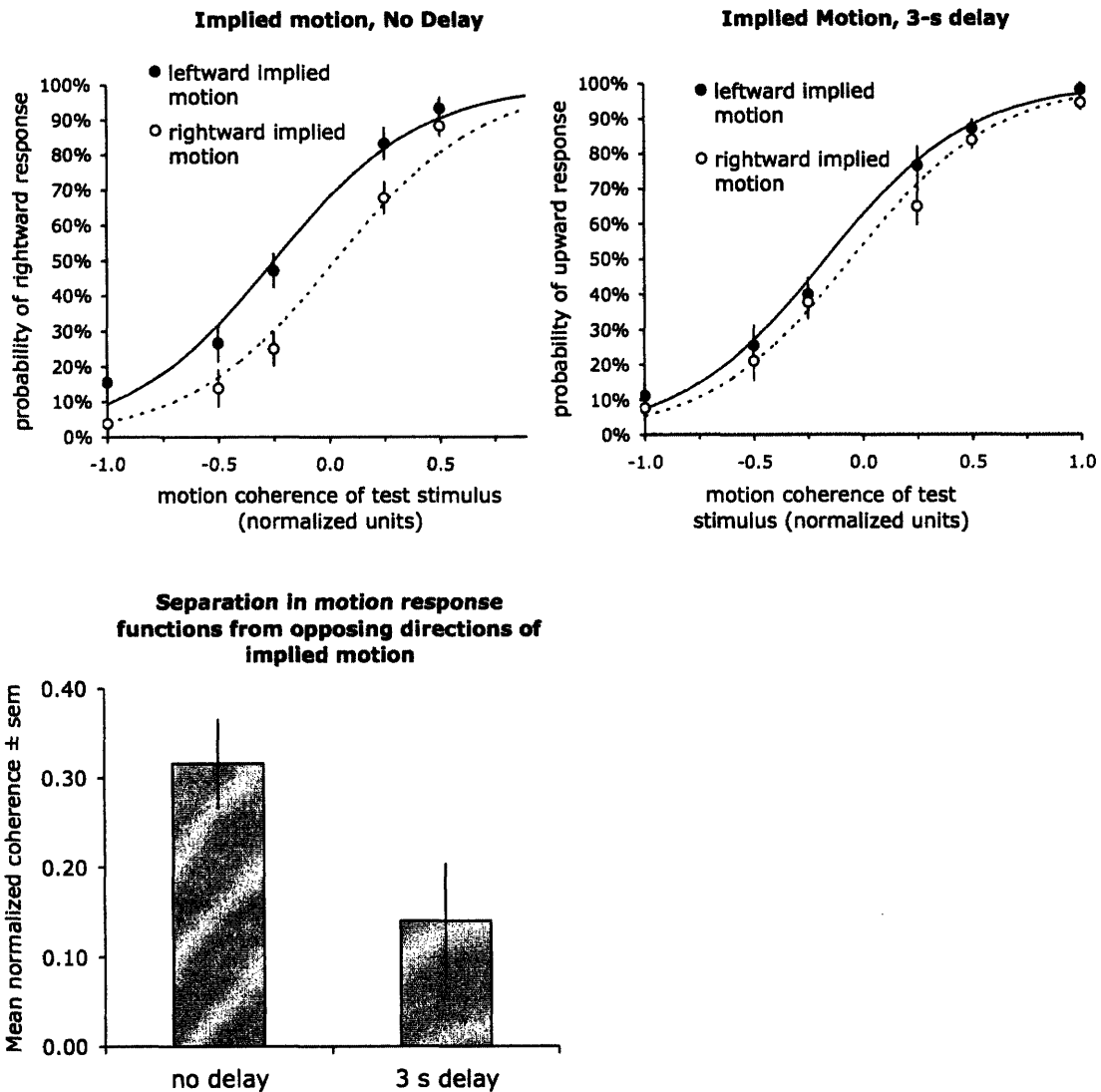


Figure 4. The effect of a 3-s delay between adapting to implied motion and viewing the test stimulus. A motion aftereffect was observed both on trials without a delay after adaptation (left) and with a delay (right). But the amount of adaptation was less than half when there was a delay.

Results and Discussion

The second experiment replicated the result of the first experiment: the null points of the leftward and rightward motion sensitivity curves in the no-delay condition were separated by $0.32 \pm .05$ units of normalized coherence ($t(19) = 6.27$; $P < 0.001$), or $11.8\% \pm 2.8\%$ in actual (un-normalized) test coherence ($t(19) = 4.14$; $P < 0.001$; Figure 4). With a 3-second delay between adaptation and test stimulus, there was also a marginal

effect of adaptation: the shift with the 3-s delay was $0.14 \pm .06$ units of normalized coherence ($t(19) = 2.16$; $P = 0.043$), or $3.8\% \pm 2.0\%$ in actual dot coherence ($t(19) = 1.86$; $P = 0.077$). A comparison of the two conditions shows that the effect was more than twice as large without the delay, both in terms of the standardized coherence (0.32 vs. 0.14, no delay vs. delay; $t(19) = 3.06$, $P = 0.007$, 2-tailed paired t-test between conditions), and in terms of the raw coherence (11.8% vs. 3.8%, $t(19) = 2.51$, $P = 0.021$).

The decay of adaptation from viewing photographs of implied motion is consistent with findings from adaptation to real visual motion (Keck & Pentz, 1977). Moreover in a pilot study we conducted using the same delay (3 s) and the same type of test probe, we found that the effect of adaptation to real visual motion (vertical sine wave gratings moving inward or outward horizontally) also declined by about the same amount: by 65% if the eyes were open during the delay (compared to 56% in the current experiment), and by 57% if the eyes were closed during the delays. These results show a similar time-course for adaptation to real motion and implied motion.

Experiment 3: Does adaptation to photographs with implied motion depend on the depiction of motion *per se*, or only on the orientation of the scene?

In the first two experiments, significant motion aftereffects were observed following viewing of photographs that depict motion, despite the fact that the static photographs contained no physical motion. It remains possible, however, that the depiction of motion *per se* is not critical to the effect; the fact that each photograph contained a scene in which a person, animal, or vehicle was oriented to the left or the right might have been sufficient to produce an aftereffect. To address this possibility, a study was conducted in which subjects viewed photographs of people, animals, or

vehicles either with implied motion or at rest. Motion aftereffects were measured with dynamic dot test probes, as in Experiments 1 and 2.

Methods

Subjects and equipment. 59 new subjects were recruited for this experiment from the Stanford community, and were randomly assigned either to the “motion” (30 subjects) or the “orientation” (29 subjects) condition.

Two subjects in the motion condition were excluded from analysis because they showed a lack of sensitivity to the coherence of the test stimulus during the experiment.

Adapting stimuli. 96 gray-scale photographs depicting motion of people, animals, or vehicles were used for the implied motion condition, and 96 images depicting people, animals or vehicles at rest were used for the orientation condition (Figure 5). To reduce possible differences between the stimuli in terms of aspect ratio or color, all photographs were made gray-scale and cropped and rescaled to 512 x 512 pixels. Most of the images in the motion condition were stimuli from experiments 1 and 2 (except for the change in aspect ratio and color). The stimuli for the orientation condition were found from Internet searches using Google Images™ and Flickr™.

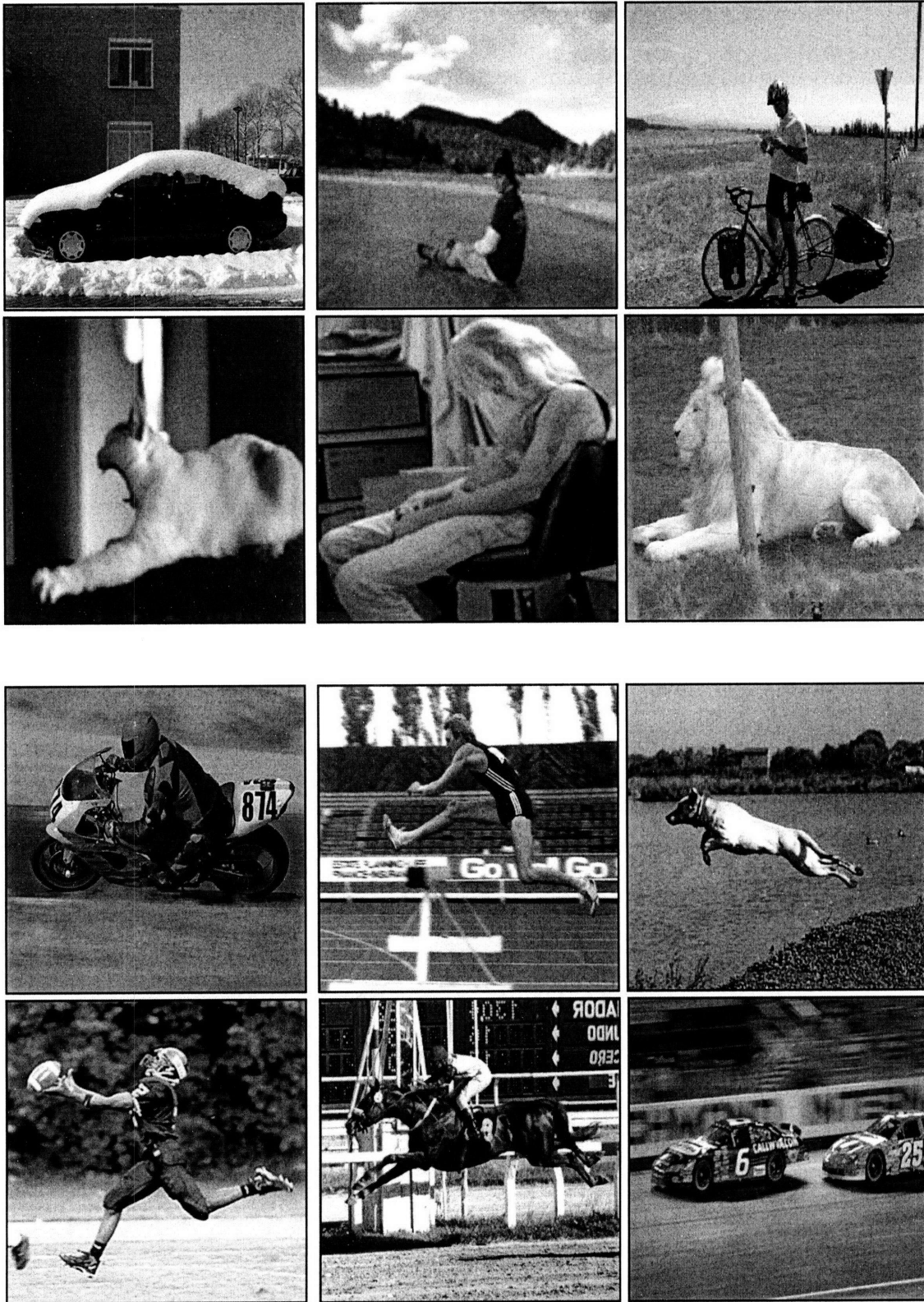


Figure 5. Example of stimuli with oriented scenes (top) and implied motion (bottom).

Norming of adapting stimuli. The stimuli were normed in two ways. First, a group of 8 subjects who did not participate in the adaptation experiment rated each of the 192 stimuli on a scale of 1 to 9 for “how much sense of motion” they felt from looking at each photograph. All 192 images were presented once each in random order without ratings (passive viewing), and then once each in random order to get 1-9 ratings. The ratings were widely different between image sets, as expected: 7.6 ± 1.0 (mean \pm SD) for the motion images, and 2.2 ± 0.7 for the orientation images. Further, none of the 96 motion images received a mean rating of less than 5.8 and no orientation images received a mean rating of more than 3.7. Secondly, to ensure that the orientation of the scene was unambiguous, 4 additional subjects made speeded, forced choice judgments on the orientation of each image (left or right). Accuracy was at ceiling (an average of 1 error per 96 images per set per subject), with mean reaction times of under 600 ms for all subjects for both stimulus types.

Procedure. As in Experiments 1 and 2, subjects first completed a baseline motion sensitivity task. The range of coherence values in this task was slightly different from the values in the baseline task of the first two experiments: there were 192 trials ranging from 1% to 100% coherence, instead of 180 trials ranging from 5% to 65%. Further, due to a programming error, all subjects were tested on the same range of motion coherence instead of a range that was scaled to their baseline performance. The values tested during adaptation were 0%, $\pm 1\%$, $\pm 2\%$, $\pm 4\%$, $\pm 7\%$, $\pm 11\%$, $\pm 17\%$, $\pm 26\%$, $\pm 39\%$, $\pm 59\%$, and $\pm 90\%$ (with positive meaning rightward and negative leftward).

There were two adaptation blocks of 48 trials each, one block with rightward pictures and one with leftward pictures. The order of the blocks was randomized and

there was no delay between viewing adapting photographs and test stimuli. All other details were identical to those in experiment 2.

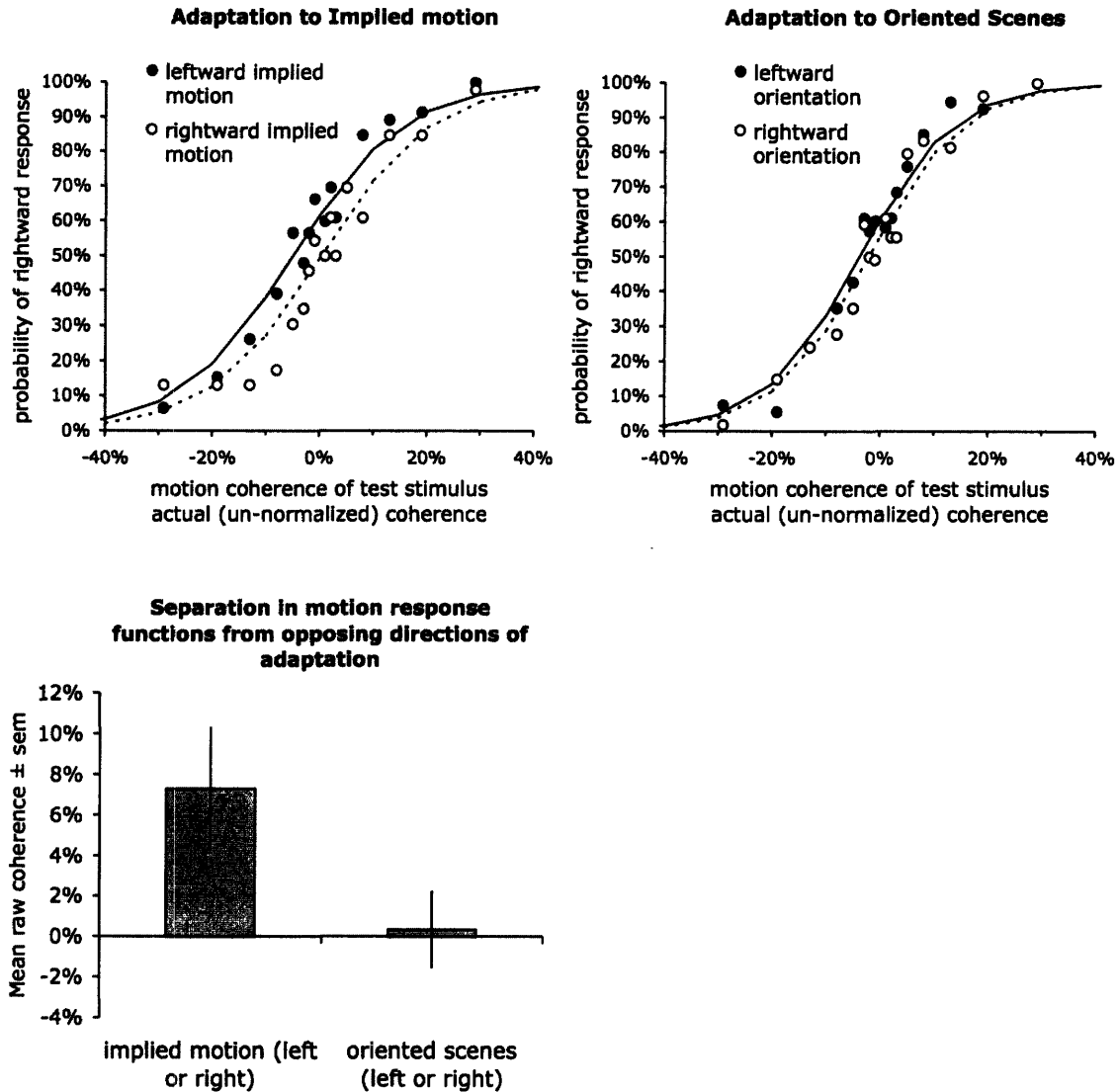


Figure 6. Adaptation to viewing photographs with implied motion or photographs of oriented scenes. Note that unlike experiments 1 and 2, the units of the graphs are in actual percentage coherence of the test stimuli, and not units of coherence normalized to each subjects' motion sensitivity. Adapting to implied motion, but not oriented scenes, caused a motion aftereffect, as demonstrated by the separation between motion responses functions.

Results and Discussion

As in the first two experiments, viewing photographs with leftward or rightward implied motion caused the subsequent test probe to be more likely to be seen as moving in the opposite direction (Figure 6). The separation between the null points of the adapt-

left and adapt-right conditions was $7.3\% \pm 3.0\%$ un-normalized coherence ($t(22) = 2.39$; $P = .045$, two-tailed t-test). This value is comparable to the effects found in the first two experiments in terms of the un-normalized coherence ($6.1 \pm 1.9\%$ for Experiment 1, and $11.8\% \pm 2.8\%$ for the no-delay condition in Experiment 2).

In contrast, the oriented scenes did not give rise to an aftereffect. The separation in the motion sensitivity functions was only $0.5\% \pm 1.9\%$ ($t(25) = 0.17$; $P = .78$), suggesting that the oriented scenes did not adapt (or presumably engage) direction-selective motion mechanisms. The difference between conditions was also confirmed by a between groups 2-tailed t-test, showing a marginally significant difference ($t(47) = 1.97$; $P = .054$).

Note that in this experiment, unlike the previous experiments, the test stimuli for all subjects had the same range of actual coherence values, not the same range normalized to their sensitivity. This presumably decreased the sensitivity of the measure, since for some subjects the shift predicted by adaptation would be small (if their sensitivity to motion coherence was high), whereas for other subjects the predicted shift would be larger (if their sensitivity to motion coherence was low). However the results can still be analyzed in terms of normalized coherence for comparison with the previous experiments by rescaling the coherence values for each subject according to baseline performance. Doing so confirms the above results, showing a separation of 0.14 ± 0.5 units of normalized activity in the motion condition ($t(22) = 3.17$, $P = 0.004$), comparable to the separation of 0.18 ± 0.5 found in the first experiment. The shift was 0.01 ± 0.03 in the orientation condition, significantly less than that found in the motion condition (between groups comparison, $t(47) = 2.40$; $P = .021$).

Together these results show that the interpretation of motion in the photographs, and not simply the presence of directional cues, contributes to the adaptation of directional motion mechanisms. These results are consistent with findings from the neuroimaging literature in which images of people in motion led to greater activation of motion sensitive brain areas than similar images of people at rest (Kourtzi & Kanwisher, 2000; Peuskens et al., 2005), as well as a bigger EEG signal in occipital areas (Lorteije et al., 2006).

Experiment 4: Does the implied motion aftereffect depend on eye movements?

In the first three experiments, motion aftereffects were observed from viewing static images that depict motion. It is possible that these aftereffects were due to people's eye movements in the direction of the implied motion, and not the interpretation of motion in the photographs *per se*. While this seems unlikely to us as it would require pursuit eye movement in the absence of a motion stimulus to track, to our knowledge eye movements while viewing such stimuli has not been reported and it nonetheless remains a possibility. We therefore considered whether motion aftereffects could be elicited by viewing photographs of implied motion in directions impossible to track with eye movements. In this experiment mirror-reversed pairs of implied motion photographs were shown simultaneously side-by-side to create implied motion either towards fixation ("inward") or away from fixation ("outward"). Motion aftereffects were assessed with the use of dynamic dot test probes containing either inward or outward coherent motion.

Methods

Subjects and equipment. 32 subjects were recruited for this experiment from the MIT community. Three were excluded from analysis for performing poorly on the baseline motion sensitivity task.

Adapting Stimuli. In the fourth experiment, the same 103 photographs used in the first two experiments were converted to gray scale and cropped 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; Figure 7). Subjects were instructed to fixate a small black and white circle (about 1 degree) at the border of the two images. These photographs were shown every 427 ms, so that 140 were seen during the initial 60-s trial and 14 during the 6-s top-up trials.

Test stimuli. The test stimuli were identical to those in Experiments 1 and 3, except that they consisted of 200 dots, 100 on each side of fixation (instead of 100 total); and they moved horizontally towards fixation or away from fixation (instead of left / right). The window of the test stimulus was the same size as that in the first two experiments and so the dot density was double. The same test stimulus was also used for inward and outward motion imagery experiments in Chapter 3.

Procedure. The procedure for Experiment 4 was nearly identical to that of Experiment 2. It differed in that there were no trials with delays between viewing the implied motion photographs and the dynamic dot test display, and in that there were 6 blocks of 24 trials each (3 blocks with inward implied motion and three with outward implied motion, in random order).

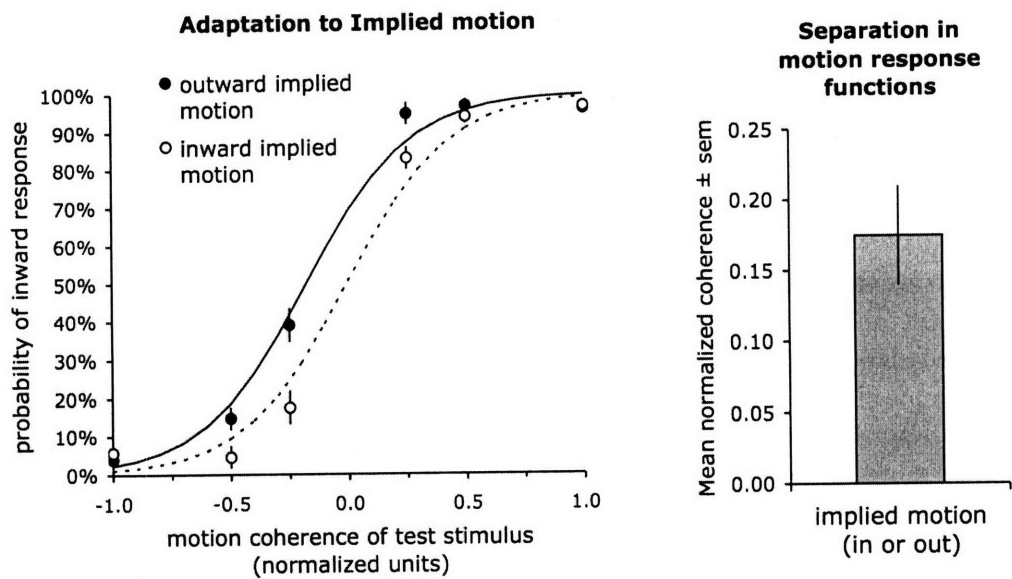
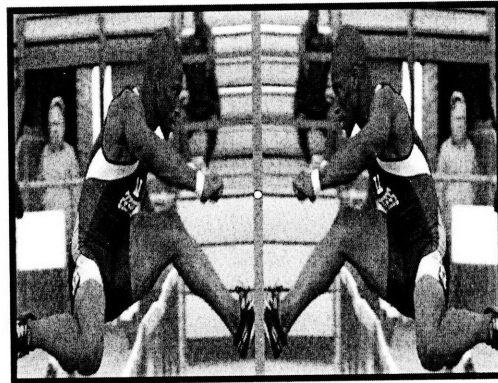
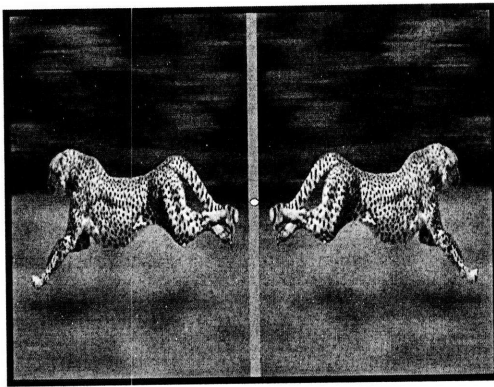


Figure 7. Adaptation to viewing photographs with inward or outward implied motion of photographs. Images were the same as those used for experiments 1 and 2, except that they were shown as gray-scale mirrored pairs, and cropped and re-scaled. A motion aftereffect was observed, as seen by the separation in the motion response curves (bottom left). Negative numbers on the x-axis (bottom left) indicate outward motion.

Results and Discussion

Subjects in the fourth 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 ($P < 0.001$) for inward vs. outward implied motion, or $5.5 \pm 1.0\%$ raw coherence ($P < 0.001$; Figure 7), comparable to the values found in the experiments with leftward and rightward implied motion. Had the previous results been

due to eye movements in the direction of implied motion (or in the opposite direction), and not to the recruitment of direction-selective motion mechanisms for representing photographs with implied motion, we would have expected there to be no effect in the current experiment.

As in the case of adaptation to inward or outward mental imagery of motion (Chapter 3), in the case of adaptation to inward or outward implied motion we cannot distinguish between the possibility that leftward and rightward motion neurons with receptive fields in the appropriate hemifield each adapt independently, and the possibility that motion circuits in which individual neurons tuned to inward or outward motion adapt. Further experiments assessing the retinotopic properties of the aftereffect to implied motion are needed to distinguish between these possibilities. In either case, this experiment provides evidence that eye movements are not the source of the aftereffects observed from implied motion.

Experiment 5: Can simultaneous viewing of real and implied motion cancel the effects of adaptation?

The first four experiments examined whether viewing implied motion and viewing real motion share common processing mechanisms by assessing transfer of adaptation from implied motion to real motion. Here we asked whether simultaneous viewing of real motion and implied motion interact: can real motion adaptation be countered by viewing simultaneous implied motion in the opposite direction? To address this question we showed subjects mirrored pairs of photographs that panned slowly behind a fixation aperture, such that the real motion and implied motion could each be either inward or outward.

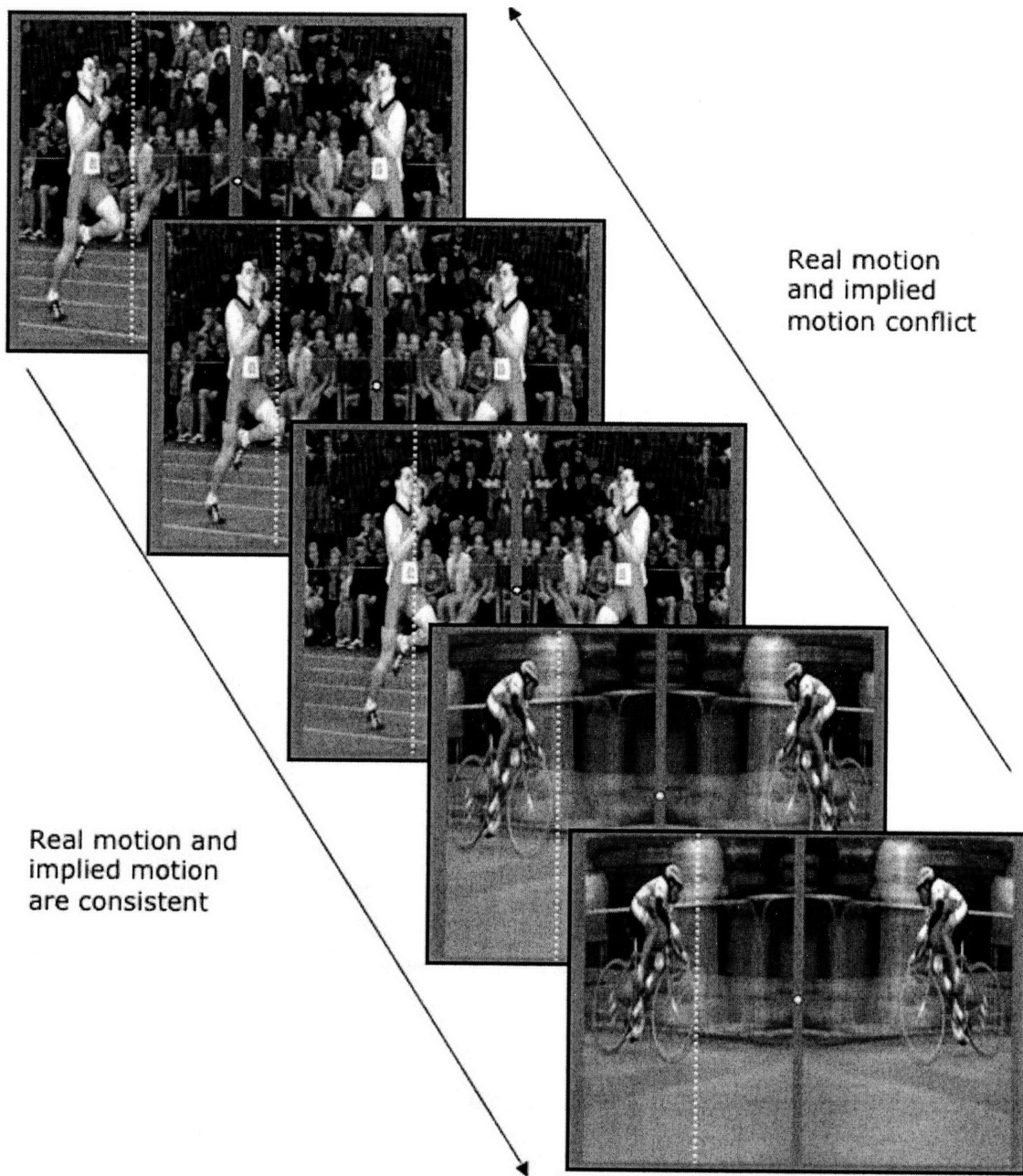


Figure 8. A schematic showing stimuli for simultaneous adaptation to real and implied motion. In this example, if the temporal sequence of images proceeds from upper left to lower right, then both real motion and implied motions are inward. If the same frames are shown in the reverse order, then the real motion is outward and the implied motion is inward, pitting the real motion and implied motion against each other. The actual amount of frame-to-frame motion is exaggerated for clarity in the figure. The dashed white outline on the left of each image is shown to compare the horizontal shift in the images; it was not shown during the experiment.

Methods

Subjects and equipment. 40 subjects were recruited for this experiment from the Stanford community, and were randomly assigned to the “real motion inward” or “real motion outward” condition. Three were excluded from analysis for performing poorly on the baseline motion sensitivity task and one for showing a lack of sensitivity to the coherence of the test stimulus during the experiment.

Adapting stimuli. The same 103 gray-scale photographs from Experiment 4 were used for adaptation, 512 x 768 pixels. However, the stimuli were shown through an aperture that was slightly narrower than the stimuli themselves (412 pixels wide instead of 512 pixels). This way the photographs could slide across the aperture without leaving a trailing blank space (Figure 8). During adaptation, each photograph was shown for 333 ms, during which it moved 1 pixel every 67 ms (approximately 0.5 degrees per second), either inward or outward. Thus the same photo pair was seen 5 times, offset by one pixel at a time, until the next photograph appeared, chosen at random. A total of 18 photographs were thus seen during each 6 s top-up adaptation trial, and 180 during each initial 60-s trial at the start of each block. The speed of one pixel per 67 ms was chosen because a pilot experiment on one experienced subject using scrambled images showed that this speed led to an aftereffect about equal in magnitude to that observed previously from our implied motion adaptation experiments.

Test stimuli. Test stimuli were identical to those used in Experiment 4, though the coherence values were slightly different (see below).

Procedure. The experiment began with a baseline motion discriminability task of 192 trials, with dot coherence ranging from 1% to 100%, as in experiment 3 (except that

the dot motion was inward or outward instead of right or left). Coherence of the test stimuli during adaptation was normalized to baseline performance: Stimuli were $\pm 100\%$, $\pm 66\%$, $\pm 44\%$, $\pm 29\%$, $\pm 19\%$, $\pm 13\%$, $\pm 8\%$, $\pm 5\%$, $\pm 3\%$, $\pm 2\%$, or $\pm 1\%$ of one unit of normalized coherence (see Chapter 2, General Methods). Following the baseline task, subjects then had 48 trials of un-adapted dot discrimination trials at the same values used for the subsequent adaptation. These trials provided an unadapted baseline condition to compare against the two subsequent adapted conditions using the same range of coherence in the test stimuli. There were then two experimental blocks of 48 trials each in which the implied motion was either inward or outward. The order of blocks was randomized.

Results and Discussion

Viewing real motion and implied motion simultaneously led to adaptation from each. For subjects viewing real inward motion (Figure 9, top left), there was an overall shift in responses such that they were more likely to see the test stimulus moving out than moving in. This can be seen in the rightward shift of the motion response functions during adaptation (black lines) compared to the preceding “no-adaptation” condition, when subjects viewed neither real motion nor implied motion. Specifically, the average null point during adaptation, that is the middle of the two black curves in Figure 9, shifted away from the no adapt function (red line) by 0.32 ± 0.10 units of normalized coherence across subjects ($t(17) = 3.17$, $P = 0.006$). This indicates that the small amount of motion in the test stimuli (about 0.5 degrees per second) was sufficient to cause a motion aftereffect in the opposite direction.

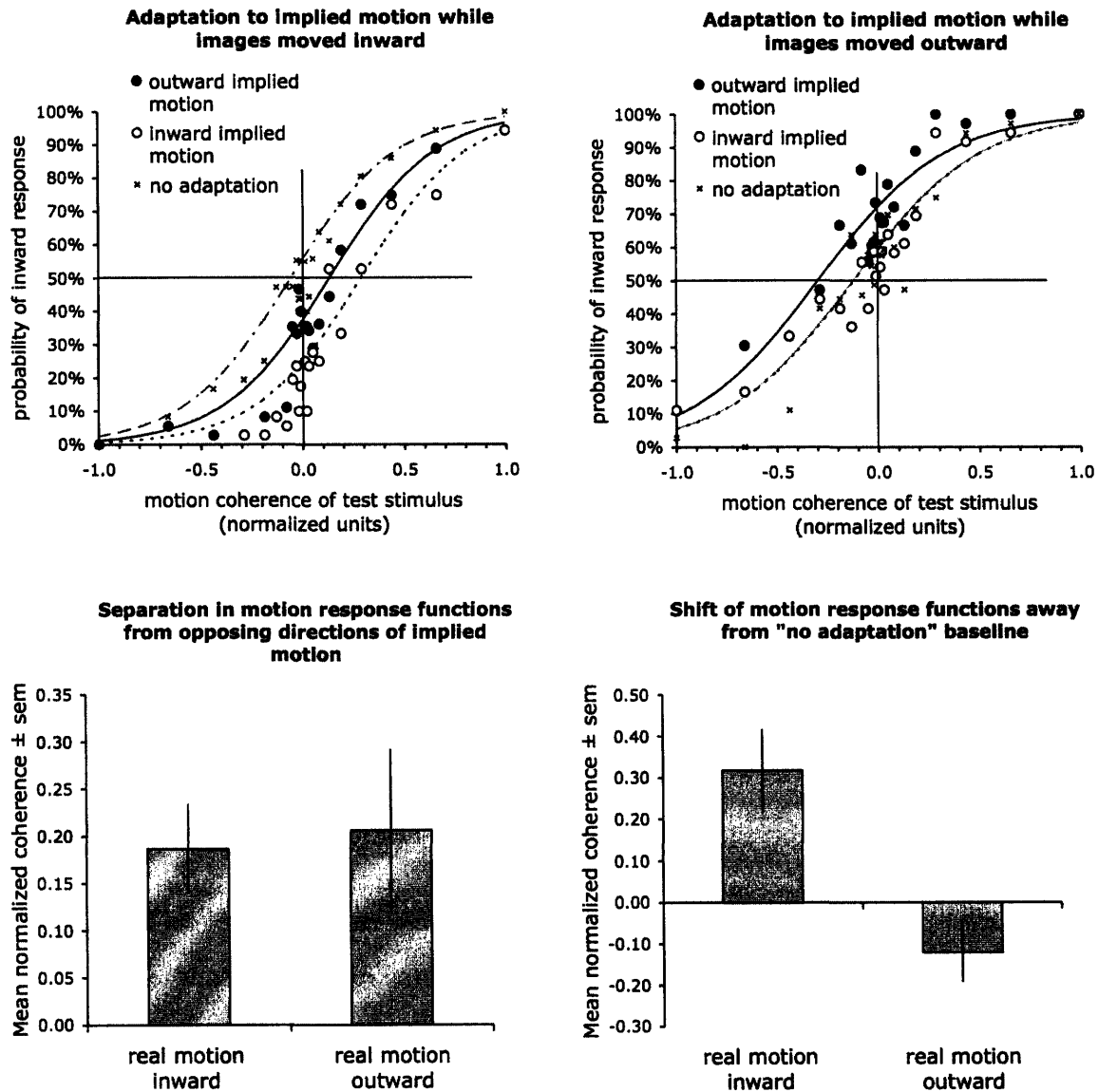


Figure 9. Simultaneous adaptation to inward or outward real motion and implied motion. Two effects can be seen. First, in both real motion conditions viewing outward implied motion compared to viewing inward implied motion increased the likelihood of seeing the dots move in. This can be seen by the separation between the black curves in each of the upper plots (black solid lines to the left of black dashed lines). The separation was about the same in each condition (bottom left bar chart). Second, the pairs of motion sensitivity functions were shifted away from the no-adapt baseline (red), in the direction predicted by an aftereffect to real motion: towards less probability of responding inward following inward real motion (upper left), and towards greater probability of responding inward following outward real motion (upper right). The bottom right panel represents the size of these shifts.

Critically, superimposed on this effect is a separation between the motion sensitivity functions from the two implied motion conditions. Just as in Experiment 4, viewing outward implied motion made subjects more likely to see the test stimulus

moving in, compared with viewing inward implied motion. The separation between the curves was 0.19 ± 0.5 units of normalized coherence ($t(17) = 3.97, P = 0.001$), or $8.7\% \pm 2.1\%$ in terms of actual, un-normalized coherence ($t(17) = 4.12, P = 0.001$). In this condition, the outward implied motion did not fully cancel the effects of inward real motion, as seen by the fact that the solid black line in Figure 9 is to the right of the red line.

When the direction of real motion was outward, the motion sensitivity functions were shifted in the opposite direction (Figure 9, top right), towards a greater likelihood of responding inward. This is indicated by a negative bar in Figure 9 (bottom right), as the leftward shift in the curves is toward outward coherence (arbitrarily assigned to negative values). In other words, the average of the two curves from the adaptation conditions (black) shifted away from the baseline, no-adapt condition (red), consistent with a motion aftereffect. This shift was not significant across subjects (-0.12 ± 0.7 units of normalized coherence; $t(17) = 1.64, P = 0.12$). But it was significantly different from the shift when real motion was inward ($+0.32$ vs. -0.12 , Figure 9, bottom right; $t(34) = 3.52, P = 0.001$, two-tailed between subjects t-test). Moreover, a significant aftereffect from the implied motion was also found in this condition, equal in size to that found during inward real motion: the separation between the null points was 0.21 ± 0.9 units of normalized coherence ($t(17) = 2.40, P = 0.028$), or $8.7\% \pm 3.6\%$ in terms of raw, un-normalized coherence ($t(17) = 2.42, P = 0.027$).

The results here show that implied motion and real motion tend to cancel each other in terms of motion adaptation when they occur simultaneously. This provides further evidence that some of the same direction-selective perceptual motion mechanisms

are involved in viewing real motion and in viewing implied motion. This does not mean, of course, that the stimuli nullify the percept of motion: one can see that the implied motion photographs are indeed moving and one can see that the photographs depict motion, even when the real motion and implied motion are in opposite directions. An interesting follow-up would be to investigate whether the perceived speeds, both of the moving photograph and of the action depicted in the photograph, are affected when the implied motion photographs move through an aperture.

Experiment 6: Implied and real motion adaptation assessed with a flickering grating test stimulus

Adaptation to inward/outward implied motion and real motion was also assessed using a different kind of test probe. Instead of dynamic dots, a vertical counterphase flickering grating (based on Culham et al., 2000) was briefly presented following several adaptation conditions. This type of stimulus is created by superimposing two low contrast identical sine wave gratings that move in opposite directions, in this case inward and outward. It is perceptually bistable such that during prolonged viewing the direction of perceived motion periodically fluctuates between the two directions (Figure 11). Prior adaptation to real motion has been shown to bias the perceived direction of motion in similar displays (Culham et al., 2000; Nishida & Sato, 1995; von Grunau, 1986).

Methods

Subjects and equipment. Eighty-seven subjects were randomly assigned to one of three adaptation conditions: inward implied motion, outward implied motion or no

adaptation. In addition, 18 subjects adapted to either real inward motion or real outward motion.

Adapting stimuli. The stimuli for implied motion adaptation were the same as those presented in the inward/outward implied motion experiment with dynamic dot test stimuli (Experiment 4). For real motion adaptation, subjects viewed a stimulus similar to the test stimulus except that only one high contrast grating was used (inward or outward) instead of two superimposed low contrast gratings. The test stimulus was identical on every trial. Thus instead of obtaining a complete psychometric function, we tested only the point that was physically neutral.

Procedure

Except for subjects in the no adaptation condition, the experiment consisted of 10 6-s adaptation trials, with a judgment on the direction of the test grating (inward or outward) made after each period of adaptation.

Results and Discussion

Adapting to inward implied motion resulted in a greater likelihood of seeing the test stimulus move outward ($80\% \pm 4\%$, mean \pm standard error of the mean) than adapting to outward implied motion ($58\% \pm 4\%$; $P = .002$, unpaired, 2 tailed t-test between subjects; Fig. 11). The responses in the no-adaptation baseline condition fell between the two adapting conditions ($72\% \pm 5\%$) as predicted, though it was only marginally different from either one ($P = .027$, $P = .094$; no adapt vs. outward and vs. inward implied motion, respectively, 1-tailed unpaired t-tests). The responses to the no-adapt condition indicate that the test stimulus was not perceptually balanced despite the

fact that it was physically balanced, with subjects showing a bias to see the neutral motion as outward. As expected, adaptation to real motion led to a reliable and robust effect:, with $97\% \pm 3\%$ outward responses following inward adaptation, compared to $1\% \pm 1\%$ outward responses following outward adaptation.

These results provide further support for the results obtained in experiments 1-5, extending the phenomenon to a different kind of test stimulus. The current experiment also shows, as expected, that adaptation to implied motion is not as strong as adaptation to real motion.

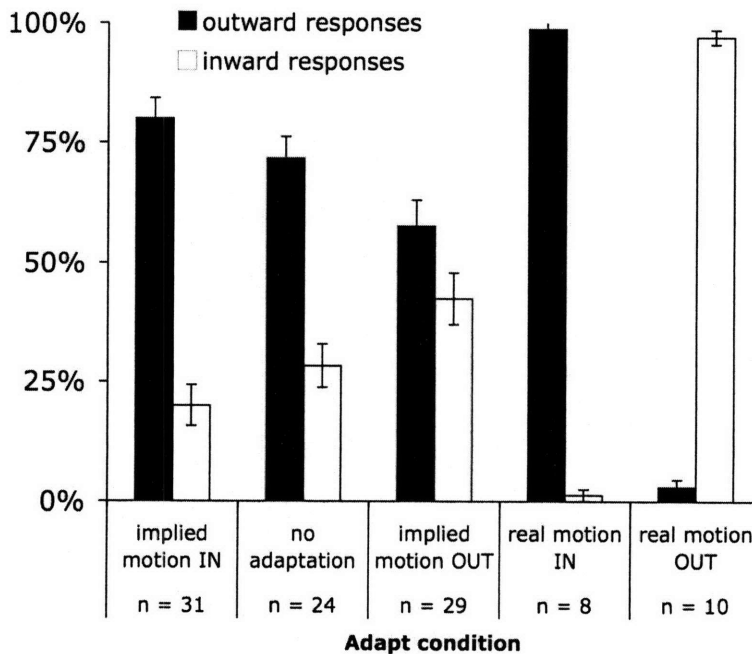
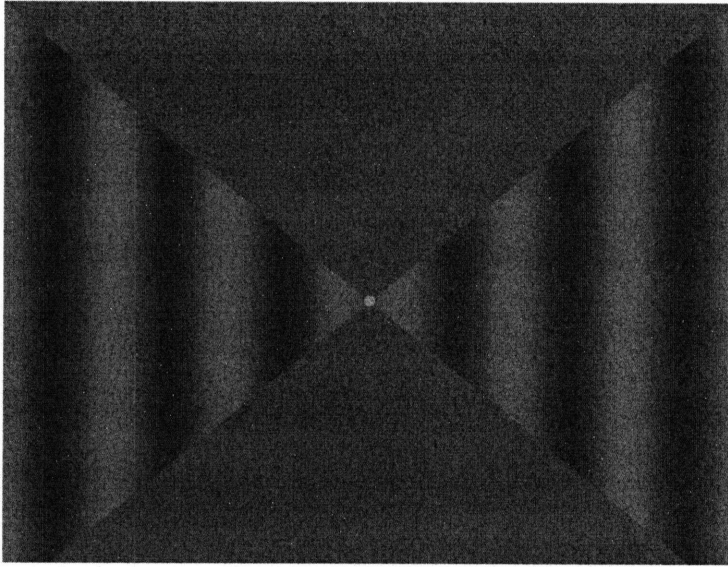


Figure 10. The percentage of “inward” and “outward” responses to the test pattern following adaptation to inward or outward implied motion, inward or outward real motion, or no adaptation. Error bars indicate 1 SEM by subject and the number of subjects is indicated below each group. Subjects who adapted to inward implied motion made significantly more outward responses than subjects who did not adapt ($P < .05$, 2-tailed unpaired t-test) or subjects who adapted to outward implied motion ($P < .01$, 2-tailed unpaired t-test), indicating the presence of a motion aftereffect and corroborating the results obtained with the dynamic dot test stimulus. Overall there was a bias to see the test stimulus moving outward. Adaptation to real motion produced a nearly complete bias such that adapting to inward real motion led to nearly 100% outward responses, and *vice versa*.

General Discussion

In each of the six experiments, viewing 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 of the direction depicted in the previous adapting photographs. The transfer of adaptation from viewing implied motion to viewing real motion is evidence that the photographic stimuli, though containing no motion, recruit direction-selective motion-responsive neurons. Below we consider a number of interpretations and potential confounds.

Stimulus confounds

Our results cannot be explained by low-level motion energy biases in the image sequences, or by apparent motion between successive frames. While any frame-to-frame pair of images will contain some motion energy, the sequence of images in our experiments was generated randomly on each trial. If a given pair of images happened to have correlated features such that their presentation in one order gave rise to a directional motion signal, then the reverse sequence would give rise to the reverse motion signal. There was an equal likelihood that any particular pair of images would be seen in one order or the opposite order, thus ruling out spurious biases in motion energy or apparent motion.

Eye movements

Further, it is unlikely that our results can be explained by systematic eye movements. While eye movements can give rise to motion aftereffects in the absence of retinal motion (Chaudhuri, 1990, 1991; Freeman et al., 2003), our use of inward/outward

stimuli in the fourth, fifth, and sixth experiments precludes optokinetic nystagmus, and argues against explanations based on directional biases in eye movements during adaptation.

Imagery

It is also unlikely that our results can be explained by aftereffects due to active visual imagery of motion. This explanation remains logically possible, especially given the results obtained from motion imagery in the previous chapter as well as prior evidence that mental imagery of motion can activate motion-sensitive brain areas (Goebel *et al.*, 1998; Grossman & Blake, 2001). Nonetheless, in practice it seems unlikely to us. Subjects were not instructed to imagine motion and were given little time to do so. Mental imagery typically requires from a few hundred milliseconds to several seconds (Cooper & Shepard, 1973; Kosslyn, 1976; Shepard & Metzler, 1971) and our stimulus presentation rates were relatively fast (2-5 Hz). One might reasonably ask, nonetheless, whether viewing the photographs elicited thoughts or recall of motion via automatic associative processes. We cannot rule this out, nor do we wish to. In fact this would seem to be a plausible mechanism to explain how motion implied in a photograph could elicit responses from perceptual motion mechanisms. But such a rapid and automatic response may be quite different from the slow, volitional process of attempting to vividly imagine something in the absence of sensory input (Barsalou, 1999), perhaps analogous to the difference between the automaticity of reading a printed word (Stroop, 1935) and the choice one may have in deciding whether to solve a printed arithmetic problem.

Regardless of whether the motion aftereffect we observed is due to imagery or the implication of motion *per se*, these results demonstrate that direction-selective adaptation

can occur in the absence of physical motion and in the absence of instructions to imagine motion.

Are the two processes – mental imagery of motion and inferring motion from photographs – related at all? Each type of representation might be thought of as “top-down”, since with imagery there is no visual input and with implied motion there is no motion input and the motion responses presumably rely on high-level knowledge of objects and scenes. This does not mean that the two processes are related. In each set of studies we have observed that adaptation transferred from the top-down process to real motion perception, but it remains possible that different motion mechanisms are adapted by each type of top-down process, and very likely the sources of the top-down effects are different. Together, though, they suggest that the feed-forward mechanisms involved in processing real motion may be able to interact with a variety of top down processes.

Attention

Another important consideration is whether our results could be explained by attentional factors and not by the inference of motion. One role of attention may be to amplify signals, as evidenced by the psychophysical amplification of motion aftereffects to attended motion (Alais & Blake, 1999) and by the increased neural signal to attended motion stimuli (Beauchamp *et al.*, 1997; Corbetta *et al.*, 1991; O'Craven *et al.*, 1997; Saenz *et al.*, 2002). It is unlikely that attention could have played such a role in the current experiments; the individual stimuli did not contain any motion at all and spurious motion arising from frame to frame transitions contained no net directional motion, as discussed above. Hence it is not clear what signal would be present for attention to amplify.

Another type of attentional mechanism, and one that has been explicitly linked to motion aftereffects, is attentional tracking (Culham et al., 2000). However, such findings could not apply directly here, as again, there were no moving stimuli to track. A further alternative is that the photographic stimuli led subjects to attend to spatial locations in a direction-specific way, for example attending to the left side of pictures with leftward motion. We cannot rule this out definitively, but to account for our results such an explanation would have to apply to inward / outward motion as well as left / right motion, and only to photographs with implied motion, not to photographs of oriented scenes. Moreover, based on the fifth experiment, it would also require that attention be oriented to a location opposite the direction of real motion in those cases when real motion and implied motion are in opposite directions.

Finally, we note that it is important to distinguish between attention as a confounding explanation and attention as a requirement. For example, it might reasonably be the case that subjects must attend to the photographs in order to recognize them and that the motion signals depends on recognition. This possibility is consistent with the finding using EEG that motion-related signals from implied motion photographs are delayed relative to bottom-up motion signals, perhaps because the signals arise from feedback from high level cortical areas processing shape and scene information (Lorteije et al., 2006).

Biases

It also appears unlikely that the results obtained in these experiments are due to a strategic or cognitive bias instead of a shift in the perception of the test stimuli. First, had the pattern of responses in the first experiment been driven by a non-perceptual bias, we

would not have predicted the decline in the motion aftereffect with a brief delay, as observed in the second experiment. Moreover, a post-experiment debriefing following the fourth experiment revealed that prior knowledge of the motion aftereffect did not explain the results: 20 subjects had never heard of the motion aftereffect (compared to 4 who had and 5 who did not respond), and when forced to guess “whether prolonged viewing of upward motion would cause a subsequent static image to appear to move up or down”, 14 responded up and 10 responded down. The size of the observed motion aftereffect did not differ significantly based on response (had vs. had not heard of motion aftereffect, $.181 \pm .03$ vs. $.28 \pm .15$ units of normalized coherence, $P = .552$, 2-tailed unpaired t-test; predict up vs. predict down: $.17 \pm .05$ vs. $.23 \pm .07$ units of normalized coherence, $P = .438$). Moreover in the fifth experiment, subjects were randomly assigned to either the oriented scenes or the implied motion conditions, each of which contained pictures with a clear directionality. Had results been due to a cognitive bias we would have expected both conditions to elicit similar effects, contrary to what we found.

Form and motion

In summary, we find that direction-selective motion adaptation can be obtained from viewing static images with implied motion. The direction-selective adaptation we report had an effect on subjects’ perception of a real visual 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 selective for the perception of actual motion in a particular direction are also activated while viewing implied motion in that same direction.

Our results can be seen in the context of 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 in the form of speedlines (Burr & Ross, 2002; Geisler, 1999) or Glass patterns (Krekelberg *et al.*, 2003; Krekelberg *et al.*, 2005; Ross *et al.*, 2000). Due to temporal integration moving targets tend to leave behind motion streaks, and these findings may reflect the fact that the visual system has exploited this regularity to infer motion trajectories from orientation. We note, however, that the inference of motion from simple orientation cues and from high-level object and scene-related cues are likely computed 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 the delayed response to implied motion photographs measured with EEG (Lorteije *et al.*, 2006), as well as the sensitivity to the depiction of action in neurons in anterior regions of the temporal lobe in monkeys (Jellema & Perrett, 2003, 2006).

Function of motion signals from implied motion

The results presented here demonstrate that viewing photographs from which one infers motion engages and adapts direction-selective motion neurons. An important question is what the role of such activity is.

At one extreme we might suppose that there is no role – that such activity is epiphenomenal and does not contribute to behavior or perception. This seems unlikely to us. First, the experiments here document a measurable effect on subsequent perceptual judgments. It seems reasonable to expect that signals which give rise to adaptation also contribute to normal processing of stimuli (though this must still be demonstrated experimentally in this case). Indeed a strong coupling between the activity of motion selective neurons and perception has been demonstrated in a variety of studies with different methodologies. For example microstimulation of cortical columns in MT in macaque can bias directional judgments of motion stimuli (Salzman *et al.*, 1990) and transcranial stimulation of the homologous region in human can modulate a perceptual motion aftereffect (Antal *et al.*, 2004). Perhaps most relevant to the current studies, TMS of human motion areas was shown to interfere with representational momentum (Senior *et al.*, 2002), the process by which a briefly viewed still action photograph is confused with another photograph of the same action taken slightly later, presumably due to the automatic extrapolation of the action sequence (Freyd, 1983).

At the other extreme, one might suppose that the directional motion signals elicited by implied motion are what allow the visual system to determine the content of the photographs. This too, seems unlikely. The cues in the photographs that signal motion presumably require significant processing of the objects and scenes, and it seems more likely that object and scene-related processing signals feed back to motion processing systems. This is the interpretation of Lorteije and colleagues who found that the motion-related signals from action photographs (Lorteije *et al.*, 2006) and the

direction-specific adaptation from such photographs (Lorteije et al., 2007) were delayed relative to bottom-up motion processing (peaking at 250 - 300 ms after stimulus onset).

A more reasonable view might be that the involvement of motion signals in viewing still-motion photographs reflects associative learning mechanisms. In the series of experiments reported here, we presented subjects with two kinds of stimuli in sequential phases. First, we presented the high level object and scene cues to motion (i.e., the photographs with implied motion). We then presented a more-or-less “pure motion” stimulus (i.e., the random dot test stimuli). We presented them sequentially in order to demonstrate that static, high-level semantic cues influence low-level processing of motion. In normal experience, of course, the object and scene cues to motion are directly coupled to the motion itself and the relationship between them can be learned from experience. Effects of associative learning on perception have been shown in a recent study (Qi *et al.*, 2006) in which an arbitrary cue was paired with an unambiguous direction of motion, such that the cue later biased the perception of an ambiguous motion stimulus. Similarly, at the single cell level, the arbitrary pairing of shapes in macaque monkey can influence the response properties of shape-selective cells in inferotemporal cortex (Miyashita, 1993), and the pairing of a static cue with a moving stimulus led to selective responses of some MT neurons (Schlack & Albright, 2006). Moreover when a moving stimulus repeatedly follows a predictable trajectory, direction selective neurons in macaque parietal cortex signal the direction of occluded motion (Assad & Maunsell, 1995). Together, these studies suggest that newly learned cues can influence the response properties of cells in extrastriate visual areas and that this in turn can influence how stimuli are perceived. Associative learning between perceptual features may be a

mechanism for implementing the kind of “unconscious inference” taken to be a hallmark of perceptual systems by Helmholtz (Barlow, 2001; Helmholtz, 1924).

Inferring the global direction of movement of even simple objects, much less biological agents with multiple moving parts, is a non-trivial problem. We presume that in normal experience the visual system uses all the cues it can in order to arrive at an interpretation as rapidly and accurately as possible, a goal which is surely of fundamental importance to interacting successfully in the environment. High level semantic cues such as those studied here, as well as mid-level cues like grouping and occlusion (McDermott *et al.*, 2001), and low-level cues like oriented edges (Geisler, 1999), together with the signals from the motion itself may provide convergent information allowing the visual system to make the best interpretations and predictions it can.

Chapter 5: Related Work and Conclusions

Abstract

An overview of two current works in progress that build on the results of the previous chapters is presented. First, to examine whether results like the aftereffect from implied motion can be found in other domains, a study using analogous methods is described in the domain of perceived eye gaze. Second, a study asks whether single cells in macaque area MT are sensitive to the direction of implied motion. Strong evidence is not found for these direction-selective responses. Finally, all the studies are briefly summarized.

Does viewing a face with implied gaze lead to gaze adaptation?

*In collaboration with Nathan Witthoft and Jennifer Yoon, Stanford University,
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The experiments in this thesis have all been within the domain of visual motion processing. The primary questions asked have been whether representations of motion that arise from mental imagery or from a perceptual inference share processing mechanisms with bottom-up motion-processing. The broader context of these questions can apply to many perceptual domains, and it is hoped that the results here do not represent a unique case restricted to visual motion. To make this point more concrete, the results of a preliminary study on “implied gaze” are discussed.

Correctly inferring the perception of gaze direction is important in humans and many social animals. Single cells in temporal cortex that are selective for the direction of gaze (irrespective of head angle) have been observed in macaque monkeys (Perrett *et al.*,

1992), and circuits representing gaze angle independent of the face identity have been reported in human STS (Hoffman & Haxby, 2000). Recently it has been shown that the perception of gaze direction, like other properties of faces (e.g., Webster & MacLin, 1999), can be adapted using psychophysical paradigms (Calder *et al.*, 2006; Jenkins *et al.*, 2006; Schweinberger *et al.*, 2007; Seyama & Nagayama, 2006). In these experiments prolonged viewing of faces with eye gaze to one side made it more likely that subsequent gazes to the same side would be seen as straight ahead.

The cues that signal gaze direction are thought to involve low-level visual properties of the eyes, such that contrast reversing the eyes severely impairs the correct interpretation of gaze direction (Sinha, 2000). However, the direction of eye gaze can also be implied in an image even if the typical cues to gaze angle are absent, for example if the head angle is to the side and the eyes are covered by dark sunglasses (Figure 1). Note that the previous reports (Jenkins *et al.*, 2006) have suggest that gaze adaptation is due to the direction of eye gaze and not the head gaze (though this will have to be tested explicitly in our paradigm with the same stimulus set). Hence if a photograph like that in Figure 1 causes gaze adaptation, we presume it is from the inferred gaze in the image and not from the head angle alone.

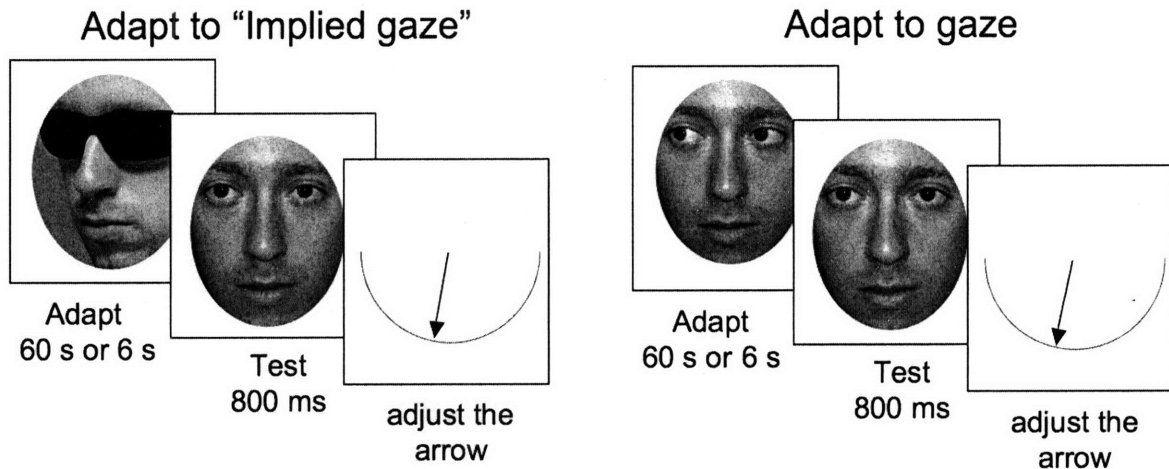


Figure 1. In one experiment, subjects adapted to “implied gaze”, either to the left (17 Ss) or to the right (16 Ss). Adaptation consisted of an initial trial with 60 s of viewing the adapt photo shown above (top left) or its mirror reversal, followed by 800 ms of a test stimulus. The subject then adjusted an arrow using the mouse to indicate the perceived direction of gaze in the test image. Nine angles of gaze were tested (± 20 , ± 15 , ± 10 , ± 5 , 0 ; negative means left) both before adaptation for a baseline and again during adaptation. In “top-up” trials the adaptation viewing time was 6 s and in the same direction as the initial trial. Subjects were instructed to look at the screen but not to fixate during adaptation. The identical procedure was used with adaptation in which the eyes could be seen, either looking to the left (XX Ss) or looking to the right (XX Ss).

In fact we found evidence of significant adaptation to such “implied gaze”. This adaptation effect was smaller than, though qualitatively similar to, that found from actual gaze adaptation (Figure 2). When subjects adapted to a photograph of rightward implied gaze, the perceived direction of gazes that were 5° or 10° to the right were judged as more directly forward, and likewise for leftward implied gaze. As with adaptation to eye gaze that is actually visible, the adaptation effects were specific to test faces with gaze in the same direction as adaptation, with little to no effect on the perception of gaze in the opposite direction (e.g., leftward gaze following rightward adaptation). These results suggest that the mechanisms used to represent the direction of gaze in photographs can also be engaged in a direction-specific manner when viewing photographs in which the gaze is implied but the eyes are not visible.

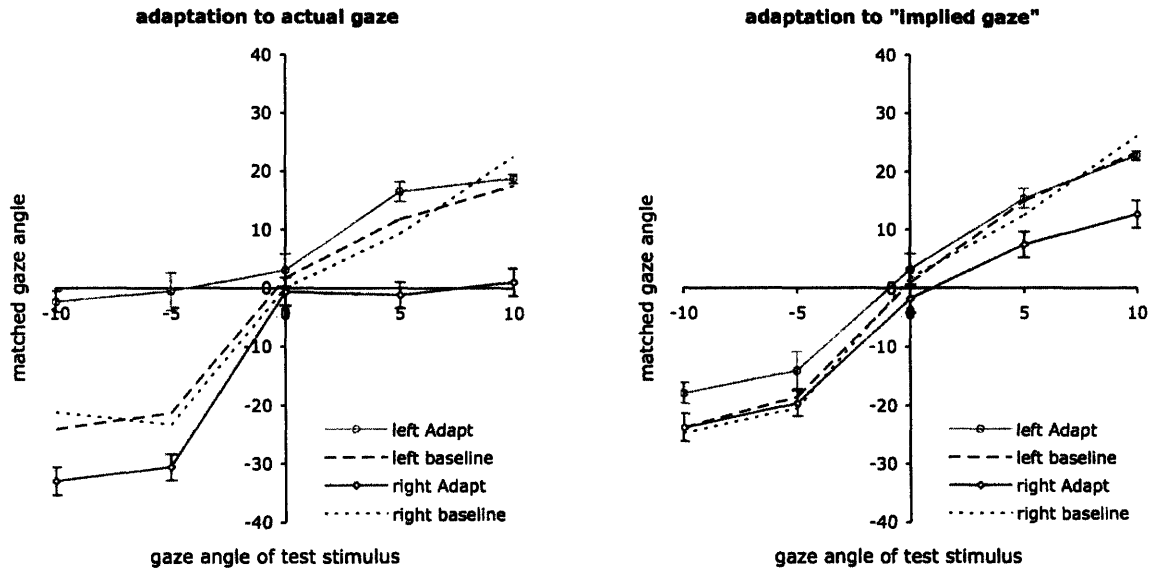


Figure 2. Adaptation from actual gaze and “implied gaze”. When subjects adapted to leftward actual gaze (green line), test faces that were 5° or 10° to the left (negative numbers on x-axis) were judged to be straight ahead, as were test faces 5° or 10° to the right following adaptation to rightward gaze (red line). The effect on the same side of adaptation was much smaller. A similar effect is seen with implied gaze, though smaller than that for actual gaze. Error bars indicate 1 standard error of the within-subjects’ difference between adapt and baseline at each angle of test.

We do not suppose that the mechanism of “implied gaze” adaptation is the same as that for implied motion adaptation. The pictorial cues to the direction of gaze are probably unrelated to the cues implying motion, and the neural circuits analyzing eye gaze are probably unrelated to the circuits analyzing visual motion (for the most part). The mechanisms may be analogous though, and it may be common in high level perceptual processing to build upon mechanisms that are used for processing more direct, bottom-up cues to the same stimulus. As discussed in Chapter 4, Schlack and Albright (2007) observed that single cells in macaque MT can become tuned to the direction of static arrows if the arrows are first associated with visual motion. They take this as evidence that associative learning, like that observed by Miyashita et al (1993) in IT cortex, can take place in MT, a presumably low-level visual processing area. Such learning mechanisms, whether in the domain of motion (Schlack & Albright, 2007),

shape processing (Miyashita, 1993), or eye gaze, may be an important way to increase the number of cues an organism can use to interpret a scene.

Do macaque MT neurons show selectivity to the direction of implied motion?

In collaboration with Jing Liu and William T. Newsome, Stanford University, Department of Neurobiology

The experiments in Chapter 4 demonstrated that viewing a series of implied motion photographs could bias judgments on the perception of subsequent real motion test probes. These studies provide evidence that direction-selective motion mechanisms are engaged and adapted by viewing photographs that depict motion, but the locus of these direction-selective mechanisms has not been determined.

As discussed in Chapter 4, there are several neuroimaging studies which report that cortical area hMT+, the presumptive human homologue of macaque MT, responds more to images with implied motion than similar images without implied motion (Kourtzi & Kanwisher, 2000; Lorteije *et al.*, 2006; Peuskens *et al.*, 2005; Senior *et al.*, 2000). However, these studies do not demonstrate directional signals in response to the images. A very recent human EEG study does demonstrate that neural adaptation transfers from real motion to viewing implied motion (Lorteije *et al.*, 2007), but the spatial resolution of EEG is not sufficient to identify the source of the directional signals. Hence the neural basis of the direction-selective responses to photographs with implied motion remains unknown. One clue from the monkey literature suggest that area MT might be a good candidate for these signals: A recent study in which monkeys were trained to associate a static arrow cue with a particular direction of motion showed that a number of MT neurons became responsive to static arrows in a direction-specific way only after the

training (Schlack & Albright, 2007). Furthermore in most of the cells responsive to the arrows, the tuning function was matched to the tuning for motion.

In a preliminary study, we asked whether MT neurons in macaque monkeys respond in a direction-selective manner to natural, implied motion images of monkeys (Figure 3). We tested 3 animals (103 neurons), each in one hemisphere. Tentative evidence of directional implied motion signals was found in the first animal tested, but not in two subsequent animals.

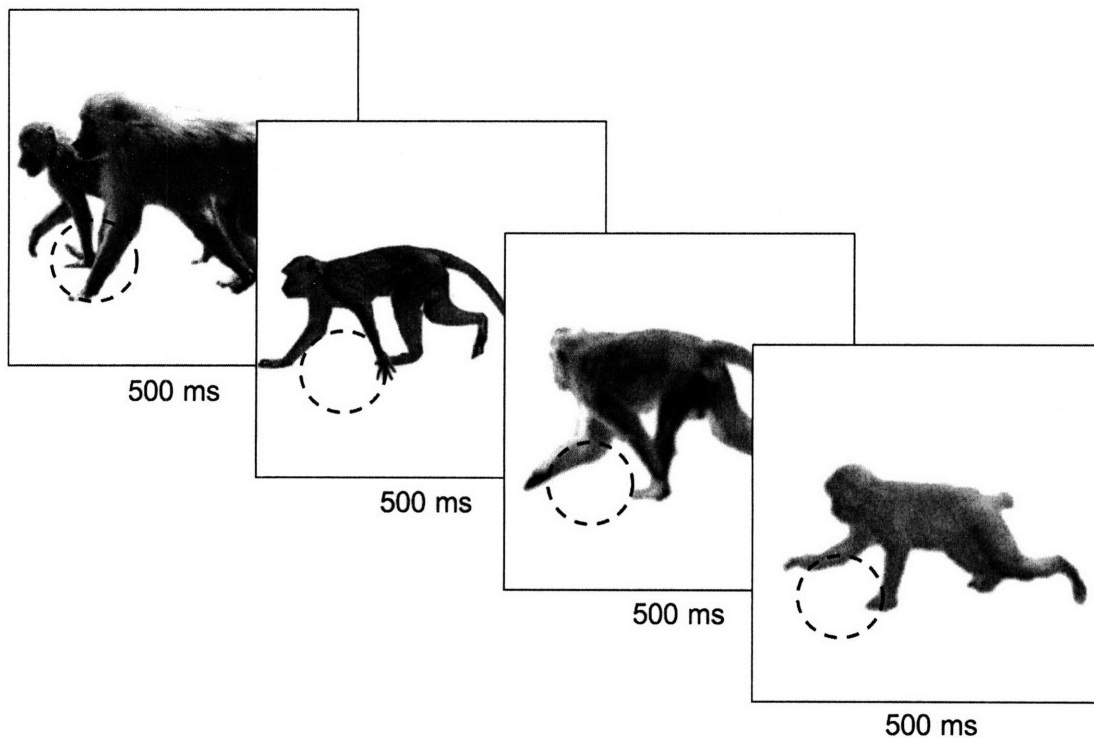


Figure 3. An example implied motion trial. A trial began when the monkey fixated a central fixation square for more than 0.5 s, after which 4 different photographs with implied motion were shown for 500 ms each. The implied motion in all 4 pictures was to the left on 50% of trials and to the right on 50% of trials, randomly intermixed. The order of the 4 images was reversed on 50% of trials to eliminate possible confounds from picture-to-picture spurious directional motion signals. During recording of each neuron, there were either 80 or 160 trials: 2 directions of motion x 2 sequences x either 1 or 2 sets of 4 images. Prior to testing with implied motion photographs, the neuron's response field was handmapped by displaying 100% coherently moving dots in various directions at different sizes and retinal locations. Only neurons showing significantly different responses to leftward and rightward real motion were tested with subsequent photographs. The dashed circle in the figure represents an approximate, typical response field as defined by the dot stimuli.

A total of 103 neurons were tested in three monkeys. In all animals the response to photographs was much lower than to dots. In the first animal tested, a greater response was found to implied motion photographs in the “preferred” direction (i.e., the direction in which real motion gave a greater response) (Figure 4, left). This result was not replicated, however, in two subsequent animals. In these two animals the responses in the preferred and non-preferred directions were indistinguishable (Figure 4, middle and right).

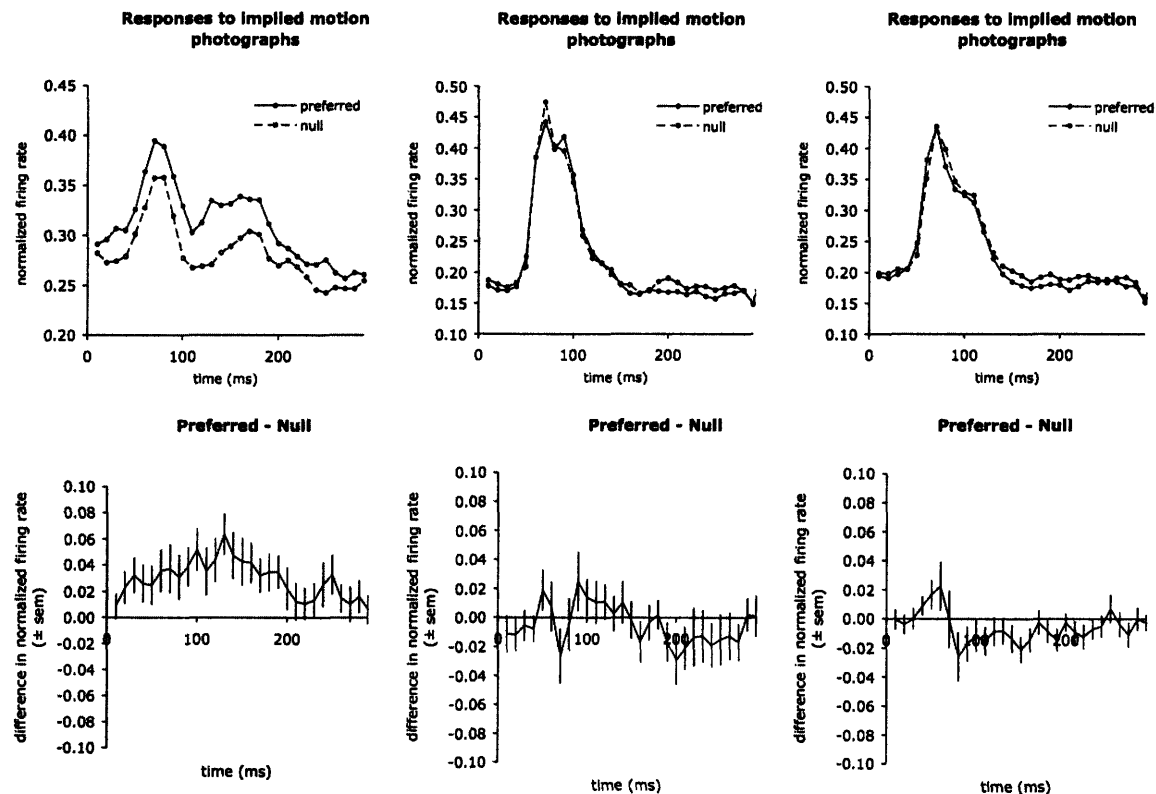


Figure 4. Responses of MT neurons in 3 monkeys to photographs with implied motion. Each row corresponds to measurements on one animal. The “preferred” direction (solid lines) was defined based on preferences to moving dots (either left or right). The “null” direction is the opposite. The firing rate of each cell was normalized to the maximum rate for that cell on any implied motion trial. On the left are the time series showing the mean normalized firing rate for photographs with implied motion in the preferred and null direction (averaged across all images and all trials and neurons for each of three animals). On the right is the times series of the difference between the preferred and null direction.

One possibility is that the first animal tested was better able to interpret the photographs than the other two. A follow-up study has been considered in which an

animal is explicitly trained to indicate the direction of motion implied in photographs with a behavioral response. If, following such training, directional signals are observed in MT neurons, in response to implied motion photographs this would provide evidence that a limiting factor in finding directional responses to implied motion photographs in macaque is whether the animal recognizes or attends to the motion in the image. An alternative that must be considered, however, is that the effect observed in the first animal was spurious, and that, at least in macaque monkey with the methods we have used, MT neurons are not responsive to the direction of implied motion. We note that for the one animal that did show a response, a few other stimulus sets were used in initial pilot testing (prior to testing with cropped images like those in Figure 3), including photographs of his trainer and other monkeys from his lab that he was familiar with. These image sets did not show any reliable directional effects and hence the cropped images that showed a directional effect might be an artifact of multiple testing.

A recent doctoral thesis (Lorteije, 2006) has also reported a failure to find directional signals to implied motion photographs in macaque MT and MST (137 MT and 26 MST cells tested in two monkeys). Stimuli of either monkeys or humans in motion or at rest were shown either in the neuron's receptive field or in the fovea while real motion was shown in the receptive field. As in our preliminary study, the preferred direction of each cell was defined by real motion response preferences. Across the population no evidence was found that MT neurons responded more strongly to implied motion in the preferred direction than the non-preferred direction, nor that the cells responded more strongly to depictions of monkeys with implied motion than depictions of monkeys at rest, irrespective of directionality. There was some evidence of a slightly

greater response to implied motion of humans compared to humans at rest, but this was interpreted as a low-level confound, as the cells that responded more strongly to humans in motion (which contained diagonal parts such as outstretched legs) tended to also respond more strongly to slanted bars than to vertical bars. As a positive control, Lorteije and colleagues do note that many cells in STS showed differential signals to photographs of implied motion versus photographs of monkeys at rest, but as many cells responded more strongly to the images of monkeys at rest as to those with motion.

Taken together, our preliminary result and that of Lorteije and colleagues (Lorteije, 2006) do not show convincing evidence of directional responses to implied motion in macaque MT. Of course failure to find clear evidence for such signals does not mean they do not exist, and in fact we are cautioned by the findings of Schlack and Albright (2007), in which MT signals to learned associations of static shaped were found, but only in a relatively small subset of neurons (19%), suggesting that sampling limitations must be considered. Moreover, even a definitive negative result could not be extrapolated to humans with certainty due to species differences. Thus the neural locus of the directional signals that adapt and are processed in common with real motion remains an open question.

Summary and Conclusions

Across a series of studies, a motion adaptation paradigm was used to demonstrate that two kinds of abstract motion representations, motion imagery and motion inferred from photographs, engage direction-selective perceptual motion mechanisms.

In the case of mental imagery, a motion aftereffect was obtained when subjects had their eyes open or closed, and across two experiments was stronger when the eyes were closed. The aftereffect was found both when the motion was vertical and when it was inward or outward, demonstrating that eye movements were not responsible for the effect. The effect also did not decline over the course of the experiment when subjects did not view repeated examples of the moving stimulus, which suggests that the top-down effects of imagery did not arise from a non-specific reactivation of a short-term perceptual memory store. The recruitment of perceptual motion mechanisms during mental imagery of motion is consistent with a large body of research demonstrating that mental imagery and other top-down processes rely, in part, on sensorimotor representations. The studies on mental imagery presented here add to this literature by demonstrating that in one domain, visual motion, mental imagery can selectively recruit perceptual mechanisms whose specific properties are matched to the properties of the mental image.

In the case of implied motion, the experiments here have shown that photographs depicting motion engage and adapt direction-selective motion mechanisms. In these experiments, subjects were not asked to imagine motion, but instead we presume that they automatically infer it from viewing the photographs. The effect was found to decay with a brief delay between viewing the photographs and viewing the test stimulus, similar

to what is found with aftereffects to real motion. The inference of motion, and not just the orientation of the depicted scene, was shown to be critical for producing the aftereffect. . As in the case of motion imagery, the aftereffect was found with inward and outward motion as well as simple translational motion, again ruling out explanations based on eye movements. The effect of adapting to implied motion was also shown to interact with real motion adaptation, such that they could cancel if they were in opposite directions. Finally, motion adaptation from viewing implied motion was also demonstrated with a second type of test stimulus, counterphase reversing gratings, in addition to the random dot displays used in the other experiments. The aftereffects we observe from implied motion are consistent with several recent results demonstrating through physiological methods that motion-sensitive brain areas also respond to implied motion. Our findings demonstrate a novel effect on perception and show that direction-selective motion signals are involved in representing the photographs.

We propose that the instantiation of directional motion mechanisms when imagining motion or when looking at a photograph that merely implies motion may be part of a broader cognitive strategy whereby appropriate sensorimotor representations are reactivated for a wide range of perceptual and cognitive processes.

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