

Neural Adaptation of Imaginary Visual Motion

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Observers made time-to-contact judgments about an imagined moving object that passed through an area of the visual field previously adapted to a single direction of real motion. The direction of imagined motion varied relative to the direction of adapting motion. When imagined motion was in the same direction as that experienced during adaptation, imagined speed was slowed; when imagined motion was in the opposite direction, its speed was increased; when adaptation and imagined motions were orthogonal, imagined speed was unaffected. The particular influence that prior adaptation has on imagined speed suggests that imagined motion and real vision may engage common neural mechanisms without being functionally equivalent. Negative aftereffects observed in imagined motion imply that the imagination represents movement as an inference from position changes of static images. © 1995 Academic Press, Inc.

Mental images have much in common with events arising from normal visual perception; images function as if they have spatial representations (Kosslyn, 1980; Finke, 1985; Finke & Shepard, 1986), they can interfere with concurrent visual tasks (Perky, 1910; Craver-Lemly & Reeves, 1992), and they appear to have the same resolution limit as those imposed on real objects imaged on the retina (Finke & Kosslyn, 1980). As researchers of imagery have noted (Farah, 1985; Kosslyn, 1987; Sergent, 1990) the comparability of images and perception suggests a deeper level of identity, an equivalence of the neural substrate in which both are represented. Positron emission tomography (Roland & Eriksson, 1987), event-related potentials (Farah, Peronnet, Gonon, & Giard, 1988), and regional cerebral blood flow imaging (Goldenberg, Podreka, Steiner, & Willmes, 1987) have implicated common processing sites for both imagined and real visual objects. In this article we offer strong psychophysical

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evidence that visual imagination can engage neural mechanisms generally identified with early stages of visual processing. Specifically, we find that judgments dependent upon imagined visual motion can be altered by prior adaptation to real motion.

Our experiments capitalize on the well-known perceptual consequences of adaptation to motion. Following prolonged inspection of motion in a given direction, one temporarily experiences illusory motion in the opposite direction upon viewing stationary objects within the adapted portion of the visual field (Wohlgemuth, 1911). This opponent-like aftereffect of motion adaptation is generally attributed to the temporary reduction in the responsiveness of visual neurons selective for direction of motion (Sutherland, 1961; Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather, 1980; Watson & Ahumada, 1985), a physiological property exhibited by neurons in the first cortical stages of motion processing (Vautin & Berkley, 1977; Hammond, Mouat, & Smith, 1985; Peterson, Baker, & Allman, 1985; Marlin, Hasan, & Cynader, 1988). Prior adaptation to motion may also affect the perceived speeds of moving objects (Thompson, 1981; Smith, 1985, Smith and Edgar, 1994) in a way that is less directionally selective; objects generally appear to move slower than normal regardless of whether motion is in the same or opposite direction of adaptation. Perceived speed of motion in directions orthogonal to the adaptation direction is unaffected.

We used the logic of the motion aftereffect (MAE) to develop a methodology for assessing the transfer of motion adaptation to imagined speed. Observers first adapted to motion within a restricted region of the visual field, and then performed a speed-sensitive judgment that involved imagining an object to move across the adapted region. If adapted cortical neurons participate in the generation of the imagined motion, judgments of the crossing time should evidence aspects of directional bias. Minimally, motion imagined orthogonal to adaptation should be distinguishable from motion imagined in the same or opposite directions to adaptation. The existence and structure of a directional bias is investigated in the following two experiments.

OVERVIEW TO THE STUDIES

The notion that prior motion adaptation might affect imagined motion was originally investigated by Corballis and McLaren (1992). In that work observers engaged in a standard mental rotation task subsequent to adaptation to rotational motion. They found little evidence that prior adaptation influenced speed of imagined rotation. In their experiments letters were presented at angles of 0°, 60°, 120°, 180°, 240°, and 300°. The primary influence that adaptation had was to initiate rotation through the larger arc of the circle for the 120° stimuli when the direction of adaptation was

counterclockwise, and similarly for the 240° stimuli when the direction of adaptation was clockwise. In addition, there were conditions in which the smallest latencies were offset from 0°. When the direction of adaptation was clockwise, the minimum latency was often observed at 60°, while the minimum latency was often observed at 300° when the adaptation direction was counterclockwise. Both of these effects may have been caused by the presentation of the cueing letters to adapted retina. Static stimuli presented to adapted retina will appear to drift for several seconds in the direction opposite to adaptation. Rotary movement induced by motion aftereffect could conceivably bias the decision as to which direction to initiate mental rotation, and it can easily account for the offset of minimum latency. The results obtained by Corballis and McLaren may thus be due to the purely visual aftereffect of perceived drift. In fact, Corballis and McLaren found no evidence in their data for an imaginal rotation speed that was contingent upon the direction of adaptation.

In order to examine how adaptation interacts with the imagination it is necessary to devise a methodology that decouples MAE on visual objects from the specification of the imagination task. One way to achieve this is to design a task in which the to-be-imagined object is presented only in unadapted retina. In this case, any influence of prior adaptation observed in the execution of the task would be attributable to the way the object is represented in the imagination. We have employed this logic in the design of our main experiment by incorporating a cueing event that followed the presentation of the adaptation stimulus and which was spatially separated from it. This methodology required a precise measurement of the areal extent of adapted retina, which we obtained in a preliminary experiment.

EXPERIMENT 1: MEASUREMENT OF RETINAL AREA ADAPTED TO MOTION

In this experiment we mapped the boundary of motion adapted retina for the particular adapting stimulus used in the imagination task by determining how far from a motion adapting texture a static test stimulus must be placed in order for there to be no perceived aftereffect (i.e., for the test stimulus to appear stationary). This information was used to place stimuli in unadapted retina for the purpose of cueing in the imagination task.

Subjects. Three observers, two naive about the purpose of the experiment, participated in this experiment. Each had prior experience observing motion aftereffects.

Stimuli. The adaptation display consisted of 200 small, white dots (1 pixel/square) seen against a black background on an Apple 13" video monitor (640V × 480H; 72 pixels/inch; 67 Hz frame rate, P4 phosphor) running in 1-bit mode (i.e., b/w). These dots were confined to a 6° × 6° square area, and during the adaptation periods the dots moved coherently leftward at 2°/s. As dots reached the left-hand edge of the virtual square they were wrapped around to the right-hand side. Located in the middle of this array of moving dots was a small,

stationary cross centered within a 20 arc min blank region; this conspicuous cross served as a fixation point. Frame-to-frame dot displacement and frame rate were adjusted to create smooth apparent motion.

The test display consisted of a narrow vertical strip composed of approximately 35 stationary dots, subtending 6° vertically and 1° horizontally. This strip of stationary dots was positioned at one of five locations relative to the retinal area upon which the adapting dots were previously imaged. Specifically, the right-hand edge of the strip of dots was either 30, 20, 10, 0, or -10 arc min from the leftmost edge of the adapted retinal area. The value of "0" placed the test target immediately adjacent to the adapted retinal region, and the value of " -10 " placed it partially within the adapted region. The fixation cross remained present at all times. Each test position was tested 10 times, with the order of trials randomized. Viewing conditions were mesopic.

Procedure. A test session consisted of an initial 150-s period of adaptation, during which the observer fixated the small blank region while viewing the leftward drifting dots. At the end of the period of adaptation, the moving dots were replaced by the vertical strip of stationary test dots. The observer's task while maintaining central fixation was to judge whether the test dots appeared stationary or not, using computer keys to signal the answer. Observers made their responses within a few seconds, and this was immediately followed by a 10-s readaptation period, followed by another test trial, and so on until 50 trials had been completed.

Results. All three observers gave essentially identical results, and the pooled data are shown graphically in Fig. 1. The incidence of illusory motion (i.e., stationary dots appearing to drift slowly rightward: the conventional motion aftereffect) decreased as the test stimulus was imaged further from the region of adapted retina. This result merely replicates earlier work (e.g., Wohlgeuth, 1911) showing that the motion aftereffect is specific to the retinal area stimulated during adaptation. For the conditions of our experiment, the motion after-

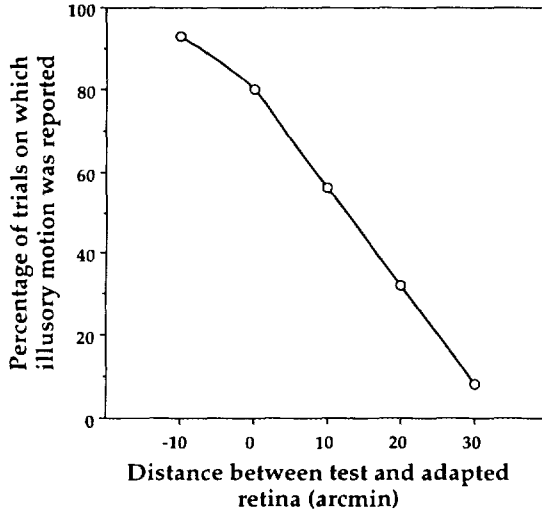


FIG. 1. Spatial spread of motion after effect. The abscissa plots the angular distance between the nearest edges of the stationary test target and the locus of adapted retina. The graph shows combined results from three observers, whose performance was essentially identical. Each data point is based on 30 trials.

effect had completely dissipated once the test dots were imaged 30 min from the nearest edge of adapted retina. This pattern of results was replicated in one observer for the other three cardinal directions of adaptation motion (i.e., upward, downward, and rightward).

Discussion

In this experiment we have sought to establish where cueing stimuli may be placed so that they do not suffer MAE when part of the retina is motion adapted. Our measurements indicate that static cueing contours should be placed no closer than 30 arc min from the boundary of adapted retina. However, the design of our imagination task mandated the presentation of a moving element in addition to the placement of static contours and the possibility that MAE boundaries differ for moving and static stimuli is potentially problematic. The retinal spread of MAE on moving patterns has not been systemically studied and there are no published reports on this issue that may be referred to. Informal evidence that MAE boundaries are not different for moving patterns comes from studies that measure the magnitude of perceived speed shift of moving patterns in adapted retina. In order to make such measurements it is necessary to use two spatially displaced motion filled apertures. One aperture is used for both adaptation and for the placement of a test pattern. The other aperture contains the matching pattern and must be placed in a retinal region free of MAE. Measurement of perceived shift is accomplished by comparison of speeds in the respective apertures. The major studies to date (Thompson, 1981; Smith, 1985; Smith & Edgar, 1994) all have adopted the standard that a 1° separation between apertures is sufficient. In our studies we have placed cueing stimuli no closer than $1/2^\circ$ to adapted retina. Even if the difference between $1/2^\circ$ and 1° is meaningful, our moving elements spend no more than 125 ms during excursions lasting several seconds in a zone that might be affected by MAE.

EXPERIMENT 2: IMAGINED TIME-TO-CONTACT FOLLOWING MOTION ADAPTATION

Subjects. Eight undergraduates from Vanderbilt University were paid \$5 per hour to participate in this experiment. Participants were naive as to the purpose of the experiment and were unfamiliar with the details of the motion aftereffect. In an interview following the experiment, observers evidenced no knowledge of the predicted pattern of results.

Stimuli. The adaptation display was identical to that used in Experiment 1 except that dot motion could be up, down, left, or right. During motion cueing a 7° white outline square replaced the adapting motion field (maintaining a common center) and a small white dot was introduced from one edge of the screen and moved towards the middle at constant speed. Cueing dot motion was directed along a ray through the fixation cross which was present throughout all phases of the trial. Upon encountering an edge of the outline square, the cueing dot abruptly disappeared. Cueing dot motions were directed either up, down, left, or right at speeds of either 4, 6, or 8°/s. Viewing conditions were mesopic.

Procedure. The basic structure of the task is described in Fig. 2. Observers first under-

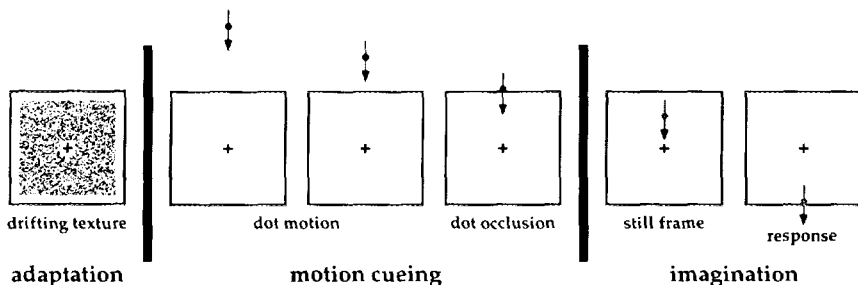


FIG. 2. We illustrate here the three epochs that define a trial; adaptation, motion cueing, and imagined motion. Dots depicted as open circles were not presented but are shown to clarify the task logic. The dot did not reappear following occlusion and the outline square was not displayed during adaptation - we show it here simply to emphasize that the adapting field was centered within the area of imagined motion. The spatial region within which elements were displayed during the cueing epoch was set to ensure that neither the dot motion nor the boundaries of the square fell within adapted portions of the visual field.

went 150 s of motion adaptation while fixating on a cross at the center of the motion field. The motion field was then replaced by an outline square and a dot that moved from the edge of the screen towards the fixation cross (motion cueing). The dot disappeared at the border of the square as if it were occluded. The observer's task was to imagine the traversal of the dot across the occluding square at the speed at which it had been moving prior to its disappearance, and to indicate by a key press exactly when he/she thought the dot would reemerge at the opposite side of the square. In experimental trials the dot did not in fact reappear and there was no feedback given to observers. Trials consisted of a 10-s readaptation period, motion cueing, and then imagined motion. Observers were instructed to maintain fixation on the central cross throughout the trial. Speed of imagined motion was computed from the time elapsing between disappearance of the dot and the observer's response.

Observers were first trained to execute this task with timing errors of less than 20% in conditions of no adaptation. Training blocks where the dot reappeared were alternated with blocks where the dot did not reappear. Observers generally completed about 500 trials of both types before reaching criterion.

Design. Each block comprised 7 trials for each of the 3 dot speeds and 4 dot directions, for a total of 84 trials per block. Each observer completed 2 blocks in the four adapting directions of right, left, up, and down for a total of 8 blocks per observer. Speed and direction were randomized over trials. Within a block the adaptation direction was held constant.

Results and Discussion

In Table 1 we present the raw data obtained from this experiment. The entries in this table are the error magnitudes (in percent) in the imagined dot speed inferred from the time-to-contact estimates:

$$\text{error} = 100 (\text{Square size}/\text{time-to-contact} - v_{\text{dot}})/v_{\text{dot}}$$

Data in Table 1 has been averaged over the 3 dot-cueing speeds. In all conditions, including practice, observers tended to overestimate the time

TABLE 1
Errors in Imagined Speed (%)

Adaptation direction	Dot direction				Derived quantities			O - S	Δ_{\perp}
	Left	Right	Up	Down	Average	Up ^a	Down ^a		
Left	-14.7	-11.3	-19.5	-12.3	-14.5	-16.1	-15.7	3.4	.4 ^b
Right	-12.7	-15.2	-20.0	-14.0	-15.5	-16.6	-17.4	2.5	.8 ^b
Up	-15.0	-15.0	-22.9	-13.5	-16.3	-19.5	-16.9	2.6 ^b	.0
Down	-15.2	-15.1	-19.0	-14.8	-16.0	-15.6	-18.2	2.6 ^b	.1
Average	-14.4	-14.2	-20.3	-13.6					

Note. O - S: error in opposite direction as adaptation minus error in same direction. | Δ_{\perp} |: absolute error difference for directions orthogonal to adaptation.

^a Speed with up/down bias removed.

^b Calculated with up/down bias removed.

required for the imagined dot to exit from behind the occluding square and so all entries are negative. There was also a general bias to imagine downward motion as faster than upward motion. In Table 1 we display the up/down errors with this anisotropy removed.

In addition to these global effects, there was also evidence that prior motion adaptation had specific and interpretable influences on imagined speed in the time-to-contact task. For all four directions of adaptation, the imagined speed in the direction *opposite* to adaptation was faster than the imagined speed in the *same* direction as adaptation. This difference is calculated in Table 1 as O - S. Furthermore, there were no effects of adaptation in directions orthogonal; speed errors in the orthogonal directions were always roughly equal. The difference between orthogonal directions is calculated in Table 1 as | Δ_{\perp} |.

These relationships are depicted in Fig. 3 where we plot the speed errors for all dot cueing and adaptation directions. In this polar plot, distance from the origin measures the magnitude of the speed error with increasing distance meaning more negative errors. Thus dots which are imagined to move more slowly are plotted further from the origin. For example, under conditions of leftward motion adaptation, a dot moving rightward is imagined to move faster than a dot moving leftward, and this is represented by the data point depicting leftward motion to be further out on the axis than the data point depicting rightward motion. The influence of adaptation on imagined speed is summarized by the way the quadrilateral for each dot direction is skewed in Fig. 3. Consistent patterns of skew were obtained for all imagined dot directions. The basic patterns depicted in Fig. 3 were obtained at each level of dot speed.

In Fig. 4 we show how imagined speed varied within each level of cued

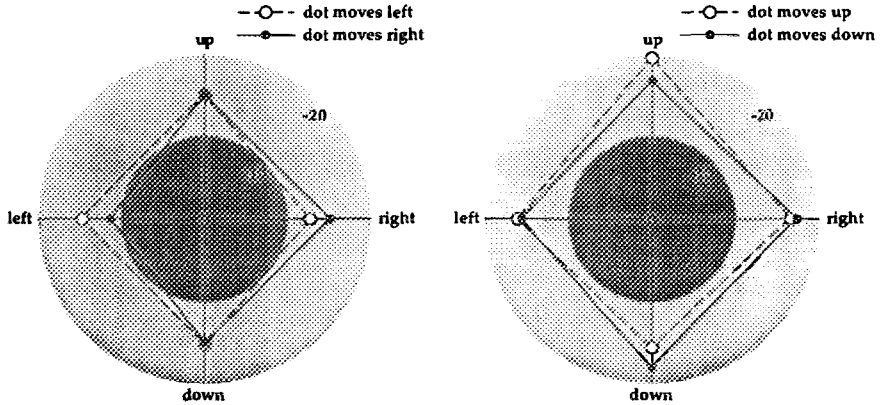


FIG. 3. Pictorial summary of the average data with the up/down bias removed. The cardinal directions—left, right, up, and down—denote the direction of the adapting motion. The filled and open circles denote the magnitude of the error in imagined speed averaged over the three dot speeds. Time-to-contact was overestimated in all conditions, resulting in negative speed errors. Points situated further from the origin represent relatively slower imagined speeds. Numbers shown are percentage errors.

dot speed. In this figure we have plotted the raw speed error relative to the appropriate cueing speed. No adjustment for the up/down anisotropy has been made. The basic pattern of $\text{speed}_{\text{opposite}} > \text{speed}_{\text{orthogonal}} > \text{speed}_{\text{same}}$ is reproduced at all 3 dot speeds. At each level of dot speed the linear trend was significant ($F(1,28) = 24.4, 5.5, \text{ and } 10.1$ for the dot speeds 4, 6, and $8^\circ/\text{s}$, respectively), while the quadratic trend was never significant ($F(1,28) = .007, .15, \text{ and } .002$, respectively). On average, speed of imagined motion in the same direction as the adapting motion was 8.4% slower than when the adapting motion was in orthogonal directions. Conversely, speed of imagined motion in the direction opposite to adaptation was 9.6% faster than speed of imagined motion orthogonal to adaptation. These speed differences are reliably discriminable (McKee, 1981).

There is no question that prior adaptation interacts with imagined speed as measured by judgments of time-to-contact. The question that arises here is whether the data uniquely implicates processes within the imagination; i.e. whether we are justified in making the inference to imagined speed from estimated time-to-contact. There are other potential explanations for the data structure that we have obtained. In particular, it may be that our data can be explained simply in terms of perceptual MAE. In fact if the imagination and ongoing perception were functionally identical, it would be difficult to rule this possibility out. In what follows we shall examine the data structures that would be obtained if the cueing elements

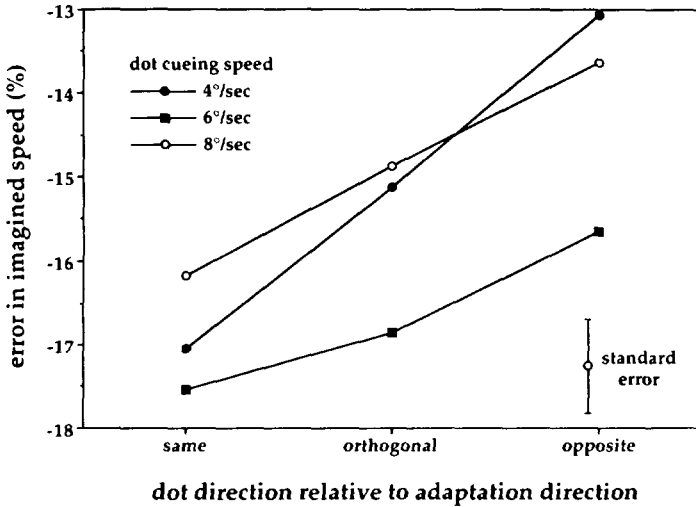


FIG. 4. Raw speed errors averaged over adaptation direction are shown for the three cueing dot speeds. For all cueing speeds, the imagined speed is smallest in the direction of adaptation, intermediate in orthogonal directions, and greatest in the direction opposite to adaptation.

were viewed with adapted retina. We shall also consider aftereffects on eye movement that can arise from prolonged viewing of unidirectional motion.

VISUAL AND IMAGINAL MOTION AFTEREFFECTS

It is necessary to distinguish the consequences of visual aftereffects from the observed data patterns in order to make an argument that the imagination has been biased by visual adaptation. We have identified three potential candidates for a visual processing account of the speed inequalities that make no reference to the imagination: MAE on the cueing dot, MAE on the static outline square, and residual eye movements induced by adaptation. The first two candidates concern the possibility that if our subjects did not hold fixation as instructed, direct fixation of the cueing elements may have corrupted the data. The third candidate addresses the possibility that even if our subjects did hold fixation, involuntary eye-movements may have generated artifactual and confounding trends in estimated time-to-contact.

Speed Shifts Produced by MAE

If subjects failed to hold fixation and looked directly at the cueing dot with adapted retina, perceived dot speeds may have been systematically biased. Furthermore, if bias in perceived speed has the same directional

anisotropy as was found in our data, then there would be no reason to invoke influence of adaptation in the imagination as an explanatory construct. The directional biasing of the time-to-contact judgments could be accounted for by the literal appearance of the dot speed. Such would be the case if the perceived speed of the moving dot was affected prior to its disappearance so that it appeared slowed when moving in the same direction as adaptation and speeded up when its motion was in the opposite direction.

Thompson (1981), Smith (1985), and Smith and Edgar (1994) have conducted parametric studies in which the perceived speed of a test pattern is assessed following motion adaptation. Unfortunately, these studies are not in complete agreement with each other. In order to make the best case against an imaginal interpretation of our data, we present a summary of all results that may be relevant. A description of these data requires reference to three distinct speeds. For notational convenience, let s_{test} be the actual speed of the test pattern, p_{test} be the perceived speed of the test pattern, and s_{adapt} be the speed of the adapting pattern. The results from these studies are then as follows:

1. If test and adaptation directions agree and
 - a. $s_{\text{test}} > s_{\text{adapt}}$, then $p_{\text{test}} \approx s_{\text{test}}$ (Thompson, 1981; Smith, 1985); or $p_{\text{test}} > s_{\text{test}}$ (Smith and Edgar).
 - b. $s_{\text{test}} \leq s_{\text{adapt}}$, then $p_{\text{test}} \leq s_{\text{test}}$ (all studies).
2. If test and adaptation directions are opposed, then
 - a. $p_{\text{test}} \leq s_{\text{test}}$ (all studies), unless
 - b. $s_{\text{test}} \leq 1^\circ/\text{s}$ in which case $p_{\text{test}} \geq s_{\text{test}}$ (Thompson).

Although most of the results reported in these studies incorporated since wave gratings as test and adaptation patterns, the basic set of inequalities that have been derived are expected to generalize to more complex patterns that contain a range of spatial frequencies. Smith (1985) showed that virtually identical shifts in perceived speed are obtained regardless of the detailed spatial frequency content of the adaptation and test patterns. The invariance of the inequalities over the specific forms of the adapting and motion-affected stimuli permits an exploration of the perceptual consequences of viewing movement of the cueing dot with adapted retina.

The implications of MAE on the cueing dot follow straightforwardly from the empirically derived inequalities in perceived speed. First, our dot speeds were respectively 2, 3, and 4 times faster than the adaptation speed of $2^\circ/\text{s}$. Test patterns with speeds that are a factor of 2 or 3 greater than the adaptation pattern have not been observed to undergo perceived slowing. Therefore MAE on the dot speed cannot account for the increase in estimated time-to-contact (decrease in speed) that was observed when the cueing dot moved in the same direction as the adaptation pattern. In

addition, we always found a rebound effect with a decrease in estimated time-to-contact (increase in speed) when the cueing dot moved in the direction opposite to adaptation. Only Thompson (1981) found positive shifts in perceived speed in this direction condition, and then only at very slow flicker (less than 2 hz) and slow speeds (less than 1°/s). For test pattern speeds moving at 2°/s and greater (flickering at 2 hz or greater) all three studies are convergent in reporting perceived slowing. The dots simulated in our study all had speeds well in excess of any test speed for which perceived speed increase has been reported. Furthermore, if MAE on the cueing dot was important, the magnitude of the rebound effect should have decreased with increasing dot speed. Such a trend exists for all adaptation rates in Thompson's data in regimes where perceived speed is greater than the actual speed. We found no reduction of the rebound effect for dots moving at 6 and 8°/s compared with dots moving at 4°/s. Thus, in all cases either the magnitude of the aftereffect on the cueing dot is expected to be negligible in magnitude, or it is of the wrong sign to explain our data. And in any event, we were careful to confine the cueing dot to retinal areas where no MAE was experienced (recall Experiment 1).

MAE on Static Outline Square

The outline square presented during the cueing and imagination phases of our study was designed to be larger than the solid angle influenced by MAE, so that even if subjects were to look directly at the square, it could not be placed entirely within adapted retina. Consequently, we expected aftereffects on the square to be small and in fact there is no perceived motion aftereffect on the outline square with the possible exception of the first presentation following the initial adaptation period of 150 s. The 10-s readaptation period that initiated each of the remaining 83 trials comprising each block does not produce a noticeable MAE drift of the outline square.

Even if the MAE on the outline square was phenomenally salient, its motion could not produce the imagined speed inequalities. Since the MAE on static images is always in the direction opposite to adaptation, the square will drift towards the cueing dot when the dot moves in the adapting direction, and away from the cueing dot when dot moves in the direction opposite to adaptation. If there is any effect at all from MAE on the outline square, it must be to reduce estimates of time-to-contact when the square drifts toward the dot, and increase them when the square drifts away. This is precisely the reverse of what was found in our data. Estimates of time-to-contact were observed to increase when the dot moved in the adapting direction, and to decrease when the dot moved opposite to

the adapting direction. Thus neither MAE on the cueing dot nor on the static square can produce the observed speed inequalities.

Involuntary Eye Movements

Involuntary eye movements comprise a third class of aftereffect that constitutes a potential source of confoundment. During the adaptation epochs preceding each imagination trial, the eyes may have been entrained in a visual motor reflex known as optokinetic nystagmus (OKN). It is also possible that subjects engaged in pursuit eye movements as they foveated the drifting texture. Both pursuit eye movements and OKN are capable of producing an eye drift bias (Cohen, Matsuo, & Raphan, 1977; Muratore & Zee, 1977) referred to as pursuit after-nystagmus (PAN) and optokinetic after-nystagmus (OKAN) respectively. Both PAN and OKAN are characterized by relatively slow eye sweeps that mimic a following of the entraining texture. The slow phase is followed by a rapid refixation and the cycle repeats. PAN drift bias generally has a smaller amplitude than OKAN (Muratore & Zee, 1979) and it requires a longer period of adaptation to create (Lisberger, Miles, Optican, & Eighmy, 1981).

The ramification of PAN and OKAN for our study is that the speed of the cueing dot may have been systemically misperceived. If subjects had attempted to fixate the cueing dot while experiencing an after-nystagmus, the pursuit eye movements required to overcome the drift bias could generate motion signals in the direction opposite to adaptation. Such an account has been given to explain MAE following prolonged unidirectional smooth pursuit (Chaudhuri, 1990, 1991). This effect, if of sufficient magnitude, could account for the inequalities observed in our imaginal time-to-contact data. In other words, subjects may have estimated time-to-contact on the basis of biased speed perceptions.

The optimal condition for the production of after-nystagmus is complete darkness with no visible contours. OKAN and PAN persist in the dark for tens of seconds. In the light, however, eye movement-tracking studies have revealed that OKAN is immediately extinguished—after only one or two cycles of slow phase OKAN (Cohen *et al.*, 1977; Lisberger *et al.*, 1981). Chaudhuri (1991) found that the presence of a static visible texture completely inhibited MAE, an indication that PAN had been discharged. This result implies that both OKAN and PAN are rapidly discharged by visible contour.

The imagination phase of our experiment was not conducted in total darkness. The video monitor provided a constant source of illumination in the room so that environmental contours were clearly visible. The outline square and fixation cross provided additional contour on the display terminal. Under these conditions, after-nystagmus is not expected to persist

long enough to have perceptual consequences. Furthermore, 10-s intervals of pursuit eye movements are not sufficient to generate PAN (Lisberger *et al.*, 1981). Indeed, after-nystagmus has never been suggested to cause biases in speed perception in any domain where more than a single dot was visible.

MAE in the Imagination

A corollary of the argument that MAE acting on the cueing dot is incapable of explaining our data is that there is no functional equivalence between perceived MAE and imaginal MAE on moving targets. The dot in the imaginal time-to-contact task is not acted upon by the MAE as if it were moving. The imagined dot instead displays the negative aftereffect associated with static images. This paradox may be resolved if imagined motion is fundamentally inferential, arising as a perceived change in position, much like the motion deduced when noting the changes in position of the minute hand of a clock. Inferred movement has the consequence that at all moments the imagination has before it a static image, an image that can suffer the negative rebound associated with static MAE. Thus, in a state of adaptation, the imagination updates its representations of position from images that have apparent negative displacement. In this way the imagined dot behaves as if it was embedded in a medium that is itself drifting in the direction opposite to adaptation.

GENERAL DISCUSSION AND SUMMARY

The existence of an interaction between imagined time-to-contact and prior adaptation implies that imagined motion relies on activity within neurons whose responsiveness is altered by adaptation to real motion. This statement is independent of the specific patterns of data that we obtained and relies only on the finding that adaptation induces an angular dependence in the speed of imagined motion that is not otherwise present. It is tempting to isolate the neural structures that are accessed by the imagination in the time-to-contact judgment. Adaptation to translational motion of the sort used in our study is generally attributed to reductions in the responsiveness of direction selective cells in V1, an early stage in the visual analysis of 3D scenes (Sutherland, 1961; Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather, 1980; Watson & Ahumada, 1985). Of course, output from these adapted V1 neurons passes to higher stages of processing while still carrying the perceptual signature of adaptation. So we cannot unequivocally pinpoint the generation site of imagined motion as V1. However, the lack of interaction between adaptation to rotation and mental rotation found by Corballis and McLaren (1982), may be instructive here. Cells that are specifically tuned for direction of rotation have been found in the media superior temporal area (MST) but

not earlier in the visual pathway (Sakata, Shibutani, Ito, & Tsurugai, 1986; Tanaka & Saito, 1989; Tanaka, Fukada, & Saito, 1989). This physiological datum suggests, albeit weakly, that the imagination does not use MST neurons in the representation of object motion, and that it operates at a site that is computationally prior to MST.

These results are consistent with earlier anatomical studies that rely upon imaging blood flow, metabolic activity, and event-related potentials (Roland & Eriksson, 1987; Farah *et al.*, 1988; Goldenberg *et al.*, 1987). Anatomical studies, however, suffer both from poor spatial resolution in mapping of brain activity and from the lack of focused prediction inherent in passive observation. Indeed, the fuzziness of the anatomical studies has made them susceptible to challenge; recent psychophysical studies of mental rotation (Corballis & McLaren, 1982; Jolicoeur & Cavanagh, 1992) have brought into question the notion that mental images share a common neural substrate with ongoing vision.

Our study demonstrates more than shared neural processes between the imagination and vision. We have also known that visual adaptation to motion creates a specific pattern of bias in judgments of imagined time-to-contact. The bias is independent of the orientation of the direction of adaptation and satisfies the inequalities

$$\text{speed}_{\text{opposite}} > \text{speed}_{\text{orthogonal}} > \text{speed}_{\text{same}}.$$

These inequalities appear to mandate an interpretation where imagined motion is functionally decoupled from perceived motion. Imagined motion behaves as if it were susceptible to a negative motion aftereffect, a phenomenon associated only with static visual images. This has led us to speculate that even though it may seem that images move around in our heads, we are really only looking at static images in different positions.

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