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Another perspective on the visual motion aftereffect

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ABSTRACT **Prolonged adaptation to motion in a given direction produces distinctly different visual motion aftereffects (MAEs) when viewing static vs. dynamic test displays. The dynamic MAE can be exactly simulated by real motion, whereas the static MAE cannot. In addition, the magnitude of the dynamic MAE depends on the bandwidth of motion directions experienced during adaptation, whereas the static MAE does not. Evidently a stationary pattern does not directly activate the neural mechanisms affected during motion adaptation, whereas a dynamic visual display does. These results imply that the traditional explanation of the MAE needs modification.**

Following inspection of motion in a given direction for a period of time, a stationary object appears temporarily to drift in the opposite direction (1); this is the well-known motion aftereffect (MAE). The MAE is a widely used inferential tool for studying the response properties of motion-analyzing mechanisms in human vision (2–4), and neurophysiologists have sought to uncover the neural concomitants of this compelling illusion (5–8). The MAE cannot be caused by transients or by retinal slip associated with eye movements, for it is observed even when the image of the test pattern is stabilized on the retina (9). Instead, the MAE is typically attributed to a temporary depression in activity within those neurons responsive to motion in the direction experienced during adaptation. When a stationary pattern is then viewed, this selective adaptation yields a shift in the balance of activity favoring neural mechanisms signaling motion in the opposite direction (10, 11). Based on two findings utilizing dynamic as well as static MAE displays, we find this explanation deficient. (*i*) A dynamic MAE can be simulated by real motion whereas a static MAE cannot and (*ii*) the magnitude of a dynamic MAE depends on the bandwidth of motion directions experienced during adaptation whereas a static MAE does not. We propose that a stationary pattern does not directly activate neural mechanisms affected during motion adaptation, whereas a dynamic visual display does. This proposal leads to a significant modification of the traditional explanation of the MAE.

Can the MAE Be Simulated by Real Motion?

Imagine viewing a cluster of black dots moving against a white background, with the directions of dot motions entirely random. Termed random dynamic visual noise (RDVN), this display has no net direction flow; the individual dots appear to be jittering about randomly (12). But now suppose this RDVN test display is viewed following prolonged inspection of dots all moving in the same direction, say upward. Following adaptation to upward motion, RDVN now appears temporarily to have a general downward direction of drift, even though statistically all directions are equally represented. This dynamic MAE is readily explained by the distribution-shift model (10, 11). Now, the unadapted DVN stimulus can be rendered perceptually identical to the dynamic MAE experienced during postadaptation viewing of RDVN simply by forcing a percentage of the dots in the unadapted DVN always to move downward; the two displays constitute metamers (13).

To quantify this metameric relation, we performed the following matching experiment (see Fig. 1 *Upper* for a summary of the conditions). Observers viewed random-dot cinematograms (12) generated by a Macintosh II computer on a monochrome video monitor [Apple 12 inch (1 inch = 2.54 cm) P4 phosphor, 480 vertical × 640 horizontal pixel resolution, 15 cd/m^2 white background, 67-Hz frame rate]. The observer maintained fixation on a cross placed midway between a pair of circular displays 3.25° in diameter within which the cinematograms appeared; the nearest edges of the two displays were separated by 4.8°. The cinematogram consisted of 100 black dots, each subtending 2 arc min from the viewing distance of 114 cm. The position of each dot changed by a fixed amount—5 pixels—from frame to frame; the resulting speed of motion was ≈2°/sec. During a 60-sec adaptation period, the dots in one circular area all drifted upward (shown in Fig. 1 *Upper* as upward arrows) while in the other circular area dots moved in all possible directions and had, therefore, no net direction of flow. During the test phase, RDVN was presented within the circular region that had displayed upward motion, and biased DVN was presented within the other circular area. Biased DVN consisted of 100 black dots, some moving in entirely random directions (represented in Fig. 1 by filled dots: noise) and the remainder (represented in Fig. 1 by open dots: signal) moving downward. Over trials we varied the percentage of signal dots in the biased DVN to find the value yielding an impression of general downward motion that was indistinguishable from the MAE experienced with RDVN.

A number of people have observed these displays, and all find that signal percentages in the neighborhood of 30–40% provide a remarkably compelling match. The data in Fig. 1 *Lower* validate and extend these observations using a forced-choice discrimination procedure.

Now consider the outcome when we assess the MAE using a display in which all dots are stationary. Adaptation to upward motion subsequently causes the stationary dots to appear to drift downward for a few seconds, which is the conventional MAE. It is impossible, however, to create *any* kind of real motion display that exactly mimics this MAE. Observers can adjust the velocity of real motion to simulate the apparent velocity of the stationary dots undergoing the MAE, but there is never any doubt that the matching and test displays are different: the stationary dots, though appearing to migrate in a given direction, simply never go anywhere.

The impossibility of matching a conventional MAE with real motion occurs, we believe, because the conventional stationary MAE display, unlike the MAE experienced with RDVN, does not directly activate the motion mechanisms

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Abbreviations: MAE, motion aftereffect; DVN, dynamic visual noise; RDVN, random DVN.

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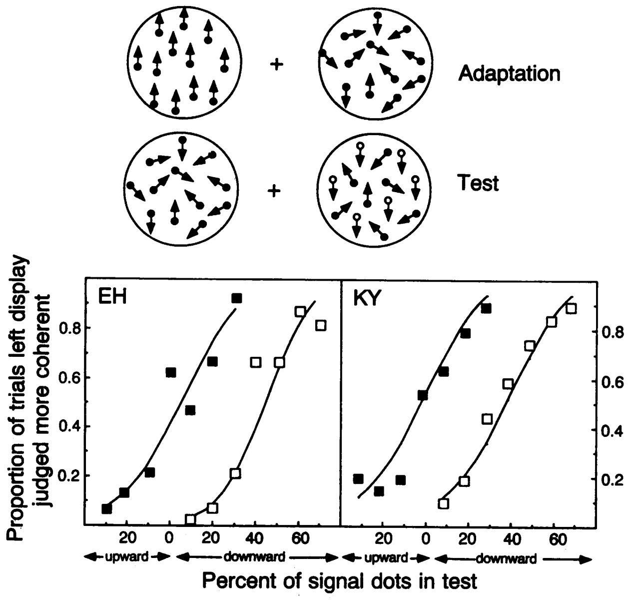

FIG. 1. (*Upper*) Summary of conditions employed to establish matches between the MAE experienced with RDVN and the motion experienced with biased DVN. (*Lower*) Relative strength of coherent motion under conditions of adaptation and no adaptation. Results are from an experiment measuring the perceptual equivalence of adapted and unadapted motion. While viewing displays like those shown in *Upper*, observers were adapted for 60 sec to unidirectional motion upward on the left and to RDVN on the right. Observers then judged in which one of two DVN test displays motion was more coherently downward. The percentage of signal dots in the left-hand test display was varied randomly from trial to trial, whereas in the right-hand comparison display the signal percentage was fixed at 40% (i.e., the value found in pilot measures to subjectively match the MAE with RDVN). Each test presentation lasted 2 sec, and between test presentations the two adaptation displays were again presented for 10 sec to maintain the level of adaptation. Results are plotted in *Lower* (one panel for each observer). The ordinate gives the proportion of trials on which the observer judged the test display imaged to the left of fixation (i.e., the test display in which signal percentage was varied) to be more coherent than the test display to the right of fixation (i.e., the display in which signal percentage was fixed at 40%); the abscissa specifies the percentage of signal dots present in the left-hand display. The right-hand curve in each graph shows results in the absence of adaptation to a given direction of motion; as expected, the two test displays are confused (i.e., performance is at 50%) when each contains 40% downward dots—i.e., when the two physically match. The left-hand curves show results under conditions of adaptation to upward motion in the left-hand display; the MAE experienced with RDVN (i.e., 0% biasing signal) is confused with biased DVN containing 40% actual motion signal downward. Each data point is based on 20 judgments, and the solid curves are best-fit by probit analysis. Note the comparable slopes of the two curves for each observer—evidently adaptation has no effect on the reliability of coherence judgments.

affected during adaptation; a metameric match cannot be made.

Is the MAE Confused with Real Motion?

We have also determined whether observers, while adapted to upward motion, can discriminate real downward motion from the illusory downward motion experienced when viewing RDVN or when viewing stationary dots. The drawings in Fig. 2 *Upper* summarize the adapting and test conditions. One hundred 2 × 2 pixel black dots were presented within a single circular display 3.25° in diameter, and the observer viewed this display while fixating a small cross (not shown) located 2.4° to the right of this display. During an initial 3-min adaptation period, either RDVN (control condition, not shown) or dots moving upward (adaptation condition, Fig. 2 *Upper*) were continuously presented. After this initial period of adaptation, a 2-sec test display and a 10-sec readaptation period were successively administered until 70 test trials had been completed; five observers were tested. For one experiment, the test display consisted of either stationary dots or dots all moving slowly upward or moving slowly downward (1 or 2 pixel jumps between frames). After each test display, the observer indicated whether or not that display contained real motion. For the second experiment, the test display consisted either of RDVN or biased DVN, with the bias causing a general drift upward or a general drift downward. The observer's task was to indicate whether the display contained random motion vs. biased motion.

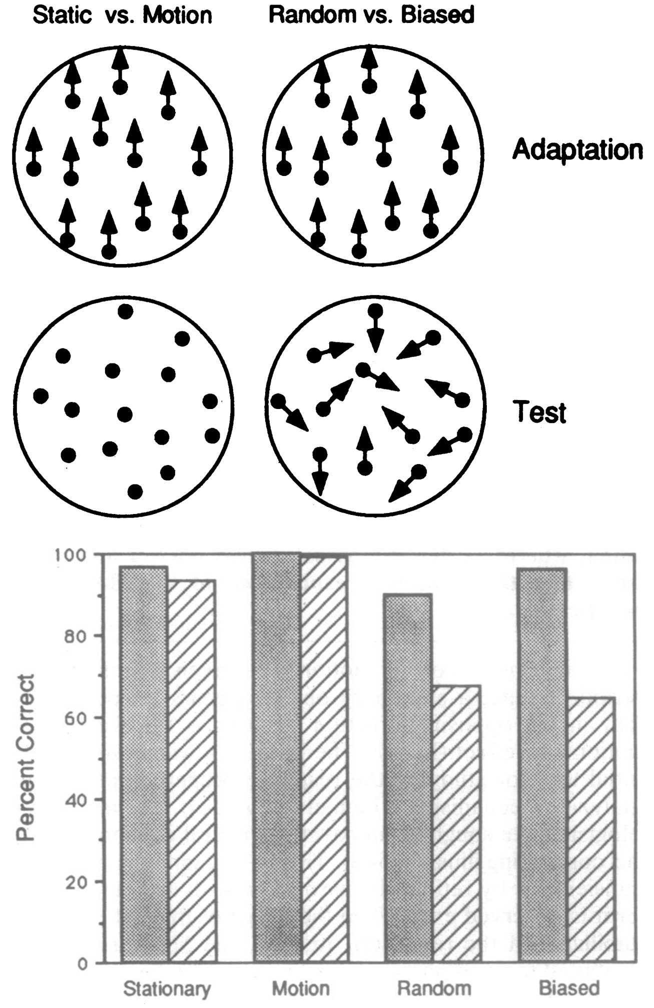

FIG. 2. (*Upper*) Schematic of test and adaptation conditions employed in discrimination experiments. Dots with arrows indicate 2°/sec motion in the direction shown; an absence of arrows indicates stationary or slowly moving dots (i.e., 0, 1, or 2 pixel jumps between frames). Not shown is the control condition, which involved presentation of RDVN during adaptation. (*Lower*) Results averaged over five observers (all of whom exhibited the same pattern of results), with at least 30 observations per condition for each observer. Stippled histograms represent discrimination performance following adaptation to RDVN; hatched histograms give performance following adaptation to upward motion. The conditions along the abscissa specify the test display.

Following adaptation to RDVN (control condition), discrimination of the test displays—static and moving—was nearly perfect (stippled histograms in Fig. 2 *Lower*). Following adaptation to upward motion (hatched bars in Fig. 2 *Lower*), discrimination of stationary vs. moving displays was

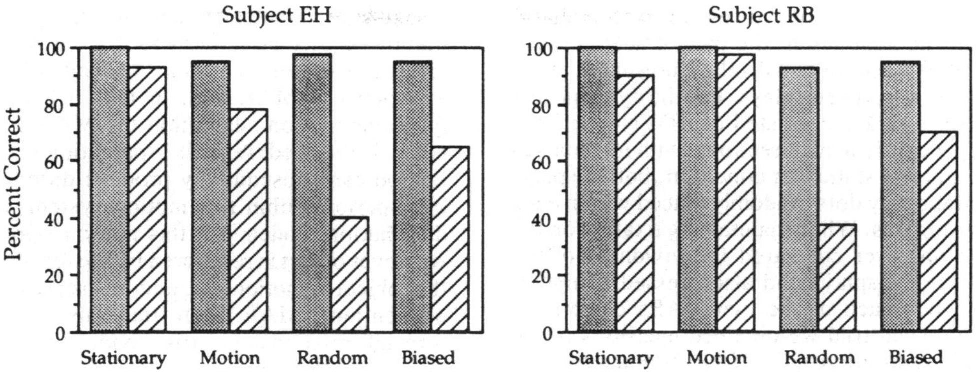

FIG. 3. Histograms showing percent-correct performance on the same task summarized in Fig. 2, only with brief, 360-msec test durations. Stippled bars give results following adaptation to RDVN (control conditions) and hatched bars give results following adaptation to upward motion (experimental conditions). The conditions along the abscissa specify the test display.

also very good, but discrimination of random motion from biased motion was impaired. In other words, observers consistently confused the MAE experienced with RDVN with biased DVN, but observers never confused the MAE experienced with stationary dots for actual movement of dots in a single direction. It is possible to cancel the MAE experienced with stationary dots by superimposing dots actually moving in the direction opposite that of the MAE (14). Observers presumably know, however, that they are viewing a display containing real motion, not just stationary dots.

For two observers, we repeated the discrimination experiment using a test display duration of 360 msec; all other procedural details were identical to those described in the first paragraph of this section. The pattern of results was essentially the same with this very brief exposure duration (Fig. 3): both observers confused RDVN and biased DVN but were better at discriminating static from slowly moving dots. At even briefer exposure durations, discrimination performance under nonadaptation conditions began to deteriorate.

These findings add further support to the idea that static stimuli do not directly activate the motion mechanisms affected during adaptation. One can, however, construct a counterexplanation for the discriminability of static and moving stimuli. Perhaps the static pattern affords positional information not available in a dynamic display. According to this argument, a static test stimulus *does* activate motion mechanisms as well as a positional mechanism responsive to zero velocity (i.e., stationary) patterns; this latter mechanism would be unaffected by motion adaptation and would be unresponsive to dynamic displays. According to this argument, observers successfully discriminate real motion from the illusory motion of a static MAE based on the presence vs. absence of activity in the positional mechanism. Testing with dynamic displays eliminates the availability of this positional information, which explains why observers confuse RDVN and biased DVN following adaptation. This counterargument entails two assumptions: (*i*) static patterns activate motion mechanisms and (*ii*) moving patterns do not activate zero-velocity, positional mechanisms. Moreover, the argument is very difficult to refute, for it can be invoked to explain any condition (e.g., brief exposure durations) where observers successfully discriminate static from moving patterns, even in the absence of adaptation. For the present, we favor the idea that motionless patterns do not activate motion-sensitive mechanisms.

Dynamic vs. Static MAE: Differential Effects of Motion Bandwidth on MAE Duration

A distinction between the conventional MAE and the dynamic MAE receives further support from an additional experiment. The adaptation and test displays consisted of a pair of circular regions 3.25° in diameter, each containing 100 black dots (each 2 × 2 pixel dot moved at 2°/sec); a small fixation cross was situated midway between the two laterally separated display areas (Fig. 4 *Upper*). During adaptation, dots in both regions changed positions every frame of the animation sequence, producing the impression of continuous motion. On each trial, the dots in one of the two circular regions all moved straight upward, whereas in the other circular region dots were constrained to move within some angular bandwidth of directions (15) centered about upward; the size of this bandwidth ranged from 0 (all dots moved upward) to 180° (dots moved in all directions ranging from leftward, through upward, to rightward). Over trials the position—left vs. right—of the variable bandwidth motion display varied randomly. Throughout the 60-sec adaptation period during which the pair of motion sequences was

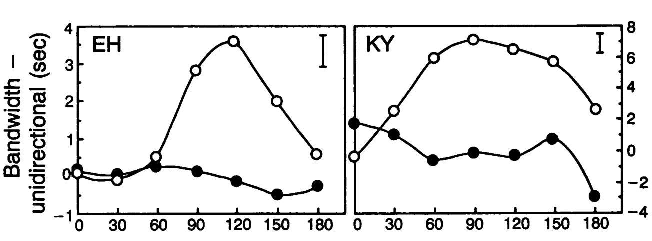

FIG. 4. (*Upper*) Schematic of test and adaptation conditions employed in MAE duration experiment. (*Lower*) The ordinate plots the duration of the MAE measured with bandwidth motion minus the duration of the MAE measured with unidirectional (i.e., upward) motion; a value of 0 indicates no difference in the strength of the two MAEs. The abscissa plots the full bandwidth (deg) of the directions present in the variable bandwidth adapting motion. Open circles denote results measured using RDVN as the test display; filled circles give results for stationary dots. Each data point is based on 10 observations and the vertical bars show the average standard error; the same pattern of results has been obtained on other observers tested less completely.

presented, the observer stared at the central fixation mark. Immediately following adaptation, the pair of adapting displays was replaced by a pair of test displays presented at the same locations as the adapting displays. For the dynamic test condition, both test displays consisted of RDVN—i.e., 100 dots moving independently in all directions, with no imposed bias in direction. For the static test condition, both displays consisted of 100 stationary dots randomly placed within each of the two circular regions. While maintaining fixation on the central mark, the observer compared the vividness of the MAE for the two test displays and also pressed computer keys to indicate when each of the two MAEs completely dissipated. Thus on each trial we obtained measures of the initial strength and the duration of the MAEs produced by the two adaptation displays.

When testing with RDVN, the strength and duration of the MAE were strongest when the adapting motion contained dots moving within a relatively broad range of directions, not just upward (Fig. 4 *Lower*, open symbols). Expanding the range of dot directions presumably engages and adapts more of the motion-selective neurons, yielding a more robust MAE; for very broad directional bandwidth, of course, the actual number of dots stimulating any given mechanism will be few, thus weakening adaptation of any given mechanism. This relation between MAE strength and adaptation bandwidth is not found, however, when testing utilizes stationary dots (Fig. 4 *Lower*, filled symbols), the condition representing the classic MAE; strength and duration of the MAE are unrelated to this seemingly important property of the adapting motion. We believe the MAE with RDVN lasts longer because this test display (which includes dots moving upward) actually prolongs recovery from adaptation, by maintaining activity within the previously adapted neurons; a stationary test display contains no such motion and, thus, has no such effect.

Conclusions

So we find that the two types of MAEs—static vs. dynamic—are distinctly different. The MAE experienced with a moving test display can be exactly simulated by a real motion display, unlike the static MAE, and its strength exhibits a directional dependence not found with the static test. These differences imply to us that a static test stimulus in fact does not directly activate the motion mechanisms affected during adaptation, whereas a dynamic test stimulus does. Using a rather different procedure, van Santen and Sperling (16) also concluded that stationary patterns fail to stimulate mechanisms used for motion detection.

Why, then, does a stationary display appear to drift following motion adaptation, if such a display fails to activate the adapted motion system? We propose that differential activity within direction-selective neurons provides a velocity signal that is automatically assigned to that visual object (or, more precisely, those visual features) registered by a separate neural system that registers information about form (17–20) and location, or position, in space (21, 22). Activity within this form system thus provides a medium of expression for information arising within the motion system (in the same way that atmospheric particles, such as smoke, allow one to visualize air turbulence); absent activity in the form pathway, motion cannot be experienced even if differential activity exists in the motion system. One must look at *something* to experience a MAE and, in fact, when nothing is viewed following motion adaptation the MAE is "stored" (i.e., its decay is retarded; ref. 23). Adaptation to a given direction of motion can subsequently produce differential activity for a brief period within this motion system, in accord with the distribution model. But this motion signal gets assigned to whatever object is registered by the form pathway even when that object is motionless, and this represents the basis of the conventional MAE. Note that this binding of motion and form information could arise simply from the synchronicity of activity within different pathways (24, 25), not a literal combination of activity from multiple pathways at some higher neural level. Regardless of the details of this process, the present results underscore the importance of utilizing dynamic test displays when exploiting the MAE as a psychophysical tool for studying the response properties of motion-analyzing mechanisms in human vision.

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