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Low-level mediation of directionally specific motion after-effects: motion perception is not necessary

M. J. Morgan[1,2]
K. Schreiber[1]
J. A. Solomon[2]

[1] Max-Planck Institute for Metabolism, Cologne
[2] City University London

Corresponding Author
Michael J. Morgan
Michael.morgan@sf.mpg.de

Abstract

Previous psychophysical experiments with normal human observers have shown that adaptation to a moving dot stream causes directionally specific repulsion in the perceived angle of a subsequently viewed, moving probe. In this paper, we used a 2AFC task with roving pedestals to determine the conditions necessary and sufficient for producing directionally specific repulsion with compound adaptors, each of which contains two oppositely moving, differently colored, component streams. Experiment 1 provides a demonstration of repulsion between single-component adaptors and probes moving at approximately 90° or 270°. In Experiment 2 oppositely moving dots in the adaptor were paired to preclude the appearance of motion. Nonetheless, repulsion remained strong when the angle between each probe stream and one component was approximately 30°. In Experiment 3 adapting dot-pairs were kept stationary during their limited lifetimes. Their orientation content alone proved insufficient for producing repulsion. In Experiments 4–6 the angle between probe and both adapting components was approximately 90° or 270°. Directional repulsion was found when observers were asked to visually track one of the adapting components (Experiment 6), but not when observers were asked to attentionally track it (Experiment 5), nor while passively viewing the adaptor (Experiment 4). Our results are consistent with a low-level mechanism for motion adaptation. It is not selective for stimulus color and it is not susceptible to attentional modulation. The most likely cortical locus of adaptation is area V1.

Introduction

Psychophysical and physiological evidence combine in suggesting that motion processing within the central visual system occurs in at least two stages (Movshon & Newsome, 1996). In the first stage, motion signals are measured within local regions of visual space by mechanisms whose preferred directions are orthogonal to their preferred axes of orientation, but nonetheless respond to all directions within ±90° of their preference, due to the "aperture problem." Veridical estimates of direction can be obtained when multiple first-stage signals are combined using the "intersection of constraints" rule (Adelson & Movshon, 1982; Ferrera & Wilson, 1990; Movshon, Adelson, Gizzi, & Newsome, 1985; Rodman & Albright, 1989).

Evidence for the two-stage model comes from experiments on transparent motion. When two sets of independently positioned dots move in opposite directions, both directions of motion are visible. Snowden, Treue, Erickson, and Andersen (1991) showed that V1 neurons stimulated by one direction of moving dots were largely unaffected when dots moving transparently in the opposite direction were added to the stimulus. Most neurons sampled from MT, on the other hand, show some degree of suppression from dots moving the opposite direction (unless they are given a binocular disparity, which makes them appear in a different depth plane; Bradley, Qian, & Andersen, 1995). This finding suggests that motion signals are averaged over a larger spatial scale in MT, possibly for the purposes of noise reduction and smoothing (Qian & Andersen, 1994).

Qian and Andersen (1994) replicated these findings, using oppositely moving dots that were paired in close spatial proximity. V1 neurons were little affected by the pairing, while MT neurons tended to be suppressed. Qian, Andersen, and Adelson (1994) had previously noted that neither direction of motion is seen in the paired dot display. It seems only to flicker.

Analogous results have been obtained with drifting gratings. They activate individual neurons (Qian & Andersen, 1994) and produce a positive BOLD response (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999) in both V1 and MT, but whereas the addition of otherwise identical, oppositely drifting gratings suppresses the responses in MT, it does not suppress the response in neurons or the magnitude of the BOLD response in V1. Apparent motion is also absent from this "counterphasing" stimulus. It too merely appears to flicker.

Some of the best evidence for the two-stage model comes from adaptation experiments. For example, Kohn and Movshon (2003) showed that adaptation to small patches of drifting grating could reduce the contrast-gain of directionally selective, MT neurons in anaesthetized, paralyzed macaque monkeys. However, this happened only when the adapting and probe stimuli were presented in the same, small, sub-area of the MT neuron's receptive field. Kohn and Movshon inferred from this result that the primary locus of adaptation is in the smaller receptive fields of V1 neurons, and that this adaptation is merely inherited by MT. We can conjecture that MT neurons would similarly inherit adaptation from V1, when the latter was stimulated with counterphasing gratings or the paired-dot stimulus.

There have been many psychophysical demonstrations of adaptation to moving stimuli. Prolonged inspection of a drifting grating or drifting dots is known to produce a selective loss of sensitivity to movement in the adapting direction (Sekuler & Ganz, 1963; Morgan, Chubb, & Solomon, 2011), a reduction of perceived velocity in the adapting direction (Thompson, 1981), and repulsion of the perceived angle of motion away from the adapting angle (Levinson & Sekuler, 1976). In this paper, we examine motion adaptation to paired dots. The two-stage model of motion perception predicts that adaptation to paired-motion stimuli or counterphasing gratings should result in selective adaptation to both directions of motion. Consistent with this prediction, we report repulsion of the perceived angle of motion away from the both angles in the adapting stimulus.

Our study is a straightforward extension of Levinson & Sekuler's (1976). They used transparently moving (i.e. unpaired) dots. Human observers were adapted to a set of dots moving at 120° (i.e. up and to the left) combined with a set moving at 300°. We shall use the notation 120/300 for this stimulus. Following adaptation, observers were shown probes of 90° and adjusted the orientation of a line to their perceived direction of movement. The probe was repelled away from the 120° component of the adapting stimulus by the same amount as it had been from an adaptor containing a single 120° component. (We refer to this as 120/120.) However, no repulsion of a 90° probe occurred from a 300/300 adaptor.

We predict a similar result with adaptation to a paired-dot moving stimulus, even though it is seen as flickering rather than moving. To test the prediction we adapted to a 30/210 paired-dot stimulus and tested with probe dot streams moving at 0 and 180°. We predicted that both probes would show clockwise repulsion. To measure the effect we analyzed psychometric functions from a 2AFC task with roving pedestals. This allowed us to determine the actual angle at which the probes appeared to the observer to move horizontally. To show that the predicted CW shift was not a static tilt after-effect, we used a control in which the paired dots formed a Glass pattern, with clear orientation but no movement.

The only previous study of adaptation to paired motion of which we are aware was by Blaser, Papathomas, and Vidnyanszky (2005), who used the same logic as ours to predict repulsion of orientation from the components. These authors adapted to 0/180 and tested at 90°. No repulsion would be expected in this case when the two sets of dots have the same motion energy, because the probe would be repelled in opposite directions by the two components. However, Blaser et al. used different colors for the leftwards and rightwards moving dots, and reported repulsion of red probes from red adaptors, and green from green. In other words, the effects of adaptation were color-specific. To test for color specificity using our own 2AFC psychophysical methods, we adapted to R0/G180 and tested with R0, R180, G0 and G180 probes.

General Methods

Stimuli were presented on a 60-Hz frame-rate Sony Trinitron monitor, viewed from 75 cm so that 1 pixel subtended 1.275 arcmin at the observer's eye. Except where otherwise stated, the viewing parameters were as close as possible to those of Blaser et al. (2005). The circular aperture size was 4.25°; the dot diameter was 0.0425°; the dot lifetime was 5 frames (80 ms); and the velocity of adapting dot movement was 2.5 deg/s. The number of dots was 256 (or 128 green and 128 red, in the transparent condition). The initial adaptation period was 40 s. Subsequent "top-up" periods were 8 s each. Background screen luminance was 50 cd/m^2 in Experiment 1, but ~0 in Experiments 2–6, as in the experiments reported by Blaser et al. The central fixation point was a 0.05° white square. (Blaser, et al. also had a central fixation point but its size is not specified.)

The luminances of the red and green dots were chosen to be equally salient in the transparent stimulus. Blaser et al. (2005) did not specify their dot luminance values but state that they were calibrated for isoluminance for each subject. (Presumably isoluminant with each other, not with the dark background.) Except in experiments with transparent motion, we used only green dots.

Eye position was measured with an EYELINK 1000 far-infrared reflection recorder.

The stimuli and a typical trial sequence are illustrated in Fig. 1. (See also Supplementary Material, **DemoAdaptRedTestRed.mp4.**) Each session began with a 40-s adaptation period, during which the observer was instructed to maintain fixation. This was followed by a sequence of 192 trials. Every 50 trials, the observer was instructed by a message on the screen to take a rest, following which a key press initiated another 40-s adaptation period. On all other trials the adaptation period was 8 s. The adapting stimulus consisted of 256 green dots randomly scattered in the circular aperture. Each of these dots moved rightwards with a limited lifetime of 5 frames (Morgan & Ward, 1980a, 1980b), at the end of which it was replaced by a dot in a random position within the aperture. Any dot that reached the edge of the aperture was wrapped to the mirror image position on the aperture, with a small horizontal shift towards the center equal to two dot diameters.

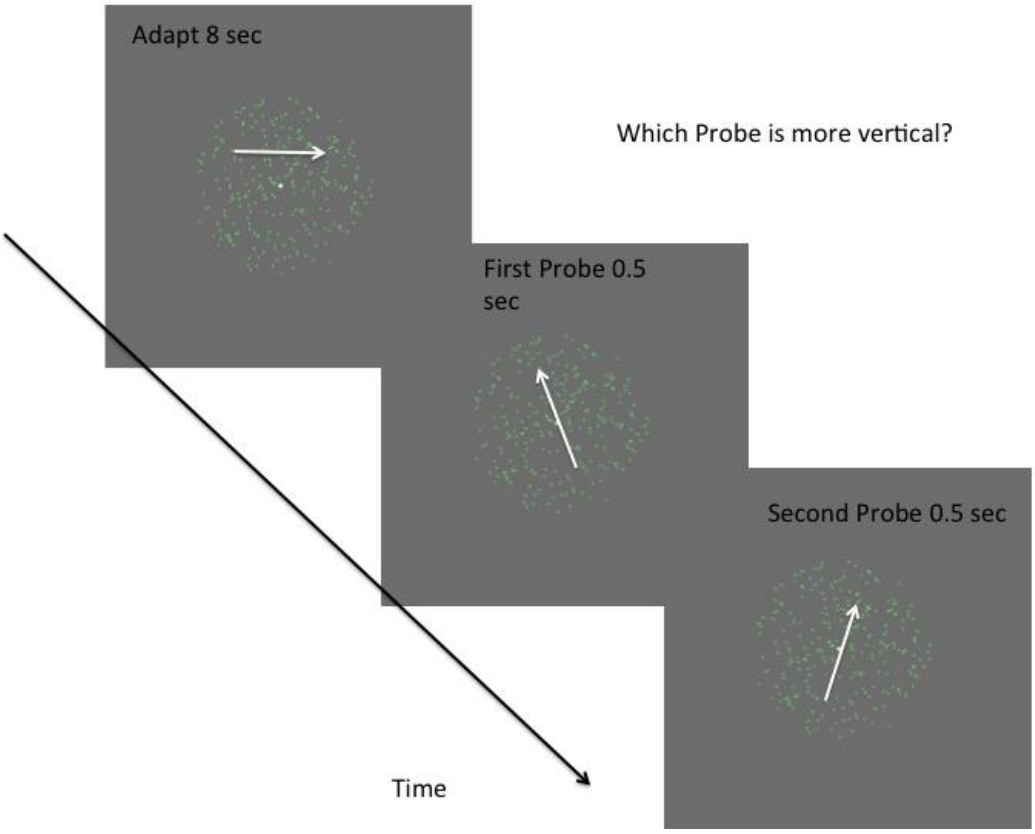

Fig. 1. Schema of the experimental procedure. In experiments with motion transparency, the adapting stimulus was replaced by equal numbers of red and green dots, moving in opposite directions.

Our psychophysical method combines 2AFC with a roving pedestal (Morgan, Melmoth, & Solomon, 2013). This combination is designed to obscure the relationship between our hypotheses and the observer's response. This is advantageous because it prevents simple cognitive biases from masquerading as a true perceptual bias (cf. Morgan, Dillenburger, Raphael, & Solomon, 2012).

Each "adaptor" was followed by two probe stimuli. A 0.2-s delay preceded each 0.5-s probe. Although the two probes moved in slightly different directions (see below), both directions were close to the "reference" direction, which could be either straight up, straight down, left, or right. The observer’s task was to press a key (1 or 2) to indicate which of the two probes appeared to move in a direction closest to the reference direction. We refer to one probe as the "pedestal." Its direction of motion was selected from the pedestal angles $p \in \left\{-10^{\circ},0,10^{\circ}\right\}$, with respect to the reference. The other probe moved in a direction that was the sum of this same pedestal and a "test level," randomly selected from the set $t \in \left\{-16^{\circ},-12^{\circ},-8^{\circ},-4^{\circ},4^{\circ},8^{\circ},12^{\circ},16^{\circ}\right\}$. We refer to this probe as the "test" stimulus. Note that the angles of the two probes could be on opposite sides of the reference. Each of the 8 × 3 × 2 kind of trial was repeated in a random sequence without replacement, making a total of 192 trials per session.

Data from each session were fit with a two-parameter signal-detection model, to obtain values of the observer’s bias (μ) and just-noticeable difference (JND; σ). These correspond intuitively (but not mathematically) to the 50% point and inverse slope of the psychometric function in the Method of Single Stimuli (MSS), as used for example by Blaser et al. (2005).

Signal-detection model

Within the context of signal-detection theory (Green & Swets, 1966), the apparent directions of the two probes can be described by normal distributions *S* and *T*, such that $S \sim N(p + m, s^2/2)$ and $T \sim N(p + t + m, s^2/2)$, where s^2 is the variance of the performance-limiting noise, *p* and *p* + *t* represent the physical directions of drift, and *μ* represents any perceptual bias, such as may be induced by adaptation. Given these definitions, the probability of choosing the pedestal is given by

$$\begin{aligned} \Pr(\text{"S"}) &= \Pr(|S| < |T|) \\ &= \Pr\left(\frac{S^2}{T^2} < 1\right) \end{aligned} . \tag{1}$$

Morgan et al. (2015) noted that S^2/T^2 is a random variable having a doubly noncentral *F*-distribution. Its denominator's noncentrality parameter is $2(p + m + t)^2/s^2$, its numerator's noncentrality parameter is $2(p + m)^2/s^2$, and both denominator and numerator have 1 degree of freedom. However, evaluating the doubly noncentral *F*-distribution can be computationally intensive. Here we provide an equivalent formulation, which can be calculated very quickly:

$$\begin{aligned} \Pr(\text{"S"}) &= \Pr\left(\frac{S^2}{T^2} < 1\right) \\ &= \left(1 + \operatorname{erf}\left[t/(2s)\right]\operatorname{erf}\left[(2m + 2p + t)/(2s)\right]\right)/2 \end{aligned} . \tag{2}$$

The participants were the three authors (MM, JS, KS), four psychophysically experienced colleagues (BD, JF, AJ, NN) not involved in the design of the experiment, and two paid volunteer undergraduates (TP and DP) who were not aware of the purpose of the experiment. Not all participants took part in all experiments.

Experiment 1

The purpose of the first experiment was to measure the size of the orientation repulsion effect using our own methods and stimuli, and to introduce the reader to the analyses used in the subsequent experiments. Observers adapted to a single component moving at 0° (horizontally to the right), and were tested with both upwardly and downwardly moving probes, randomly interleaved within a single session (sampling without replacement). On each trial, after a top-up adaptation, two stimuli were presented in temporal succession and the observer had to report which of them was closer to the vertical. (See **General Methods.**)

Results (Experiment 1)

Examples of the raw psychometric functions from which we derive estimates of bias and JND are shown in Fig. 2. These were derived from a single testing session with one naive observer (TP) comprising 192 trials (3 pedestals × 8 test levels × 2 reference directions × 4 repeats). The first row shows results with one reference direction (90°: see arrow to the right), the second row shows the other reference direction (270°). The vertical axis shows the probability that the observer chooses the pedestal, rather than the test (horizontal axis). The solid symbols show the data, each point being based on only 4 repeats, which explains the quantization of the probability to only 5 levels. The third row shows the data from the first two rows combined, with a reversal of the test and pedestal values of the first row, to take account of the reverse bias expected for the 90 and 270 cases.

The data in Fig. 2 are best summarized within the context of signal-detection theory. Nonetheless, a rough estimate for the size of the motion after-effect can be obtained from inspecting the raw psychometric functions. First consider those obtained with pedestals of zero. With a zero pedestal and a zero test level, we expect the observer to choose the pedestal 50% of the time, even if they have a perceptual bias. Furthermore, if the rightward moving adaptor produces CCW biases (i.e. positive angles) in the observer's percept of both probe stimuli, then the observer should be less likely to choose any particular probe (as more vertical) when an additional CCW angle is added to it. Results in the top row (central panel) are consistent with this prediction. Observer TP invariably selected the pedestal as more vertical, whenever an CCW angle was added to the test. Conversely, probes containing a CW (negative) test level may appear closer to vertical, making observers less likely to select the pedestal. The observer should be least likely to select the pedestal when the cue level is exactly opposite to the observer's bias, and the psychometric function should be symmetric around this value.

Now consider the case where there is a non-zero pedestal. If the pedestal is in the same direction as the observer’s bias, both probes will seem shifted from the vertical by an amount equal to the bias and the pedestal. Test levels in one direction will make the test look more vertical than the pedestal, test levels in the other direction make it look less vertical. Consequently, the psychometric function should be sigmoidal in the region around the point (0, 0.5). See the top right and middle left panels for examples.

Finally, consider the case where the pedestal and bias are in opposite directions. In this case, a small test value (positive or negative) can make the motion of the test indiscriminably different from vertical, and consequently the observer should only rarely select the pedestal. Results of this nature can be seen in the top left and middle right panels.

Inspection of the raw data in Fig. 2 makes clear that adaptation to rightward motion produced a positive (CCW) bias in the perception of upward moving probes (top row of panels) and a negative (CW) bias in the perception of downward moving probes (middle row). Biased functions like these can be compared to the unbiased functions obtained from "non-frame dependent" participants in a rod-and-frame task (see Morgan, et al., 2015, Fig. 3).

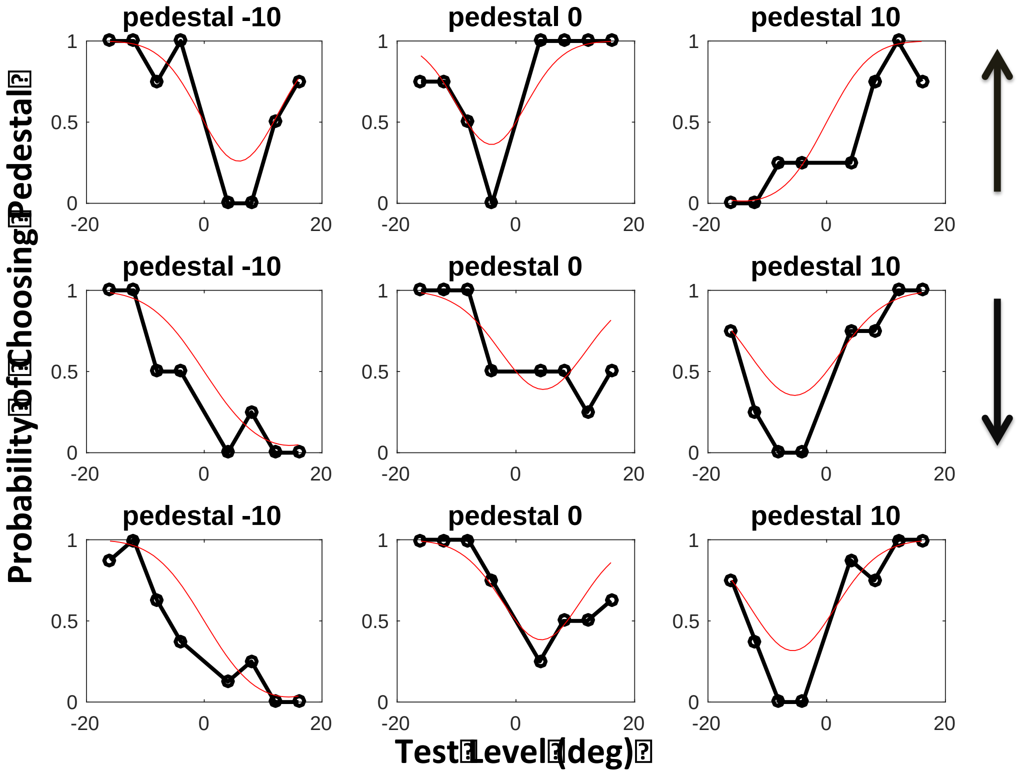

Fig. 2. Psychometric functions obtained from one observer (TP) in Experiment 1. The arrows show the direction of the reference. The bottom row shows the data for the top two rows combined, with reversal of the pedestal and test levels in the top condition. For further explanation see the text. Note that the Test Levels (horizontal axis) are added to the pedestal value in the test stimulus. Positive values are CCW.

Red curves in Fig. 2 show the fit of the signal-detection model. This 2-parameter model was simultaneously fit to all 96 trials depicted in the top row; it was fit again to all 96 trials depicted in the middle row; and finally it was fit to all 192 trials in the bottom row. The results of these fits are summarized in Fig. 3. The sign of the bias is in the direction expected if the probes are repulsed from the 0° adaptor. Thus, upwards moving dots are apparently displaced CCW (positive bias) and downwards moving probes are displaced CW (negative bias). The rightmost bar for each observer shows the net repulsion effect, obtained by combining the same direction of test. This is positive in all observers. One observer (JS) had a large overall CW bias, which inverted the repulsion to an apparent attraction with the upward reference, but his combined data were in the repulsion direction. Values of bias (left-hand panel) and JND (right-hand panel) are quite similar, as is commonly found when applying MSS to the measurement of classical perceptual biases such as the Muller-Lyer (Morgan, Hole, & Glennerster, 1990) and in 2AFC measures of the "rod and frame" effect (Melmoth, Grant, Solomon, & Morgan, 2015). To test whether the biases were significantly different from zero we used a log-likelihood analysis, comparing the two-parameter fit (μ ; σ) to a constrained fit with μ set to zero. Under the null hypothesis (i.e. $\mu = 0$), twice the difference in log likelihoods between the two fits is distributed as X^2 with df=1 (Hoel, Port, & Stone, 1971). Values of this test statistic for the 6 observers were 23.7872, 5.3444, 19.5877, 20.6917, 28.5069, and 8.0290. All these values are larger than that (5.024) required to reject the null hypothesis at the α=0.025 level of significance.

These results confirm the report by Levinson & Sekuler (1976) that there is repulsion of a moving dot stream away from the direction of an orthogonal adapting stream.

Experiment 1

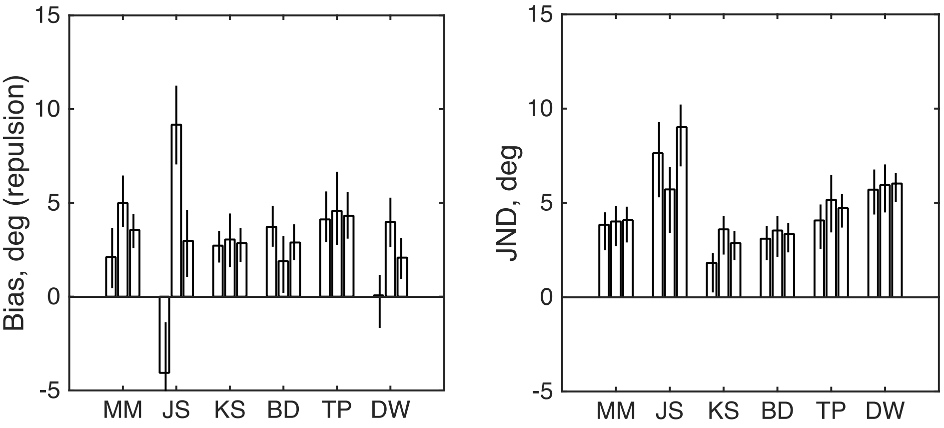

Fig. 3. Results of Experiment 1. The left-hand and right-hand panels show maximum-likelihood estimates of bias (μ) and JND (σ), for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with an upward reference (2) trials with an downward reference, and (3) all trials fit together. Each error bar contains the central 95 percentiles of a parametric bootstrap distribution (sample size: 1600).

Experiment 2

Having confirmed the repulsion effect of Levinson & Sekuler (1976) with our own method, we used it to determine whether there is adaptation to paired motion (Qian, et. al., 1994). Six observers were tested with adaptation to 30/210 (i.e. oblique) adaptors. Two of these six (MM, KS) were, in addition, adapted to 150/330. (See General Methods.) The results for 30/120 were combined with those for 150/330, after reversal of test and pedestal values for the latter, so that a positive bias would represent repulsion. Trials with leftward and rightward references were randomly interleaved. Data were analyzed in the same way as in Experiment 1.

Results (Experiment 2)

Psychometric functions for one observer (MM) are shown in Fig. 4. In this case, unlike Fig. 2, we find the same direction of bias for both reference directions, so the third row shows the results for the first two rows combined, without reversal of sign. Summary results are shown in Fig. 5. All observers show a net bias (bar 3) in the predicted direction, although BD has a strong CCW bias that destroys the symmetry of her data. Test statistics for our log-likelihood analysis were: 127.2109, 35.9124, 32.8900, 2.3710, 40.2409, 10.3021, and 6.9878. Thus we can reject the null hypothesis ($\mu = 0$) for six of our seven observers. A t-test for the significance of the net biases being drawn from a distribution of observers with zero mean gives the result $t(6)=8.47$; p=0.00015.

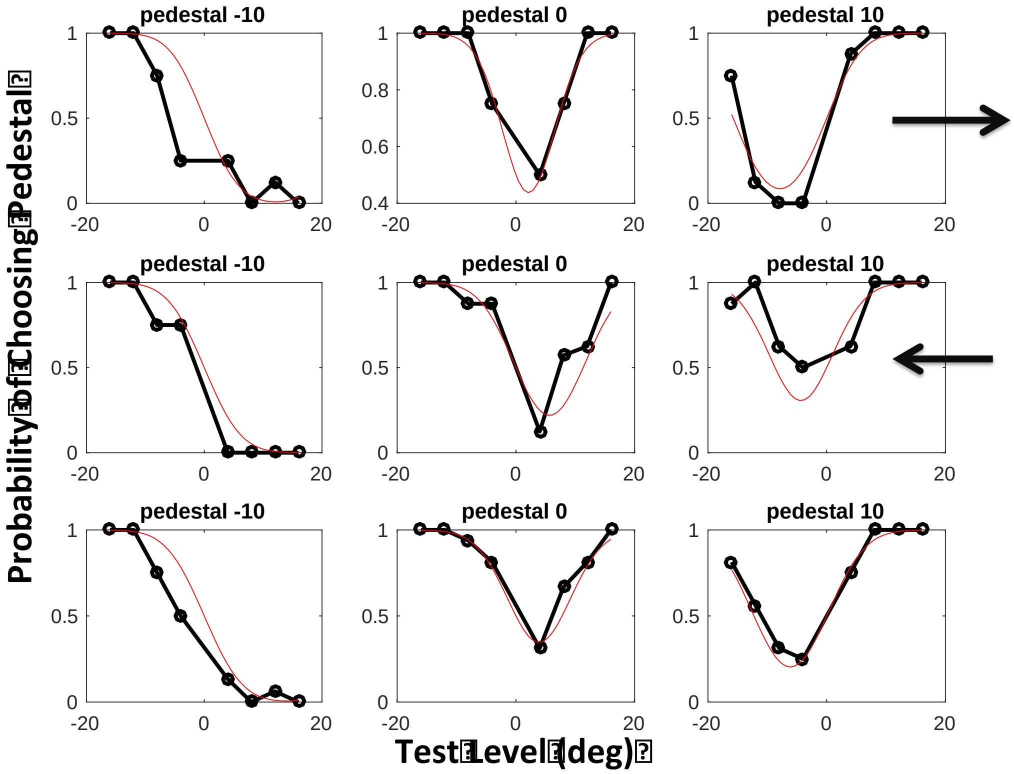

Fig. 4. Psychometric functions obtained from one observer (MM) in Experiment 2, based on a total of 381 trials. The arrows show the reference direction. The bottom row shows the data for the top two rows combined. For further explanation see the text.

Experiment 2: paired motion

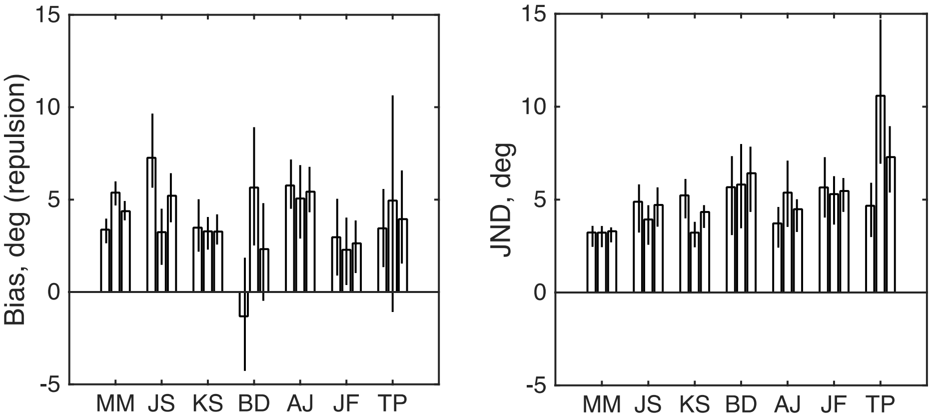

Fig. 5. Results of Experiment 2, in which the adapting stimulus consisted of paired dots moving in opposite directions. The left-hand and right-hand panels show maximum-likelihood estimates of bias (μ) and JND (σ), for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with a rightward reference, (2) trials with a leftward reference, and (3) all trials fit together. Each error bar contains the central 95 percentiles of a parametric bootstrap distribution (sample size: 1600). As in Fig. 3, the μ values are expressed as the angle of repulsion.

Experiment 3

Although the results of the previous experiment may seem compelling evidence for directionally specific adaptation, there is an alternative interpretation based on the static tilt after-effect (Gibson & Radner, 1937; Meese & Georgeson 1996). Indeed, the paired-dot stimulus had a strongly striated appearance, along the axis of motion. These "motion streaks" could have affected the apparent orientation of similar streaks in the probe stimuli, and the latter could have affected judgments of motion direction (Geisler, 1999).

Levinson and Sekuler (1976) discussed this objection to their interpretation of transparent motion adaptation, and rejected it on the cogent grounds that adaptation to a single component direction is directionally specific. For example, adaptation to 120/300 produces CW repulsion of a 90° probe, as does adaptation to 120/120: but adaptation to 300/300 produces no repulsion. If adaptation were based on motion streaks, then 120 and 300 adaptors should have the same effect, since they differ only in direction, not in orientation.

To satisfy ourselves on this point, we replicated Levinson & Sekuler's experiment with three observers (MM, AJ, JS), and obtained the same results (not shown here). However, this rebuttal of streaks is not completely convincing for the case of paired dots, because it is possible that streaks are stronger in this case than for a single direction of moving dots. We therefore designed a stimulus that had a strongly oriented structure but no motion. This consisted of the paired dots used in the previous experiment, but they did not move during their lifetime. Observers BD, AJ, and JF were adapted to 30/120. Observer JS was adapted to 150/330. Observers MM and KS experienced both conditions in different sessions. The results for 30/120 were combined with those for 150/330, after reversal of cue and pedestal values for the latter, so that the overall bias would represent a repulsion. The stimulus had a strongly striated appearance, as would be expected from a Glass pattern (Glass, 1969), but had no motion along the axis of the striations. Such motion as there was in the pattern was orthogonal to the striations, arising from the nonuniform distribution of motion energy imposed by the orientation structure (c.f. Morgan & Tyler, 1995, who used a cylindrical lens to study the Pulfrich effect with random dynamic noise).

Results (Experiment 3)

The summary results are shown in Figure 6. For only one of the six observers (KS, who had a strong overall CW bias) was the net bias significantly different from zero. (Values of the test statistic for the log-likelihood analysis were 0.9485, 3.2081, 8.5696, 1.2002, 0.0056, and 0.9527.) A group *t*-test showed that the difference from zero was not significant: $t(5)=1.582$, p=0.1745. This was in contrast to the paired motion case [Experiment 2; $t(5)=7.12$; p=0.00084]. Another paired *t*-test showed that the difference between the two experiments in those observers who did both was also significant: $t(5)=4.644$; p=0.0056. We conclude that the adaptation found with moving, paired dots is unlikely to be explained by the static tilt after-effect.

Experiment 3: Glass Patterns

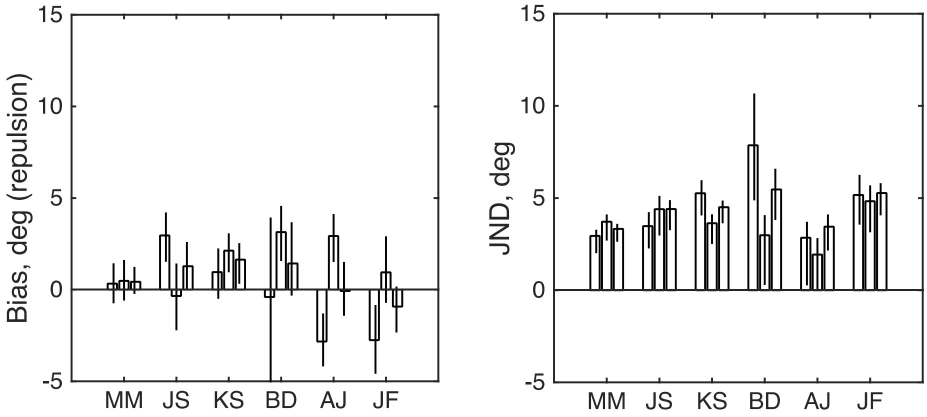

Fig. 6. Results of Experiment 3, in which the adapting stimulus consisted of stationary, paired dots. The left-hand and right-hand panels show maximum-likelihood estimates of bias (μ) and JND (σ), for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with a rightward reference, (2) trials with a leftward reference, and (3) all trials fit together. Each error bar contains the central 95 percentiles of a parametric bootstrap distribution (sample size: 1600).

Experiment 4

Blaser et al. (2005) described directionally specific repulsion of a 90° probe, following adaptation to both a transparent and a paired-dot stimulus with 0/180 components. This adaptation is unexpected, because the two components should cancel out. However, the two sets of moving dots were colored red and green, and the adaptation was found to be color-specific. We tried to repeat this result using our own stimuli and psychophysical methods. We adapted to a 0/180 transparent stimulus of rightwards-moving green dots (0°)

and leftwards-moving red dots (180°). Next we tested with interleaved upwards (90°) and downwards (270°) references, exactly as in Experiment 1. (For a demo see Supplementary Material **DemoAdaptTransTestRedandGreen.mp4.)** In separate sessions, the probe dots were either red or green. If there were a color-contingent motion adaptation effect from a transparent stimulus, we would find opposite directions of repulsion with the two different probe colors.

Fig. 7 shows three bars for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with a upward reference, (2) trials with a downward reference, and (3) all trials fit together. Results for the two colours are combined with appropriate sign reversal so that a positive effect indicates repulsion. Clearly, there was no significant net bias. Values of the test statistic for the log-likelihood analysis were 2.2334, 0.1068, 0.0061, 0.0567, and 0.9399. Thus we cannot reject the null hypothesis (μ = 0) for any of our five observers.

We conclude that our psychophysical technique does not produce any evidence for significant color-specific, directionally selective motion adaptation from a transparent stimulus.

Experiment 4 Red-Green Transparent Motion

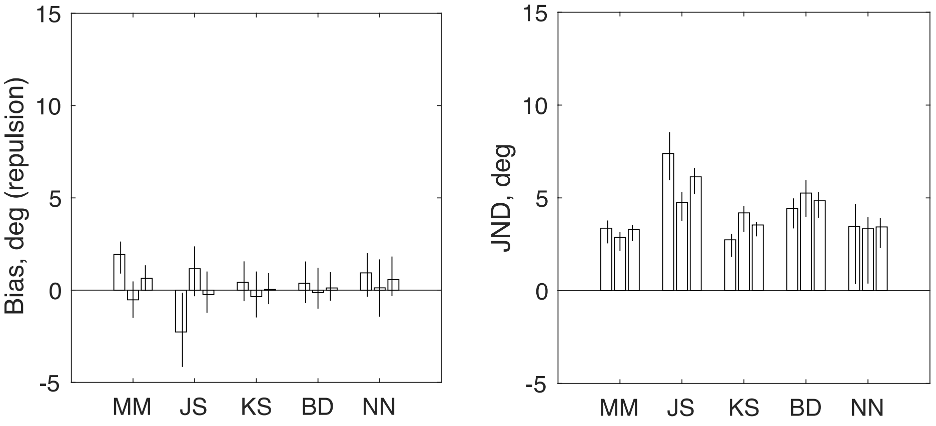

Fig. 7. Results of Experiment 4. The left-hand and right-hand panels show maximum-likelihood estimates of bias (μ) and JND (σ), for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with an upward reference, (2) trials with a downward reference, and (3) all trials fit together. Trials with green probes and red probes have been combined. Each error bar contains the central 95 percentiles of a parametric bootstrap distribution (sample size: 1600).

Experiment 5

We wondered whether Blaser et al. (2005) obtained a color-contingent adaptation by involuntarily attending to one of the components in the adapting stimulus. After attending to red, for example, there might be an adaptation specific to the movement direction of the adapting red dots. This would be a direction-specific adaptation, not a color-specific effect. Just such an effect has been reported (Lankheet & Verstraten, 1995), albeit it with a different stimulus array and a different psychophysical procedure. (They used

MSS to find the null point in the signal-to-noise ratio.) To examine this possibility, we repeated Experiment 5 but with attention to one component of the transparent stimulus. Observers attempted to follow the motion of either the green or the red dots "in the mind's eye" but without actually tracking. We admit that these instructions are not very precise, and could elicit a number of different strategies, such as attempting to follow individual dots attentively, or attending to a particular apparent depth plane. We verified informally with the EYELINK recorder that observers were not tracking the target. In blocks with ATTEND TO RED the probe stimuli were red. In blocks with ATTEND TO GREEN they were green. Thus, a possible direction-specific adaptation was confounded with a possible color-contingent adaptation, as in the Blaser et al. experiment. (Though not, we think, in Lankheet & Verstaten, 1995, where the color of the probes was not the same as that of the attended component.)

Results (Fig. 8) showed no significant net effect of attended color on adaptation. Values of the test statistic for the log-likelihood analysis were 1.5563, 0.0711, 2.9851, 0.6382, 3.5382, and 3.841 for the 5 observers (MM, JS, KS, BD, TP). Thus we cannot reject the null hypothesis (μ = 0) for any of our five observers.

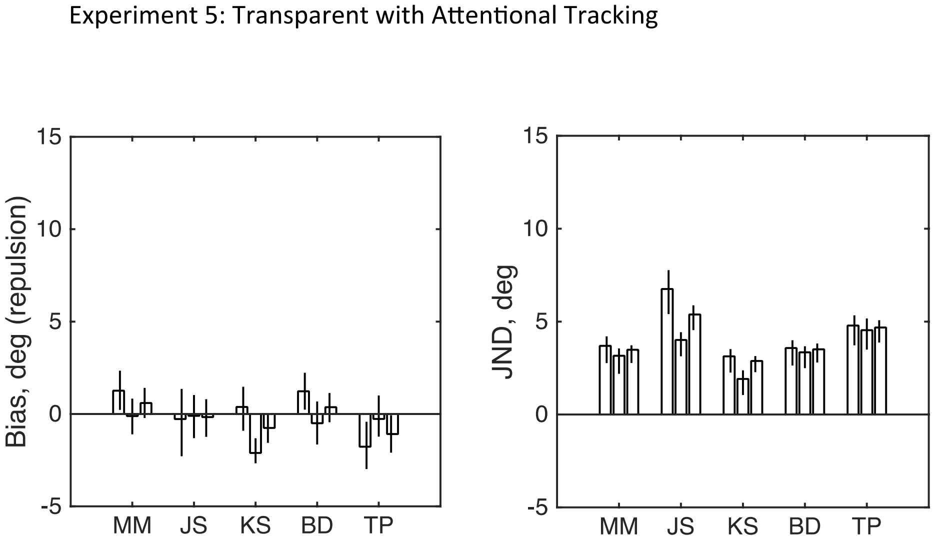

Fig. 8. Results of Experiment 5. The left-hand and right-hand panels show maximum-likelihood estimates of bias (μ) and JND (σ), for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with a rightward reference, (2) trials with a leftward reference, and (3) all trials fit together. Trials with attend-to-green and attend-to-red probes have been combined. Each error bar contains the central 95 percentiles of a parametric bootstrap distribution (sample size: 1600).

Experiment 6

A possible explanation of adaptation to transparent motion is pursuit eye tracking (see Discussion). To test the possible role of tracking, we adapted observers to a transparently moving stimulus, while they were instructed to pursue a white fixation point moving with the same velocity as of one of its components. The actual movement of the fixation point was a saw-tooth; it moved instantaneously to the left-hand side of the circular aperture (Fig. 1), when it reached the right-hand edge.

Fig. 9 shows the results for observers MM, JS, KS, BD, AJ, JF, and TP. All observers showed an aftereffect in the expected direction (repulsion from the direction of tracking). Values of the test statistic for the log-likelihood analysis were 31.7869, 16.6479, 1.4562, 106.4826, 16.3963, 20.7043, and 4.5260. Thus we can reject the null hypothesis ($\mu = 0$) for 6 of our observers, but not for KS. Overall, despite the high variance between observers, the data can reject the null hypothesis that the 7 observers are drawn from a population with mean of zero [$t(6)=2.55$, p=0.0437].

Experiment 6: Transparent with Pursuit

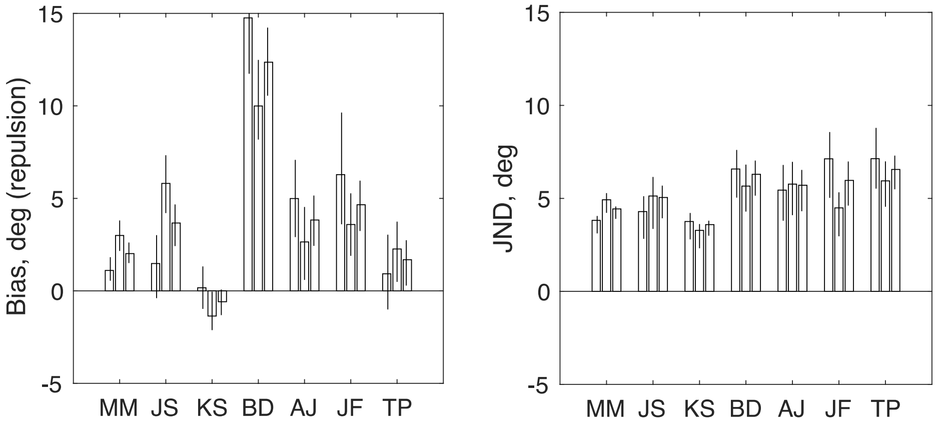

Fig 9. Results of Experiment 6. The left-hand and right-hand panels show maximum-likelihood estimates of bias (μ) and JND (σ), for each observer. From left to right, the three bars for each observer show estimates derived from (1) trials with an upward reference, (2) trials with a downward reference, and (3) all trials fit together. Each error bar contains the central 95 percentiles of a parametric bootstrap distribution (sample size: 1600).

Discussion

The results of our first experiment (Experiment 1) confirm the finding by Levinson and Sekuler (1974) that a horizontal moving adaptor causes repulsion in orthogonal probes (0° and 270°). The results of our Experiment 2 support the claim by Blaser et al. (2005) that motion adaptation can be produced by a paired-dot stimulus (Qian, et al., 1994). We found that a 30/210 paired-dot adaptor caused directional repulsion in both 0° and 180° moving probes. The finding of adaptation to paired motion, added to the further finding by Levinson and Sekuler that adaptation to one component of a transparently moving stimulus is no weaker than to a single component, gives strong psychophysical support to the two-stage model of motion processing (Adelson & Movshon, 1982; Movshon & Newsome, 1996). According to the two-stage model, elaborated to include adaptation, V1 neurons respond to one component of paired-dot or transparently moving stimuli as if the other component were absent. V1 neurons also adapt to their input (Kohn & Movshon, 2003), and these two facts taken together imply that they would adapt to paired-dot and transparent stimuli, as we and Sekuler and Levinson found. MT neurons, on the other hand, merely inherit their adaptation from V1, and they combine, to a greater or lesser extent, motion in opposite directions within their receptive field. This is generally held to explain why paired-dot stimuli are not seen to move, although the linking hypothesis here has not been made clear or justified. Presumably it is that perception should be linked more to later stages in a processing hierarchy than to earlier, because later stages are closer the response buttons or tongue.

On the other hand, our results (Experiment 4) did not confirm the factual basis for the claim (Blaser, et al. 2005) that there is repulsion of a 90° probe from both components of a 0/180 paired-dot adaptor. Such repulsion would not be expected from our logic, since the two adapting components would cancel out. Blaser et al. attempted to prevent this cancellation by making the oppositely moving dots of different colors, and testing with single colors. Since our experiment was a conceptual replication (Schmidt, 2009) rather than an exact replication we cannot be certain why our results are different. Differences include the psychophysical method (2AFC rather than MSS, which has one stimulus and two possible responses), statistical methods of analysis, the use of colors that appeared equally salient to the observer, rather than equiluminous, and the absence in our experiment of stationary dots of the opposite color to the moving probe, which were present in Blaser et al.

Differences in the outcomes of different psychophysical procedures have already been noted elsewhere and perhaps deserve more attention. Mather & Sharman (2015) have argued that the claim for adaptation based on imagining the adaptor (Winawer, Huk, & Boroditsky, 2010) depends on response bias with the MSS. When the decision was changed from "which direction is the probe moving" to "in which half of the stimulus array is there coherent movement," the effect of a imaginary adaptor disappeared. Similarly, using a 2AFC procedure, Morgan (2014) failed to find spatiotopic adaptation of tilt adaptation, which had been reported by Turi & Burr (2012) using the MSS. In another example, again using 2AFC, Morgan (2014) failed to find an effect of attentional load during motion adaptation, which had been reported by Taya, Adams, Graf, and Lavie (2009) using the MSS. On the other hand, there are good reasons for rejecting response bias as an explanation for the paired-motion findings of Blaser et al. (2005), since they showed that participants were unable to report the association between color and motion in a forced-choce task.

Concerning statistical procedures, we have little to say. Blaser et al. (2005) present only group data in their paper. Individual psychometric functions were not analyzed, and the significant result applies to the group data (Blaser, personal communication). It is possible therefore, that some observers, including those that were naïve, did not show a significant effect. This is an important difference from our analysis, which considers the observers separately, except where we report population *t*-tests.

Although our manipulation of attention did not produce a directional after-effect, Lankheet and Verstraten's (1995) manipulation of attention did. The reason for this discrepancy remains unclear. One possibility is that our observers used a less effective strategy for maintaining one component "in the mind's eye." Another obvious difference is that we used a directional repulsion effect, while Lankheet & Verstraten (1995) measured the dynamic motion after-effect with a signal-noise ratio method.

We tried informally to find a dynamic motion after-effect after attending to transparent red-green motion, by using probes comprised of stationary dots. (Each dot had a limited lifetime of 5 frames.) This produced a clear motion after-effect after adaptation to a single direction (red dots only; see **DemoAdaptRedTestDVN.mp4**); but all we could see after transparent adaptation (**DemoAdaptTransTestDVN.mp4**), with or without selective attention, was the vague motion orthogonal to the axis of adaptation predicted (and found) by Grunewald and Lankheet (1996). The generality of the attention-contingent adaptation clearly needs further investigation. Raphael, Dillenburger, & Morgan (2010) examined the effect using transparent streams of expanding/contracting black/white dot streams. An effect was found, but it was noisy and inconsistent over observers. The main effect was a massive, idiosyncratic bias towards reporting "expanding" or "contracting."

Another possible mechanism for the after-effect of transparent motion is pursuit tracking of one of the two components. It is known that tracking of a moving texture can produce a compelling motion after-effect opposite to the direction of tracking, even though the tracking tends to stabilize the moving stimulus on the retina (Anstis & Gregory, 1965). Both an extra-retinal motion signal (Freeman, Sumnall & Snowden, 2003) and adaptation to the stationary background (Morgan, Ward, & Brussel, 1976) may be involved. Tracking was not controlled in the experiments of Blaser et al. (2005) and Lankheet and Verstraten (1995), and is thus a possible explanation of the positive findings. However, in a different kind of after-effect due to attentional tracking, Verstraten, Hooge., Culham, & van Wezel (2001) found no evidence that involuntary pursuit was involved, so we cannot assert that pursuit is a general explanation for adaptation following attentional tracking. Nor did we find an after-effect of tracking in all our observers (only 6 out of 7 observers in

Experiment 6). Future experiments on adaptation to transparent motion, and experiments on "attention" to motion generally, clearly ought to control for pursuit eye movements.

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Supplementary Material

Demonstration Movies. The mp4 movies available at https://owncloud.sf.mpg.de/index.php/s/KltJeAUADngWadO show representations of the stimuli used in the experiments. These are not identical to the actual stimuli. The frame rate is nominally 50 Hz instead of the 75 Hz used in the experiments, and the colors will depend on the viewing platform. Colors should be adjusted if possible so that red and green dots are equally salient. All the movies were designed to be viewed in a repetitive loop: adapt-probe-probe-adapt-probe-probe-adapt….

DemoAdaptRedTestRed.mp4 shows the basic 2AFC design used in the experiments. The adapting stimulus (5 s) consists of red dots moving at 30°, with a limited lifetime of 5 frames. This is followed, after a 0.2-s blank interval, by the two probe stimuli (0.5 s each), in sequence. In this case, the first and second probes move with angles of 5° and –5°, respectively. Although they are equally far from the horizontal (0°), the probes should look asymmetrical following adaptation, with the 5° stimulus appearing roughly horizontal and the –5° stimulus shifted clockwise.

DemoAdaptTransTestRedandGreen.mp4 presents an adaptor consisting of red and green dot streams moving in opposite directions. This is followed by red probes, moving in the same direction as the adapting red dots. As in the previous movie, these probes are moving at +5° and –5°, respectively. The adaptor is then repeated, and followed by green probes. If there were a color-contingent adaptation, the red probes would appear to move in different directions from the green probes.

DemoAdaptRedTestDVN.mp4 presents a single-direction red adaptor, followed by tests of dynamic visual noise, consisting of stationary but limited-lifetime (5 frame) probes. The probes should appear to drift in the opposite direction to the adaptor.

DemoAdaptTransTestDVN.mp4 is similar to the previous movie, but the adaptor consists of red and green dots moving in opposite directions. This is followed by two red probes. The adaptor is then repeated and followed by two green probes. The probes may show a drift in the opposite direction to one of the adapting components because of unequal luminance balance, but the question is whether this direction is different for the differently colored probes. Another question is whether the apparent direction of the probes is altered by attending to one of the differently colored adapting components (Lankheet & Verstraten, 1995). Another effect that may be observed is transparent motion in the tests, orthogonal to the adapting axis (Grunewald & Lankheet, 1996).