



The direction aftereffect is driven by adaptation of local motion detectors

William Curran ^{a,*}, Colin W.G. Clifford ^b, Christopher P. Benton ^c

^a School of Psychology, Queen's University of Belfast, Belfast, BT7 1NN, UK

^b School of Psychology, The University of Sydney, NSW 2006, Australia

^c Department of Experimental Psychology, University of Bristol, Bristol, BS8 1TN, UK

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Abstract

The processing of motion information by the visual system can be decomposed into two general stages; point-by-point local motion extraction, followed by global motion extraction through the pooling of the local motion signals. The direction aftereffect (DAE) is a well known phenomenon in which prior adaptation to a unidirectional moving pattern results in an exaggerated perceived direction difference between the adapted direction and a subsequently viewed stimulus moving in a different direction. The experiments in this paper sought to identify where the adaptation underlying the DAE occurs within the motion processing hierarchy. We found that the DAE exhibits interocular transfer, thus demonstrating that the underlying adapted neural mechanisms are binocularly driven and must, therefore, reside in the visual cortex. The remaining experiments measured the speed tuning of the DAE, and used the derived function to test a number of local and global models of the phenomenon. Our data provide compelling evidence that the DAE is driven by the adaptation of motion-sensitive neurons at the local-processing stage of motion encoding. This is in contrast to earlier research showing that direction repulsion, which can be viewed as a simultaneous presentation counterpart to the DAE, is a global motion process. This leads us to conclude that the DAE and direction repulsion reflect interactions between motion-sensitive neural mechanisms at different levels of the motion-processing hierarchy.

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1. Introduction

Adaptation-induced aftereffects are ubiquitous in the human visual system, occurring across a range of basic visual attributes, including orientation (Clifford, 2002; Gibson & Radner, 1937; Wenderoth & Johstone, 1988), curvature (Gibson, 1933), spatial frequency (Blakemore, Nachmias, & Sutton, 1970), and motion direction (Clifford, 2002, 2005; Kohn & Movshon, 2004; Levinson & Sekuler, 1976; Patterson & Becker, 1996; Schrater & Simoncelli, 1998); and even extend to more complex stimuli, such as faces (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Watson &

Clifford, 2003; Webster & MacLin, 1999). In almost all of these cases,¹ adaptation to the relevant stimulus characteristic (say orientation or direction of motion) causes the perceived difference between a subsequently viewed test stimulus and the adapting stimulus to be greater than their physical difference. Take the direction aftereffect as an example. After adapting to a unidirectional motion, and then being presented with a test stimulus whose direction differs from the adapting stimulus by (say) 30°, observers report the adaptor-test direction difference to be as great as 40°–60° (Levinson & Sekuler, 1976; Schrater & Simoncelli, 1998).

¹ While the tilt aftereffect is typically repulsive, 'attractive' aftereffects have been reported for very small and very large adapting-test orientation differences.

* Corresponding author.

E-mail address: w.curran@qub.ac.uk (W. Curran).

The debate surrounding the functional significance of adaptation typically falls into two camps. On the one hand, it has been argued that adaptation-induced aftereffects are caused by ‘fatigue’ of neurons sensitive to the adapting stimulus (Sutherland, 1961), and that such aftereffects expose a design fault of the visual system. More recent explanations view aftereffects as being a consequence of the system reducing its sensitivity to redundant information (i.e. unchanging components of the signal), thus freeing up valuable neural resources for coding any changes that may occur in the environment (Mather & Harris, 1998; Clifford, 2005). The former, ‘fatigue’ explanation is almost certainly incorrect for a number of reasons. First, cortical adaptation has been found to show a degree of pattern specificity (Movshon & Lennie, 1979), rather than simply depending on the adapting neuron’s response rate as predicted by the fatigue model; second, the time taken to recover from adaptation in some visual aftereffects can be quite different to that expected from neural fatigue (Stromeyer, 1978); and third, it cannot account for storage of the MAE when testing does not immediately follow adaptation (Spigel, 1962).

Many repulsive effects observed following adaptation can also be obtained without prior adaptation by simultaneously presenting the test and ‘inducing’ stimulus. The simultaneous counterpart to the tilt aftereffect is the tilt illusion, and direction repulsion is the simultaneous counterpart to the direction aftereffect. That many aftereffects have a simultaneous-presentation counterpart raises the question of whether an aftereffect and its simultaneous counterpart are expressions of similar neural mechanism(s). Again, take the direction aftereffect (DAE) as an example. The phenomenon is direction tuned, such that the effect peaks at an adaptor-test direction difference of approximately 30°–40° (Levinson & Sekuler, 1976; Patterson & Becker, 1996; Schrater & Simoncelli, 1998). Its simultaneous-presentation counterpart, direction repulsion, shows direction tuning peaking at an inducer-test direction difference of 20°–45° (Braddick, Wishart, & Curran, 2002; Marshak & Sekuler, 1979; Mather & Moulden, 1980). Another striking similarity is that both phenomena have been reported to exhibit ‘direction attraction’ for very small and very large inducer-test direction differences (Braddick et al., 2002; Schrater & Simoncelli, 1998). Such tuning similarities are consistent with, but are not confirmatory of, the notion that both the DAE and direction repulsion reflect activity of similar mechanisms. More extensive comparisons are required before we are in a position to categorically state that these two phenomena are driven by similar or different neural interactions. One way of testing whether or not this is the case is to determine at which level of visual processing the two phenomena occur.

There is considerable evidence that motion processing is a hierarchical process in which the initial extraction of local motion measures are followed by a ‘pooling’ of these measures at a later global-processing stage (Morrone, Burr, & Vaina, 1995; Albright, 1984; Welch, 1989). One might ask ‘at which of these two levels—local or global—are the DAE

and direction repulsion induced?’ A number of studies have, either directly or indirectly, asked this question of direction repulsion. Grunewald (2004) failed to find that direction repulsion exhibits interocular transfer, therefore suggesting that the phenomenon is monocular in origin. Because monocular-driven cortical neurons do not exist beyond area V1, whose neurons have small receptive fields, Grunewald’s findings support the notion of direction repulsion being driven by local motion detector adaptation. However, it should be noted that Grunewald used very sparse dot stimuli (dot density = 1 dot/deg²) to avoid binocular rivalry (binocular rivalry describes how, when presented with different information to each eye, the different retinal inputs arriving at the cortex compete to dominate perception). Kim and Wilson (1997) avoided this rivalry problem by presenting a central test stimulus to one eye and a surrounding inducing stimulus to the other. They found robust interocular transfer of direction repulsion with this centre-surround configuration. Furthermore, the fact that the effect persisted for non-overlapping moving patterns suggests that direction repulsion may occur after the pooling of local motion measurements.

The apparent uncertainty in the psychophysical literature regarding the locus of direction repulsion is reflected in the neural modeling literature, which, depending on the model you choose, supports either the local motion approach (Hiris & Blake, 1996; Nawrot & Blake, 1991) or the global motion position (Kim & Wilson, 1996, 1997; Wilson & Kim, 1994). In Blake et al.’s model, direction repulsion is generated by inhibitory interactions at the level of motion-sensitive units involved in local-motion processing. These units are described as monocular and as having comparatively small receptive fields, and they can be identified with neurons in primary visual cortex. In contrast, Wilson and Kim proposed that direction repulsion is a consequence of inhibitory interactions between pattern unit detectors. Physiological studies (Albright, 1992; Movshon, Adelson, Gizzi, & Newsome, 1986) have identified primate middle temporal (MT) neurons that have response characteristics similar to Wilson and Kim’s pattern units; thus Wilson and Kim’s model predicts that direction repulsion is a consequence of inhibitory interactions between MT neurons.

We have recently found that, when using a mixed-speed inducer, direction repulsion magnitude is determined by the global speed of the inducing stimulus (Benton & Curran, 2003). This provides compelling evidence that global motion interactions play a major role in driving direction repulsion. In contrast to direction repulsion, there has been relatively little research asking where in the motion-processing hierarchy the DAE is induced. While Patterson and Becker’s finding (1996) that the DAE persists under stereoscopic viewing conditions places the DAE’s locus somewhere in visual cortex, we are aware of only one study which attempts to identify the cortical location of the adaptation underlying the DAE. Kohn and Movshon (2004) report that motion adaptation changes the direction tuning

of macaque MT neurons, and that these tuning shifts are consistent with the perceived repulsive nature of the DAE; however they find that this is not the case for V1. Extrastriate area MT contains predominantly motion-sensitive neurons with larger receptive fields than the V1 neurons projecting to them (Snowden, 1994), suggesting that an important role of this area is to extract global motion information by pooling local motion signals arriving from V1. Thus Kohn and Movshon's data suggests that neuronal adaptation underlying the DAE may occur at the global motion processing level.

The following series of experiments seeks to elucidate further at which stage of motion extraction—local or global—the DAE is induced. Our first experiment reveals that the effect undergoes interocular transfer, thus confirming that it involves the adaptation of binocular cells. The remaining experiments employ 'speed-tuning', 'mixed-speed' and 'speed-notch' paradigms in an attempt to tease apart the role that local and global direction sensitive mechanisms have in inducing the DAE. We will show that, unlike direction repulsion, the DAE is driven by adaptation at the local motion extraction stage.

2. Experiment 1: Interocular transfer of the direction aftereffect

2.1. Observers

Three naïve observers and one of the authors participated in the experiment.

2.2. Apparatus and stimuli

The adaptor and test stimuli were random dot kinematograms (RDK), presented within circular apertures (7.96 deg^2), with each RDK containing equal numbers of black and white dots against a mean luminance background. Dot diameter was 1.9 arc. min. Dot density in each stimulus was set to 64 dots/ deg^2 . Stimuli were presented on a Sony G520 monitor. Mean luminance was 33.6 cd/m^2 , and viewing distance was 138 cm. The monitor was driven by a Cambridge Research Systems VSG 2/5 graphics board at a framerate of 120 Hz. Stimuli were viewed using a mirror stereoscope, allowing us to control which eye(s) the adapting and test stimuli were presented to.

2.3. Procedure

During the initial motion adaptation phase (60 s duration) observers were presented with a random dot stimulus moving either 45° to the left or 45° to the right of vertical (upwards) at a constant speed of 5.0 deg/s . The adaptor direction chosen (left or right from vertical) was the same for all subsequent top-up phases. Both adaptor and test stimuli had a central spot to help maintain fixation. In the test phase immediately following adaptation, observers had to judge whether the subsequent test stimulus (speed

2.5 deg/s ; duration 200 ms) was moving left or right of vertical. Test phases alternated with adaptation 'top-up' phases of 10 s duration. The test stimulus motion direction was chosen by an adaptive method-of-constants procedure (adaptive probit estimation), a method that dynamically updates the set of stimuli being presented depending on the observer's previous responses (Treutwein, 1995; Watt & Andrews, 1981). The stimulus values are selected to optimize the estimation of the 'point of subjective equality' (PSE), in our case the direction the test stimulus was moving when it was perceived as moving vertically up. All pairwise adaptor-test eye combinations were tested; i.e. adapt left–test left, adapt left–test right, adapt right–test left, and adapt right–test right. In any given block of trials, the 'test eye' conditions (same as or different to the 'adaptor eye') were randomly interleaved. The interval between switching adaptor eye was at least 2 h. Half the psychometric functions were generated following adaptation to motion 45° clockwise to vertical up, and half were generated following adaptation to motion 45° counter-clockwise to vertical up; thus controlling for any potential difference between subjective and objective measures of vertical. Observers generated up to eight psychometric functions per condition (monocular and interocular),² with each psychometric function being derived from 64 trials.

2.4. Results and discussion

Fig. 1a. plots example psychometric functions obtained from one of the observers. Psychometric functions denoted by the solid and dashed lines are for the monocular and interocular conditions, respectively. The psychometric functions to the left of centre were obtained from those conditions in which the adaptor moved 45° to the left of vertical up; and psychometric functions to the right of centre are from those conditions in which the adaptor moved 45° to the right. Fig. 1b plots DAE magnitude for the same observer when adaptor and test stimuli are viewed by the same eye and by different eyes. The first thing to note is that interocular transfer (IOT) occurs for the direction aftereffect, thus confirming that the effect is mediated by binocular cell adaptation. The second point of note is that DAE magnitude is visibly reduced in the interocular condition relative to the monocular condition. When taken as a ratio of the DAE magnitude under monocular viewing, DAE interocular transfer is approximately 63–75%. (CB 63.4% SE ± 6.3 ; SD 66% SE ± 7.8 ; CC 73.1% SE ± 15.7 ; DA 75% SE ± 4.9 SE). Given that partial IOT of aftereffects is considered to reflect adaptation at early cortical stages of motion processing (Nishida & Ashida, 2000), this incomplete transfer of the DAE points to the possibility that it may occur before the extraction of global motion signals. The remaining experiments sought to investigate this issue.

² Two observers generated 8 psychometric functions per condition, and two generated 4 psychometric functions per condition.

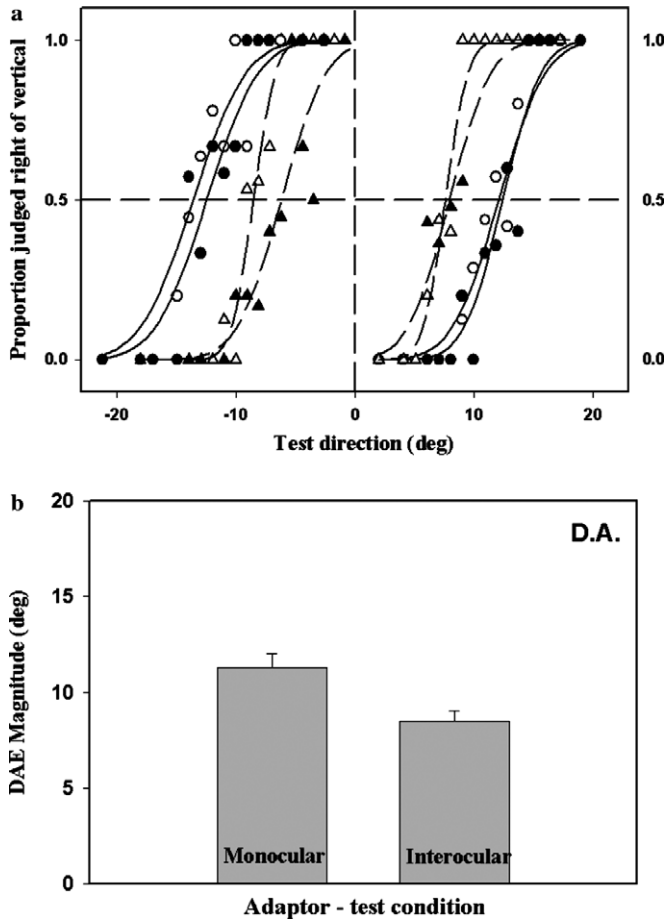


Fig. 1. (a) Example psychometric functions from one observer in experiment 1, and (b) the monocular and interocular DAE calculated from the functions. Solid lines plus circles and dashed lines plus triangles are for the monocular and interocular conditions, respectively. Negative and positive x -axis values denote directions to the left and right of vertical up. The psychometric functions to the left of centre in 1a were obtained using an adaptor moving 45° to the left of vertical up; psychometric functions to the right are from those conditions in which the adaptor moved 45° to the right. Error bars in this and subsequent figures are ± 1 standard errors of the PSEs.

3. Experiment 2: Speed tuning of the direction aftereffect

In a similar vein to our earlier research on direction repulsion (Benton & Curran, 2003; Curran & Benton, 2003), Experiments 3 and 4 measure the DAE induced by mixed-speed adaptor stimuli. In order to interpret the data accurately, a necessary pre-requisite is to measure to what extent the DAE is speed tuned.

3.1. Observers

Four observers, two authors and two naïve, participated in this experiment.

3.2. Procedure

As in the previous experiment observers adapted to a random dot pattern moving $\pm 45^\circ$ from the vertical

(upwards), with both adaptor and test stimuli centred on a fixation spot. Stimulus aperture size and dot density were identical to Experiment 1. Unlike in Experiment 1, observers viewed the stimuli binocularly. Observers were tested with adaptor stimulus speeds ranging from 0.625 to 15.5 deg/s. Test stimulus speed remained fixed throughout the experiment at 2.5 deg/s. The interval between testing with different adaptor speeds was at least 2 h. The observers' task was the same as in Experiment 1.

3.3. Results

Fig. 2 plots direction aftereffect magnitude as a function of adaptor speed, which is similar for all four observers. The data clearly demonstrate an inverted U-shaped speed tuning function of the DAE,³ which peaks between adaptor speeds of 2.5 and 5 deg/s, and which is well described by a log-Gaussian function. This is reminiscent of the speed tuning of direction repulsion reported previously (Curran & Benton, 2003).

The non-linear character of the DAE speed tuning allows us to test directly whether the DAE is a local or global motion phenomenon. Previous research has shown that the perceived speed of a mixed-speed stimulus lies close to the mean of the component speeds (Watamaniuk & Duchon, 1992), a finding which we have replicated (Benton & Curran, 2003). If the DAE occurs after the extraction of global motion it follows that, if one uses a mixed-speed adaptor, DAE magnitude will be determined by the mean speed of the adaptor. Furthermore, increasing the range of speeds present in the adaptor, while keeping mean speed constant, should have no effect on DAE magnitude. If the DAE occurs before global motion extraction, at the level of local motion processing, there are a number of possible local models. These range from a local-maximum model, in which DAE magnitude is determined by the dot speed which produces the greatest DAE; to a local-minimum model, in which DAE magnitude is determined by the dot speed which produces the weakest DAE. There is any number of intermediate models in which DAE magnitude is determined by some weighted speed average. Of course it is not possible to test all the possible perturbations of local DAE models. We have, therefore, restricted ourselves to testing the local minimum, local maximum, and a simple local-mean model which predicts that DAE magnitude is determined by the mean DAE induced by the local speeds in the adaptor. In the latter case DAE magnitude will be predicted by first calculating, from individual speed tuning functions, the DAE of each speed in the mixed-speed stimulus and then averaging these calculations. The remaining experiments attempt to test which, if any, of the above models (local and global) best accounts for the DAE.

³ It should be noted that the peak of the function is likely to be strongly influenced by where the test speed is positioned. For the purposes of the follow-up experiments, the important point is that the speed tuning is non linear when the test speed is kept fixed.

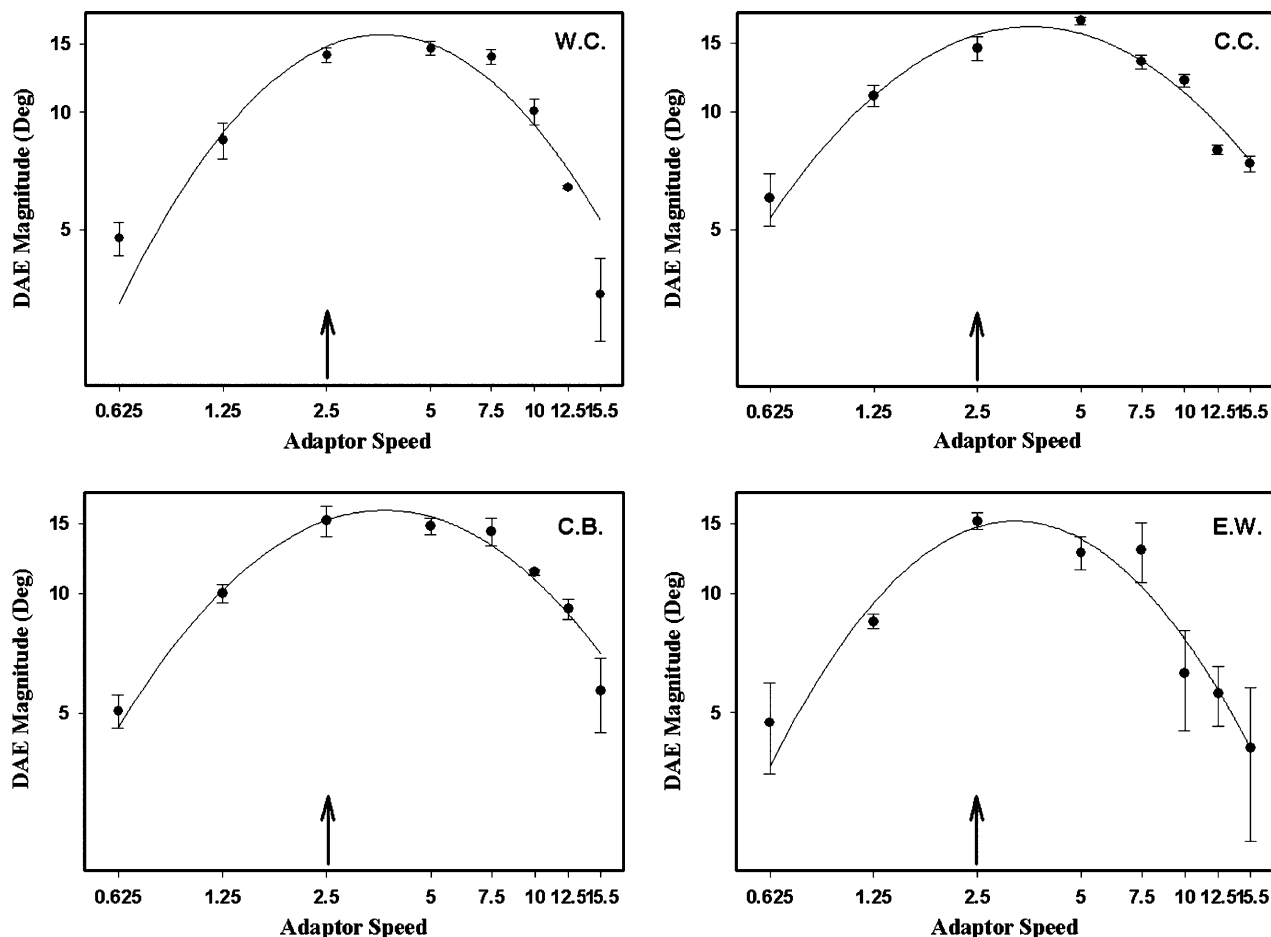


Fig. 2. Direction aftereffect magnitude plotted as a function of adaptor speed for four observers. The test speed was 2.5 deg/s (highlighted by the arrow), and the adaptor speed was set to 0.625, 1.25, 2.5, 5.0, 7.5, 10.0, 12.5, or 15.5 deg/s. The solid lines show log-Gaussian functions fitted to the data. Each datum point is the mean of four PSEs.

4. Experiment 3: Mixed-speed adaptor stimuli and DAE magnitude

4.1. Procedure

The same four observers from Experiment 2 participated in this experiment. Again, as in Experiment 2, the test stimulus speed remained fixed at 2.5 deg/s. The adaptor speed, however, contained dots whose speeds were drawn from one of five rectangular speed distribution widths (in which all speeds within a defined range had equal probability). Each adaptor speed distribution was centred on 5 deg/s; thus ensuring that all five adaptors moved at the same mean speed. The distribution widths were 0°, 2°, 4°, 6°, and 8°. In the zero degree speed distribution stimuli all dots moved at 5 deg/s; in the 8° speed distribution dot speeds were evenly spread between 1 and 9 deg/s.

4.2. Results

Fig. 3a plots DAE magnitude (filled circles) as a function of speed distribution. Included in this figure are DAE magnitude predictions based on three possible local-DAE

models, in which perceived DAE is determined by the local maximum DAE (upper dashed line), the local minimum DAE (lower dashed line), or a local-mean DAE (middle dashed line). Each of the three local predictions was made using the parameters from the curve fit to the data in Experiment 2. The solid line plots the DAE magnitude which would be predicted if it were driven by global motion adaptation. There is little to distinguish between the predictions of the global, local-mean, and local-maximum models; all of which essentially predict that DAE magnitude should be relatively unaffected by increasing adaptor speed distribution. A local-minimum model, on the other hand, predicts a rapid decrease in DAE magnitude as speed distribution is increased. The data obtained from the observers are essentially flat; thus ruling out a local minimum explanation. They do not, however, distinguish between the other two local models and the global model. We therefore repeated the experiment, but this time centred the adaptor speed distributions on the 10 deg/s point of the speed tuning function. Shifting the speed distribution to this point on the tuning curve results in the global and local-maximum models making radically different predictions.

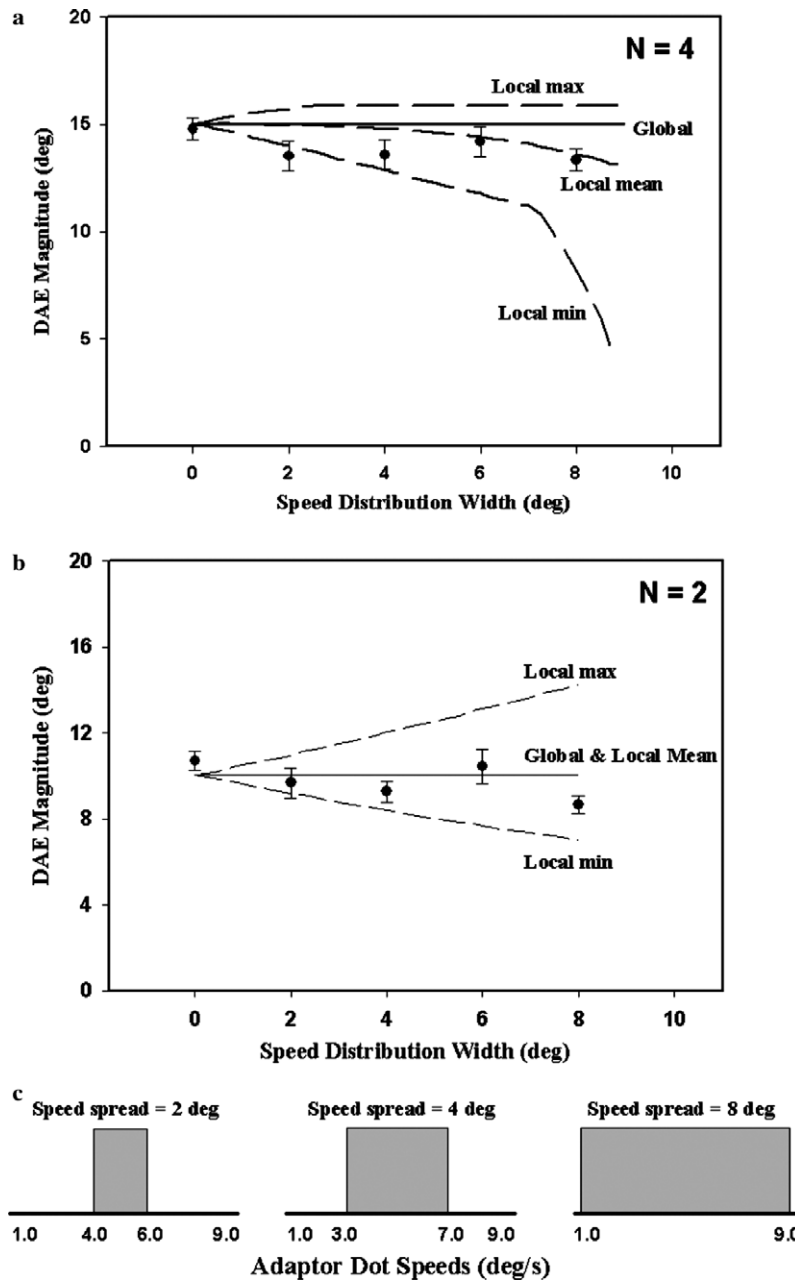


Fig. 3. (a) The results of Experiment 3, in which DAE magnitude was measured as a function of varying the ‘speed distribution’ of dots in the adaptor stimulus. Mean dot speed was kept fixed at 5 deg/s. Dot speeds in the adaptor stimulus were evenly sampled from one of five speed distributions widths; 0°, 2°, 4°, 6°, and 8°. The upper, middle, and lower dashed lines plot the DAE magnitude as a function of speed distribution predicted by a local-maximum, local-mean, and local-minimum model of the DAE, respectively. The solid line plots DAE predictions based on a global motion model of the DAE. The pattern of results rules out a local-minimum model explanation for the DAE. (b) The results of the second part of Experiment 3, which used five speed-distribution adaptors whose mean speed was fixed at 10 deg/s. Note that the global motion model (solid line) and the local-mean model make identical predictions. The data lie close to these predictions, thus ruling out both the local-minimum and local-maximum models. (c) Schematic representation of three speed distribution adaptors with a mean speed of 5 deg/s. Dot speeds were evenly spread over the gray speed ranges shown.

Data from two observers, one an author the other naïve, are plotted in Fig. 3b. Note that the local minimum and maximum predictions rapidly diverge from the global and local-mean models as a function of speed distribution. The local-mean and global model predictions, on the other hand, are identical. Again, the data reveal that DAE magnitude remains constant as speed distribution is increased.

The combined data from Fig. 3a and b clearly rule out both the local minimum and local-maximum models. However, they do not distinguish between the global and local-mean models. In the final experiment, we introduced a speed notch to the adaptor stimulus’s speed distribution in order to tease apart the predictions of the local-mean and global models.

5. Experiment 4: Using a ‘speed notch’ adaptor to disentangle local and global predictions

5.1. Procedure

In this experiment, the adapting stimulus contained dots travelling at speeds ranging from 1 to 9 deg/s; i.e. the stimuli had a speed distribution of 8° centred on 5 deg/s. As an additional manipulation we removed a central range of speeds from the adaptor and measured DAE magnitude as a function of the width of this ‘speed notch’ (see Fig. 4b). The speed notch width ranged from 0° to 4°. In the 0° speed notch condition dot speeds were evenly distributed between 1 and 9 deg/s. In the 4° speed notch condition, dot speeds were evenly distributed between 1 and 3 deg/s, and between 7 and 9 deg/s (see Fig. 4b). As in previous experiments, the test stimulus speed remained fixed at 2.5 deg/s.

5.2. Results

Fig. 4a plots DAE magnitude as a function of speed notch size. Included in the plot are the DAE predictions made by the local and global models. Note that the local-mean model and the global model, which are of particular interest in this experiment, predict very different patterns of

DAE with increasing speed notch width. While the global model predicts that DAE magnitude will be unaffected by the speed notch manipulation, the local-mean model predicts that DAE magnitude will decrease monotonically with increasing speed notch width. The perceived DAE magnitude (filled circles) follows a pattern which is very similar to that predicted by the local-mean model.

Two potential objections against the local-mean model may be raised at this point. First, it could be argued that the DAE is, in fact, a global motion processing phenomenon and that our data are a consequence of observers’ global motion percepts being compromised by the presence of a notch in the adapting speed distribution. However, this would not explain the observed similarity between the local model prediction and DAE magnitude under the zero speed notch condition. Second, one might ask whether it is reasonable to expect a global speed signal generated from a stimulus containing a distribution of speeds to be as strong or as effective an adaptor to a stimulus that has all elements moving at the same speed. It has previously been demonstrated that the perceived speed of a mixed-speed stimulus is equal to the mean speed of the stimulus components (Watamaniuk & Duchon, 1992). Furthermore, we have reported identical direction repulsion effects when using either a single speed distractor or a mixed-speed distractor,

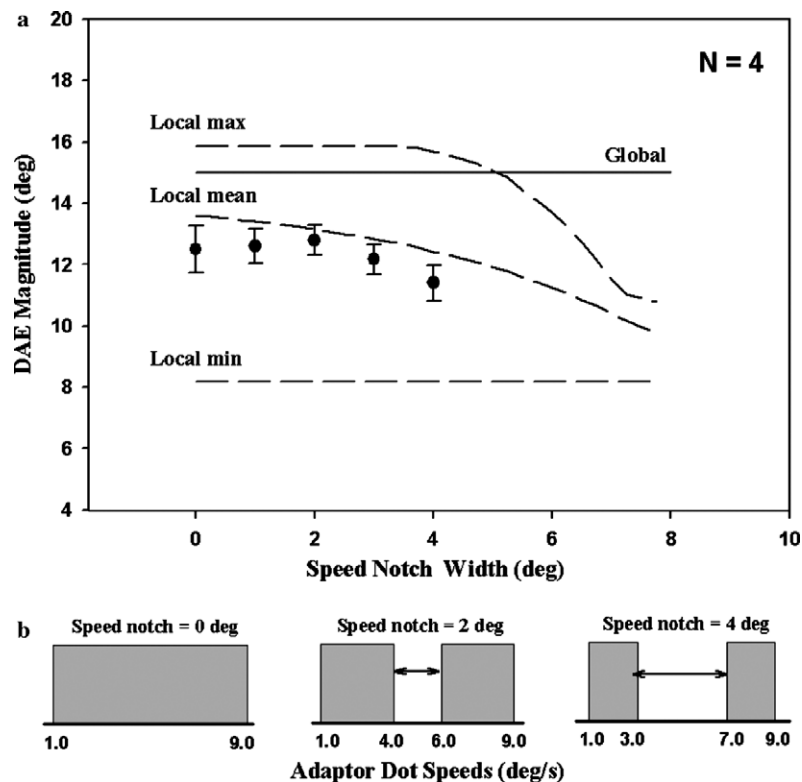


Fig. 4. (a) The results of experiment 4, in which DAE magnitude is plotted as a function of speed notch width. The speed distribution of the adaptor dots was centred on 5 deg/s, and the DAE was measured using five speed notch values; 0°, 1°, 2°, 3°, and 4°. As in previous figures, the dashed and solid lines plot DAE magnitude predicted by the local and global models. The data are most consistent with the local-mean model. (b) Schematic representation of the adaptor speeds used in the speed notch experiment. Each dot within the adaptor was assigned a velocity, which was kept for the duration of the stimulus. The dot speeds were evenly spread over the gray speed ranges shown in the figure. An adaptor with a speed range of 1.0 to 9.0 deg/s and a speed notch of 4° would contain dot speeds evenly spread between 1.0 and 3 deg/s and between 7 and 9 deg/s.

with the former adaptor assigned the mean speed of the latter (Benton & Curran, 2003). These previous findings suggest that it is reasonable to expect mixed-speed and single speed stimuli to be equally effective adaptors.

6. Discussion

The experiments reported in this paper are an attempt to identify at which level of motion processing—local or global—adaptation driving the DAE occurs. Reported similarities between the DAE and its simultaneous presentation counterpart (direction repulsion) are suggestive of a common neural mechanism underlying both phenomena. For instance both phenomena are direction tuned and peak at similar inducer–test direction differences (Levinson & Sekuler, 1976; Schrater & Simoncelli, 1998; Marshak & Sekuler, 1979; Braddick et al., 2002). The results of our ‘speed-tuning’ experiment (Experiment 2) add to these similarities between the two phenomena by revealing that, like direction repulsion, speed tuning of the DAE is well described by a log-Gaussian function. Previous research in our labs has demonstrated that interactions between neural mechanisms sensitive to global-motion play a major role in driving direction repulsion (Benton & Curran, 2003). We decided to use a similar approach in ascertaining whether the DAE is driven by adaptation of local or global motion detectors.

If the DAE is an expression of adapted global motion mechanisms, then the mechanisms in question should be binocularly driven; consequently one would expect the phenomenon to exhibit interocular transfer. While the presence of interocular transfer would not rule out a local-motion-adaptation account of the DAE, its absence would certainly rule out a global-motion explanation. The results of our first experiment clearly demonstrate that the DAE does exhibit interocular transfer, and establish that the underlying adapted neural mechanisms are binocularly driven. That the interocular transfer found in this experiment was partial suggests that the effect may be mediated by neural adaptation as early as V1; this in turn suggests that the direction aftereffect may reflect adaptation of local motion detectors.

The log-Gaussian functions fit to the data from Experiment 2, which marks out the speed tuning of the DAE, were used to predict DAE magnitude based on three local models and a global model. The results of Experiment 3 clearly rules out two of the local models—the local-maximum model and the local-minimum model - but fail to differentiate between a global motion account and the remaining local-motion account, the local-mean model. A ‘speed notch’ paradigm was used in the final experiment in an attempt to tease apart the DAE magnitude predicted by the global model and the local-mean model. While the global model predicted that DAE magnitude would be unaffected by removing an increasingly wider central band of speeds from a speed-distribution adaptor stimulus, the local-mean model predicted a monotonic decrease in DAE magnitude as a function of the speed notch increase. Our data reveal an effect of speed notch on DAE magnitude very similar to

that predicted by the local-mean model. It could be that the global model, which assumes a single global motion, is incomplete; particularly when testing it with stimuli containing large speed notches. With small speed notches an adaptor stimulus appears to contain one global speed; however, if the speed notch is sufficiently large, the stimulus takes on the appearance of two transparently moving global speeds (Bravo & Watamaniuk, 1995).

The clear implication of these experiments is that direction repulsion and the direction aftereffect, which have similar direction and speed tuning characteristics, are nonetheless driven by adaptation of neural mechanisms at different levels of motion processing. We have demonstrated previously that direction repulsion is driven by adaptation of global motion mechanisms. Although the results presented here do not directly identify the cortical level at which the DAE occurs, they clearly demonstrate that the DAE is not determined by the global motion of the inducer. Rather, it seems as if the local motion information is driving the effect. We therefore conclude that the direction aftereffect is driven by adaptation of local-motion detectors, adaptation which occurs before the pooling of local motion signals into a global-motion signal.

As pointed out in the introduction there has been only one previous attempt to identify at which stage of motion processing adaptation underlying the DAE occurs (Kohn & Movshon, 2004). While their results are suggestive of the DAE being driven by adaptation of MT neurons, Kohn and Movshon note that, their data can also be modelled by weakening feedforward input from V1 into a recurrent model of MT circuitry. This account assumes that adaptation in V1 weakens the input to those MT cells providing recurrent excitation more than it weakens the input to inhibitory MT cells. The results from the experiments reported here support this latter interpretation.

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