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Short Communication

Changes in Perceived Speed Following Adaptation to First-order and Second-order Motion

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To investigate whether or not adaptation to second-order motion can cause changes in perceived speed, measurements of perceived speed were obtained for two varieties of motion: (i) contrast-modulated two-dimensional static noise (second-order motion); and (ii) luminance-modulated noise (first-order motion). The test stimulus (either first-order or second-order) was presented to one side of a central fixation spot and a comparison stimulus (always first-order) was simultaneously presented on the opposite side. The observer's task was to indicate which of the two motion stimuli appeared to drift faster. The perceived speed of the test stimulus was measured with and without prior adaptation to motion on one side of the fixation spot only (that of the test stimulus). The modulation depth of the adaptation stimulus was always half that of the test stimulus and all test patterns were equated for visibility. The pattern of results for second-order motion was similar to that for first-order motion. Typically, adaptation reduced perceived speed, particularly when the adaptation speed was faster than the test speed. However, when the adaptation speed was low relative to the test speed, increases in perceived speed were found. Cross-over adaptation effects between first-order and second-order motion were also observed. Robust velocity aftereffects were found for second-order motion when the noise was dynamic or was high-pass filtered, suggesting that first-order (luminance) artifacts were not responsible for the velocity aftereffects observed. We conclude that the perceived speeds of first-order and second-order motion appear to be encoded in human vision using similar computational principles (but not necessarily utilizing the same mechanism), since the same pattern of results was found for the two varieties of motion. Copyright © 1996 Elsevier Science Ltd

First-order motion   Second-order motion   Adaptation   Perceived speed

INTRODUCTION

First-order motion is defined by spatiotemporal translation of the luminance or colour distribution across the retinal image. In the luminance domain the mechanisms that encode first-order motion have been successfully modelled as detectors that either act as filters oriented in space–time (or spatiotemporal frequency) [e.g. Adelson & Bergen (1985)], or measure intensity gradients over space and time [e.g. Marr & Ullman (1981)]. Second-order (Cavanagh & Mather, 1989) or non-Fourier motion (Chubb & Sperling, 1988), however, is defined not by spatiotemporal variations in luminance or colour but variations in derived image parameters such as contrast, flicker rate and disparity.

In the case of stimuli that give rise to second-order motion but do not contain any systematic cues to image motion in the luminance domain [e.g. the "drift-balanced" stimuli described by Chubb & Sperling (1988)], the responses of first-order motion detectors will be ambiguous. Current computational models of second-order motion perception utilize similar principles to those employed in models of first-order motion processing but incorporate one or more additional processing stages that serve to expose second-order motion to conventional motion analysis. These models fall into two classes. Firstly, it has been suggested that first-order and second-order motion are detected by separate, but qualitatively similar, mechanisms operating in parallel [e.g. Chubb & Sperling (1988); Derrington & Badcock (1985); Werkhoven *et al.* (1993); Wilson *et al.* (1992)]. Secondly, it has been proposed that first-order and second-order motion are detected by the same mechanism (Johnston *et al.*, 1992).

Recent psychophysical and physiological evidence suggests that first-order and second-order motion are initially encoded by separate mechanisms (Harris & Smith, 1992; Mather & West, 1993). For example, Ledgeway and Smith (1994) found that observers were

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unable to integrate the frames of a multiframe motion sequence in which the frames alternated between sinusoidal variations in luminance (first-order) and similar variations in contrast (second-order), suggesting that first-order and second-order motion are initially detected by separate mechanisms. However, some motion phenomena such as the coherence of plaid patterns containing both first-order and second-order components (Stoner & Albright, 1992) and cross-adaptation effects between first-order and second-order motion patterns (Holliday & Anderson, 1994; Ledgeway, 1994; Turano, 1991) suggest that the two types of motion are combined at some stage in the visual system. Wilson *et al.* (1992) have developed a model based upon this scheme, in which the outputs of separate first-order and second-order motion-detecting pathways are pooled to compute the resultant direction of local motion. The general processing scheme embodied within this model is consistent with the response properties of some motion-sensitive cells in feline cortex (Zhou & Baker, 1993).

Although many experiments have investigated the mechanisms that encode the direction of second-order motion, few studies have addressed the factors which govern the perceived speed of second-order motion. However, recent attempts have been made to clarify this issue [e.g. Johnston & Clifford (1995); Ledgeway & Smith (1995a); Witt *et al.* (1994)]. Ledgeway and Smith (1995a) found that although the perceived speed of a contrast-modulated (CM) noise image was typically slower than that of a luminance-modulated (LM) image of the same physical speed, when the stimuli were equated for visibility their perceived speeds were identical. They also reported that the perceived speed of second-order motion is dependent on the stimulus modulation depth in a manner analogous to that of conventional luminance gratings (Stone & Thompson, 1992; Thompson, 1982).

In the luminance domain adaptation techniques have proved to be valuable for studying speed coding. Prolonged exposure to the motion of conventional gratings can alter the perceived speeds of subsequently viewed test patterns [e.g. Thompson (1981); Smith (1985)]. For example, Smith and Edgar (1994) found, in agreement with previous studies, that the perceived speed of test gratings could be reduced by up to 60% following adaptation to gratings drifting in the same direction with similar or higher speeds. They also reported robust increases in perceived speed (up to 150%) when the adaptation speed was low, the test speed high and both gratings drifted in the same direction. Similar but more moderate effects were found when the adaptation and test stimuli had opposite directions of drift. They interpreted these results in terms of a model in which speed sensitivity emerges by comparing the levels of activity in two broadly-tuned, overlapping temporal frequency channels, one low-pass and the other band-pass. The effect of adaptation is to reduce the sensitivity of each temporal mechanism in direct proportion to its sensitivity to the adaptation stimulus.

Although the mechanisms that encode the direction of second-order motion are susceptible to adaptation, as revealed by direction-specific threshold elevation [e.g. Ledgeway & Smith (1992); Turano (1991)] and biases in the perceived direction of dynamic test patterns (Ledgeway, 1994; McCarthy, 1993; Nishida *et al.*, 1994), it is not known if post-adaptation biases in perceived speed, similar to those found for first-order motion stimuli, can be induced with second-order motion stimuli. In the present study we sought to address this issue by conducting a speed-matching experiment using a spatial two-alternative forced-choice (2AFC) task to measure the perceived speeds of second-order and first-order motion stimuli both prior to and following adaptation to motion. All possible combinations of first-order and second-order adaptation and test patterns were examined in order to compare same-adaptation and cross-adaptation effects. Perceived speed measurements were obtained for a range of adaptation and test speed combinations.

METHODS

Observers

Two observers participated in the main experiment and both had normal or corrected-to-normal acuity. Observer T.L. was one of the authors and observer S.M.C. was a paid volunteer who was unaware of the purpose of the experiment. The second author (A.T.S.) also served as an observer for a number of subsidiary (control) measurements (see Discussion).

Apparatus and stimuli

The apparatus and stimuli were essentially identical to those used in a previous study and a full description can be found in Ledgeway and Smith (1995a). A general description of the apparatus and stimuli employed in the present paper is given below.

Two motion stimuli were presented simultaneously to horizontally adjacent parts of the observer's field of view. One motion stimulus was composed of either CM (second-order motion stimulus) or LM (first-order motion stimulus) two-dimensional static noise and was displayed on a MANITRON monochrome monitor with a refresh rate of 100 Hz and white (P4) phosphor. The other motion stimulus, which was always a first-order sine grating, was displayed on a X–Y display (HP1332A with white P4 phosphor) at an update rate of 122 Hz. The two displays were gamma-corrected and each had a mean luminance of *ca* 30 cd/m^2. Independent control of the spatial frequencies, contrasts, drift directions and drift speeds of the two motion stimuli was possible. Each motion stimulus subtended an angle of 6 × 6 deg and was viewed binocularly at a distance of 0.67 m. A small fixation spot was located at the centre of the observer's field of view, between the two images.

The first-order motion stimuli contained two-dimensional static noise in order to control for any possible confounding effects of the noise present in the second-order images on their perceived speeds. The motion stimuli were generated in real-time using the following techniques. Two-dimensional static noise was produced by randomly assigning elements (groups of image pixels) to be either "black" or "white" with probability 0.5. The size of the static noise elements was 6 × 6 arc min and the mean Michelson contrast of the noise was 0.5. LM noise was produced by the addition of a vertically oriented sine grating of spatial frequency 1 c/deg with noise. This resulted in an image in which the luminance of the noise was spatially modulated in the horizontal dimension. The luminance modulation could be made to drift at any desired speed, either leftwards or rightwards, by displacing the sinusoid prior to addition with the noise, which remained stationary. CM noise was produced in a similar manner with the exception that the static noise was multiplied by, rather than summed with, the drifting 1 c/deg sinusoid. For the purposes of multiplication the sinusoid was unsigned (range 0 to +1) and the noise was signed (range −1 to +1).

For the second-order motion stimuli the amplitude of the sinusoidal modulation in noise contrast (contrast modulation depth) could be varied in the range 0.0–1.0 defined as:

$$\text{modulation depth} = (C_{\max} - C_{\min})/(C_{\max} + C_{\min})$$

where $C_{\max}$ and $C_{\min}$ are the maximum and minimum local contrasts, respectively, in the image. In a similar manner the amplitude of the modulation in noise luminance for the first-order motion stimuli (luminance modulation depth or contrast) could be varied in the range 0.0–0.5 defined as:

$$\text{modulation depth} = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$$

where $L_{\max}$ and $L_{\min}$ are the maximum and minimum luminances, respectively, in the image averaged over adjacent pairs of noise elements of opposite polarity.

Procedure

To measure the effects of adaptation on perceived speed, a method similar to that used in previous studies [e.g. Smith & Edgar (1994); Thompson (1981)] was employed. This involved presenting an adaptation stimulus (either LM noise, CM noise or, in control conditions, an unmodulated noise field) in one half of the observer's visual field only: either to the left or right of the fixation spot. Following adaptation, speed matches were measured by means of a 2AFC procedure involving the simultaneous presentation of a test motion stimulus (either LM or CM noise) and a comparison motion stimulus (always LM noise) to different parts of the observer's field of view. The test motion stimulus was always presented in the same half of the visual field as the adaptation stimulus and the comparison motion stimulus was presented in the other (unadapted) half of the visual field. As aftereffects are confined to the region of the visual field where adaptation occurs, this arrangement made it possible to assess the effect of adaptation by comparison with a motion stimulus that was unaffected by adaptation. The adaptation and test motion stimuli always had the same direction of drift (either rightward or leftward) but the test and comparison motion stimuli always drifted in opposite directions towards the fixation spot in order to facilitate fixation.

All possible combinations of first-order and second-order motion adaptation and test patterns were examined in order to compare same-adaptation and cross-adaptation effects on perceived speed. The suprathreshold visibilities of the first-order and second-order motion stimuli were equated approximately by presenting them at the same multiple of their individual direction-identification thresholds. The modulation depth of the second-order motion test stimulus (the stimulus to which the observers were least sensitive) was fixed at 1.0* and the modulation depths of the first-order test and comparison stimuli were scaled (0.4 for T.L. and 0.52 for S.M.C.) so that they were presented at the same multiple (*ca* 30) of threshold. In line with previous studies [e.g. Thompson (1981); Smith & Edgar (1994)] the modulation depths of the adaptation stimuli were always half those of the test stimuli (in terms of multiples of threshold), in order to avoid reduction of the perceived modulation depth of the test stimulus which might in itself cause a reduction in perceived speed.

At the beginning of each run of 30 trials, the adaptation stimulus was presented for 1 min. This was followed by a brief inter-stimulus-interval during which an homogeneous blank field (luminance 30 cd/m^2) was presented for 0.5 sec and then the test and comparison motion stimuli were presented simultaneously for 1 sec. This was immediately followed by a homogeneous blank field and a tone to indicate to the observer that a response was required. The observer's task was to indicate, using one of two response buttons, which of the two motion stimuli presented during the test phase appeared to be drifting faster. Adaptation was then "topped-up" for 5 sec, before the test and comparison motion stimuli were presented again, and so on.

Six drift speeds were used for the adaptation motion stimuli (1.25, 2.5, 5.0, 10.0, 15.0 and 20.0 deg/sec) and the test stimuli had one of two drift speeds (either 2.5 or 15.0 deg/sec). Within any one run of trials the drift speeds of the adaptation and test motion stimuli were constant but the drift speed of the first-order motion comparison stimulus on each trial was determined by a PEST routine (Taylor & Creelman, 1967) which tracked the 50% performance level (i.e. the drift speed at which the perceived speeds of the test and comparison motion stimuli were equal). For half of the runs of trials, the adaptation and test stimuli were presented to the left of the comparison stimulus and for the remaining runs the

*The modulation depths of the test stimuli drifting at 2.5 or 15 deg/sec were the same (1.0) when they were presented at the same multiple of threshold because in line with previous studies that have used similar stimuli [see Ledgeway & Smith (1995a) Fig. 3] we found that sensitivity to both first-order and second-order motion composed of static broadband carriers is approximately flat for 1 c/deg stimuli drifting below about 15 Hz but thereafter decreases rapidly.

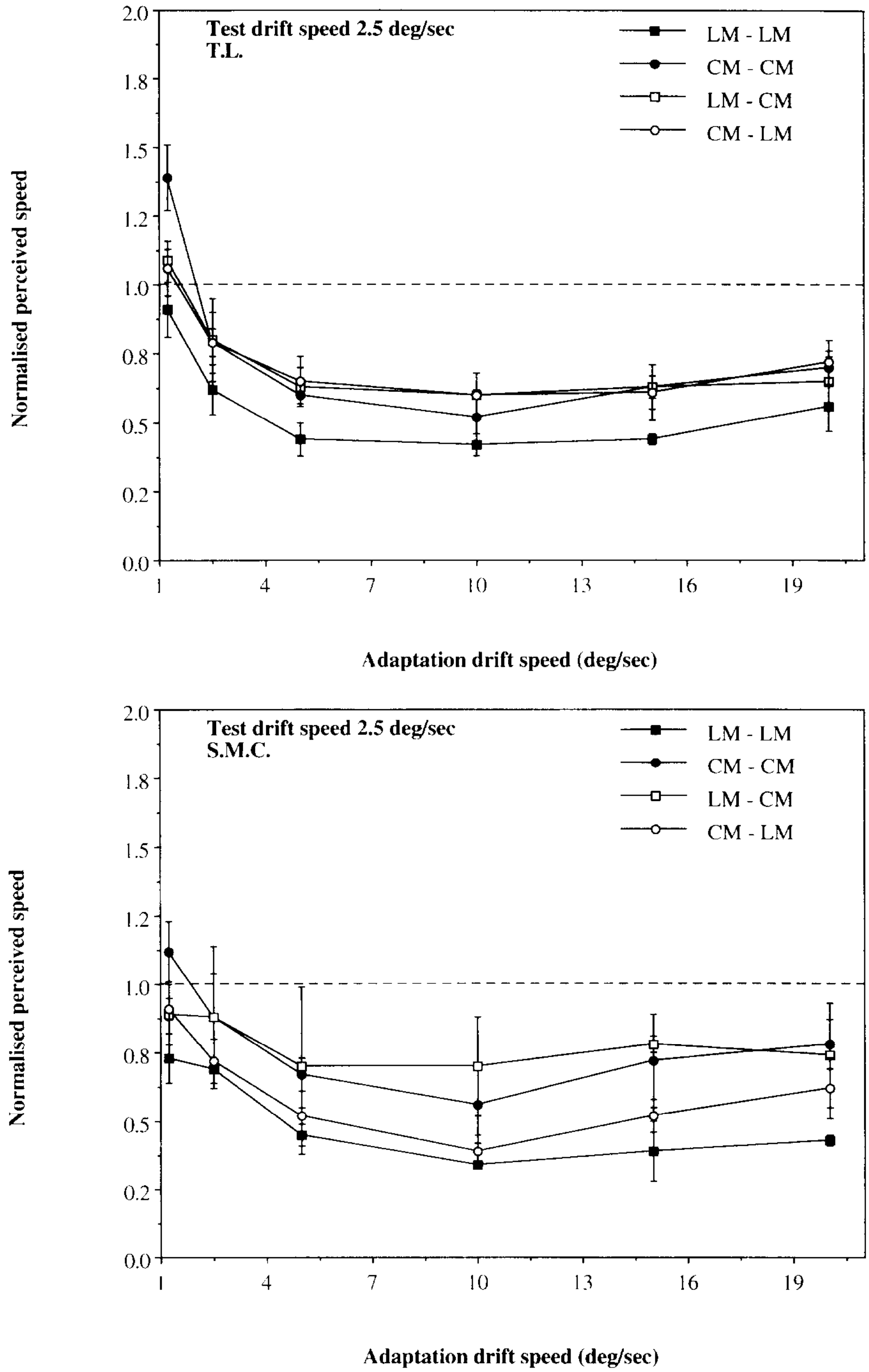
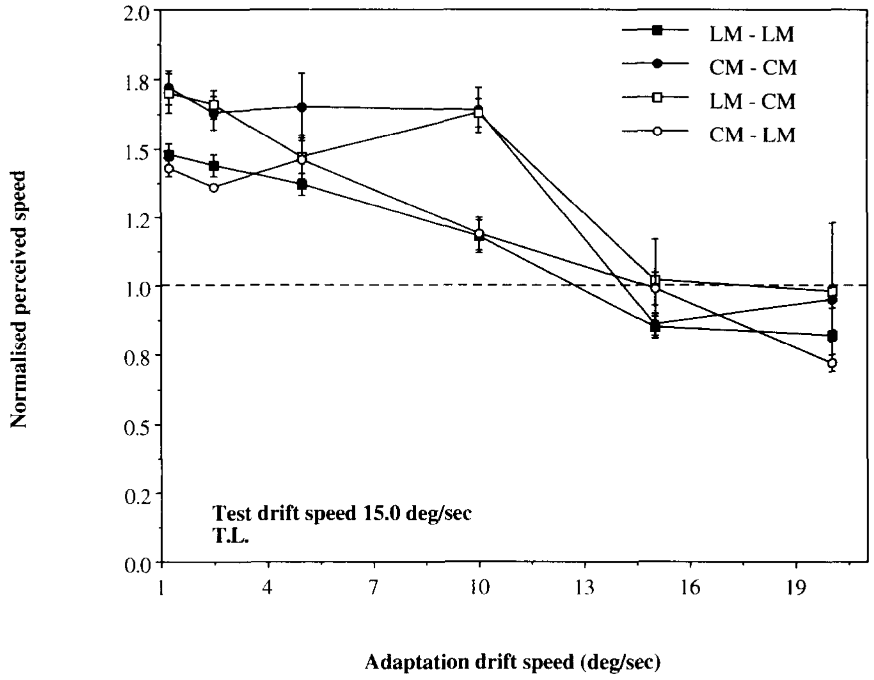


FIGURE 1. Post-adaptation changes in perceived speed for two observers for first-order and second-order motion test stimuli drifting at 2.5 deg/sec. The first-order motion stimuli were composed of LM two-dimensional static noise and the second-order motion stimuli were composed of CM noise. The adaptation and test stimuli had the same direction of drift. Same-adaptation conditions (i.e. when the adaptation and test stimuli were both composed of either LM noise or CM noise) are indicated by either LM–LM or CM–CM and data points are represented by the filled squares and circles, respectively. Cross-adaptation conditions (i.e. when the adaptation and test stimuli were different motion stimuli) are indicated by either LM–CM (i.e. adapt LM, test CM) or CM–LM and data points are represented by the open squares and circles, respectively. Values on the ordinate >1 (above the dashed horizontal line) indicate increases in perceived speed and values <1 indicate decreases. The vertical lines above and below each data point (where visible) represent ± 1 S.E.

positions were reversed. Thus, any hemifield differences in perceived speed (Smith & Hammond, 1986) were counterbalanced. Observer T.L. completed four runs of trials for each adaptation and test condition and observer S.M.C. completed at least two runs of trials for each condition.

In order to obtain baseline (control) measurements of perceived speed in the absence of adaptation to motion, the perceived speeds of the test stimuli following adaptation to an unmodulated static two-dimensional noise field were also measured for each observer. We considered that an unmodulated static noise field, rather



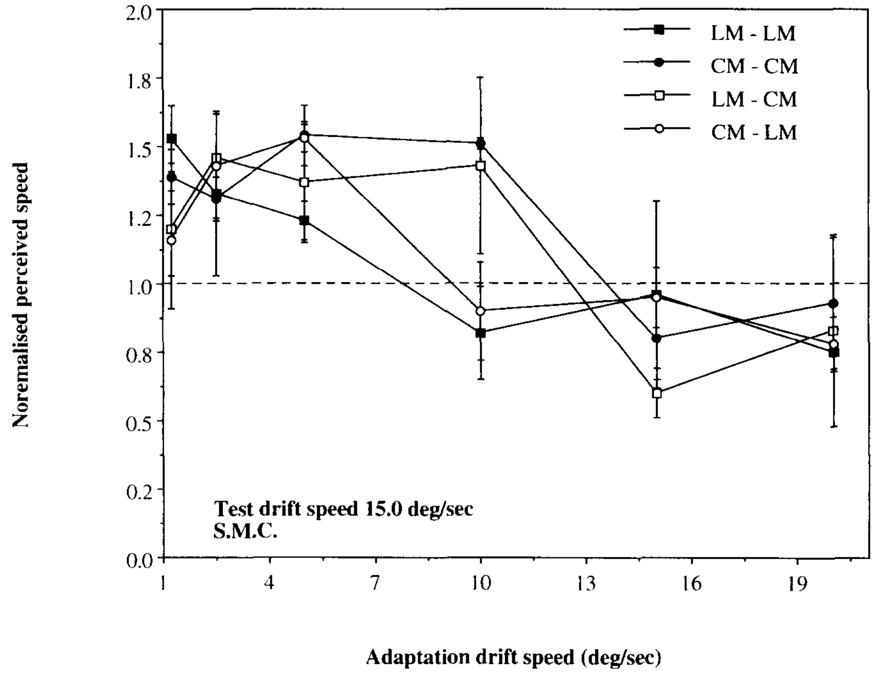


FIGURE 2. Same as Fig. 1 except that the drift speed of the test stimuli was 15.0 deg/sec.

than an homogeneous blank field, was the appropriate stimulus to use for the control condition in order to disambiguate any effects of the presence of noise in the adaptation motion stimuli on the perceived speeds of the test stimuli. The size and mean contrast of the elements comprising the unmodulated noise field were identical to those present in the first- and second-order motion stimuli.

RESULTS

From the resulting data obtained for each condition the speed match was taken as the mean drift speed of the first-order comparison stimulus calculated over the last three trials presented. This particular metric was chosen as the speed match because it was found empirically that it exhibited less variance between runs of trials than estimates derived using alternative techniques [e.g. Weibull (1951) fits]. All results are expressed in terms of the ratio of perceived speed after adaptation to motion to perceived speed after adaptation to static unmodulated noise (see above). Thus, a value of 1 indicates no effect of adaptation to motion on perceived speed, higher values indicate an increase in perceived speed and lower values a decrease. Figures 1 and 2 show the data for the two observers expressed in this way as a function of both the adaptation speed and the modulation characteristics of the adaptation and test stimuli (e.g. LM noise and CM noise).

Post-adaptation speed matches obtained for test stimuli drifting at 2.5 deg/sec

It is apparent from Fig. 1 that for most combinations of adaptation and test stimuli the net result of adaptation to motion is a reduction in the perceived speed of the test stimulus. When the speed of the adaptation stimulus was greater than or equal to that of the test stimulus, adaptation to motion resulted in a reduction in perceived speed of *ca* 38% for both observers averaged over all four conditions. This is in close agreement with previous studies that have investigated changes in the perceived speed of first-order (luminance-defined) stimuli using similar methods to the present experiment [e.g. Smith & Edgar (1994); Thompson (1981)]. This phenomenon appears to occur not only for second-order motion adaptation and test stimuli but also for all four combinations of same- and cross-adaptation conditions examined, which exhibit similar patterns of results across the different adaptation speeds. Although some variability in the absolute magnitude of the effects obtained for these conditions is evident, this may be due in part to difficulties in equating the first-order and second-order motion stimuli precisely for suprathreshold visibility. It is also apparent from Fig. 1 that when the adaptation speed was lower (1.25 deg/sec) than the test speed (2.5 deg/sec) changes in perceived speed were generally much smaller than those obtained for the higher adaptation speeds or in some cases absent, in line with previous studies.

Post-adaptation speed matches obtained for test stimuli drifting at 15.0 deg/sec

The speed-matching data (Fig. 2) exhibit greater variability both between observers and between the different combinations of adaptation and test stimuli than those for the 2.5 deg/sec test speed conditions. When the speed of the adaptation stimulus was greater than or equal to that of the first-order or second-order motion test stimulus (15.0 deg/sec) the perceived speed of the latter was, if anything, reduced as a result of adaptation. The average reduction in perceived test speed across the same- and cross-adaptation conditions was 10% for observer T.L. and 18% for observer S.M.C. There were also systematic increases in perceived speed when the adaptation drift speed was less than the test drift speed. Adaptation to stimuli drifting at speeds <15.0 deg/sec produced a mean increase in perceived speed of 50% for observer T.L. and 32% for observer S.M.C. If anything, somewhat greater increases in perceived speed were found when the test stimulus was composed of CM noise rather than LM noise (irrespective of the nature of the adaptation stimulus). However, further experimentation would be required to establish the reliability of this finding. At present it is sufficient to conclude that second-order motion stimuli show qualitatively similar changes in perceived speed following adaptation to those found for first-order motion stimuli. When the adaptation speed is similar to or greater than the test speed, reductions in perceived speed occur following adaptation to motion, and when the adaptation speed is less than the test speed, increases in perceived speed occur. This basic pattern of results was found across all four same- and cross-adaptation conditions examined and suggests that the visual system may utilize the same computational strategy in order to derive estimates of the speed of the two types of motion.

DISCUSSION

The results of the present study are important for several reasons. Firstly, they demonstrate that adaptation to second-order motion not only produces biases in the perceived direction of subsequently viewed second-order motion stimuli [e.g. Ledgeway (1994); McCarthy (1993)] but can also bias their perceived speeds. Secondly, the results clearly demonstrate that same- and cross-adaptation velocity aftereffects are possible with first-order and second-order motion stimuli and that when all motion stimuli are equated for visibility, adaptation can produce remarkably similar changes in perceived speed (in terms of both their magnitude and direction). Thirdly, the similar patterns of results found for the first-order and second-order motion stimuli suggest that in human vision the coding of the speeds of first-order motion and second-order motion are likely to be achieved by either the same mechanism or separate mechanisms that employ similar computational principles. This suggestion gains additional support from the findings of two recent studies which have demonstrated that the perceived speeds of the two varieties of motion show a similar partial dependence on stimulus modulation depth [e.g. Johnston & Clifford (1995); Ledgeway & Smith (1995a)]. In terms of current computational models of motion processing the similarities found in the present experiment between the processing of first-order and second-order motion are consistent with both models which propose that the two types of motion are processed by a single pathway in the visual system [e.g. Johnston *et al.* (1992)] and models which suggest that first-order and second-order motion signals are initially detected separately and then pooled at a later processing stage in order to extract the resultant image direction and speed [e.g. Wilson *et al.* (1992)]. We favour the latter interpretation because the balance of current psychophysical and physiological evidence (see Introduction) supports the existence of separate motion-detecting mechanisms for each type of motion.

An important point to be considered concerns the degree to which the present results reflect adaptation to second-order motion *per se* rather than adaptation to first-order (luminance) motion artifacts that could, in principle, arise in second-order motion stimuli [for a detailed analysis see Smith & Ledgeway (1995, 1996)]. For example, it has been suggested [e.g. Derrington (1987, 1994)], at least for the case of CM gratings, that

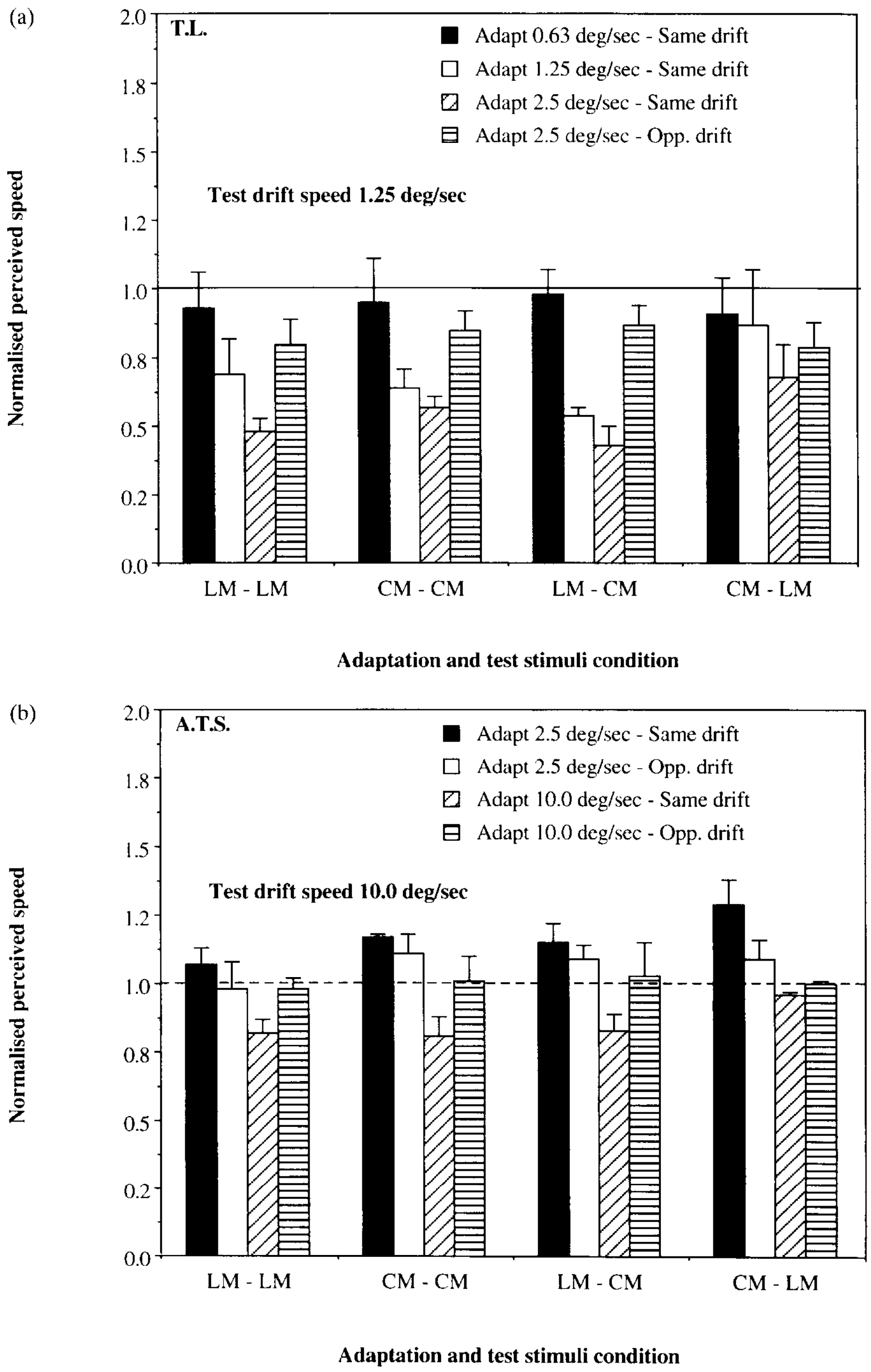


FIGURE 3. Histograms showing post-adaptation changes in perceived speed for two observers for motion stimuli containing dynamic, rather than static, two-dimensional noise carriers. This was achieved by replacing the noise sample on each image update with a different stochastic noise sample. Results are plotted separately for each adaptation speed, the drift directions of the adaptation and test stimuli (either same drift or opposite drift) and the modulation characteristics of each pair of stimuli (either LM or CM noise). For observer T.L. (a) the mean Michelson contrast of the dynamic noise carrier was 0.25, the drift speed of the test stimuli was 1.25 deg/sec and all test stimuli were presented at approximately 12 times their respective direction-identification threshold. For observer A.T.S. (b) the mean Michelson contrast of the carrier was 0.5, the drift speed of the test was 10.0 deg/sec and all test stimuli were presented at approximately four times threshold. Values on the ordinate >1 (above the dashed horizontal line) indicate increases in perceived speed and values <1 indicate decreases. The vertical line above each bar (where visible) represents ± 1 S.E.

when the carrier contrast is high, early non-linearities in the visual system may create global first-order components (distortion products) at the same spatiotemporal scale as the contrast-modulation and that these may be utilized to extract motion. However, Smith and Ledgeway (1995, 1996) measured direction thresholds for CM two-dimensional noise patterns similar to those used in the present experiment and found that thresholds were little affected by increasing the carrier contrast and did not vary in inverse proportion to the noise contrast, as would be predicted if performance was based upon distortion products. Therefore, we feel it is unlikely that

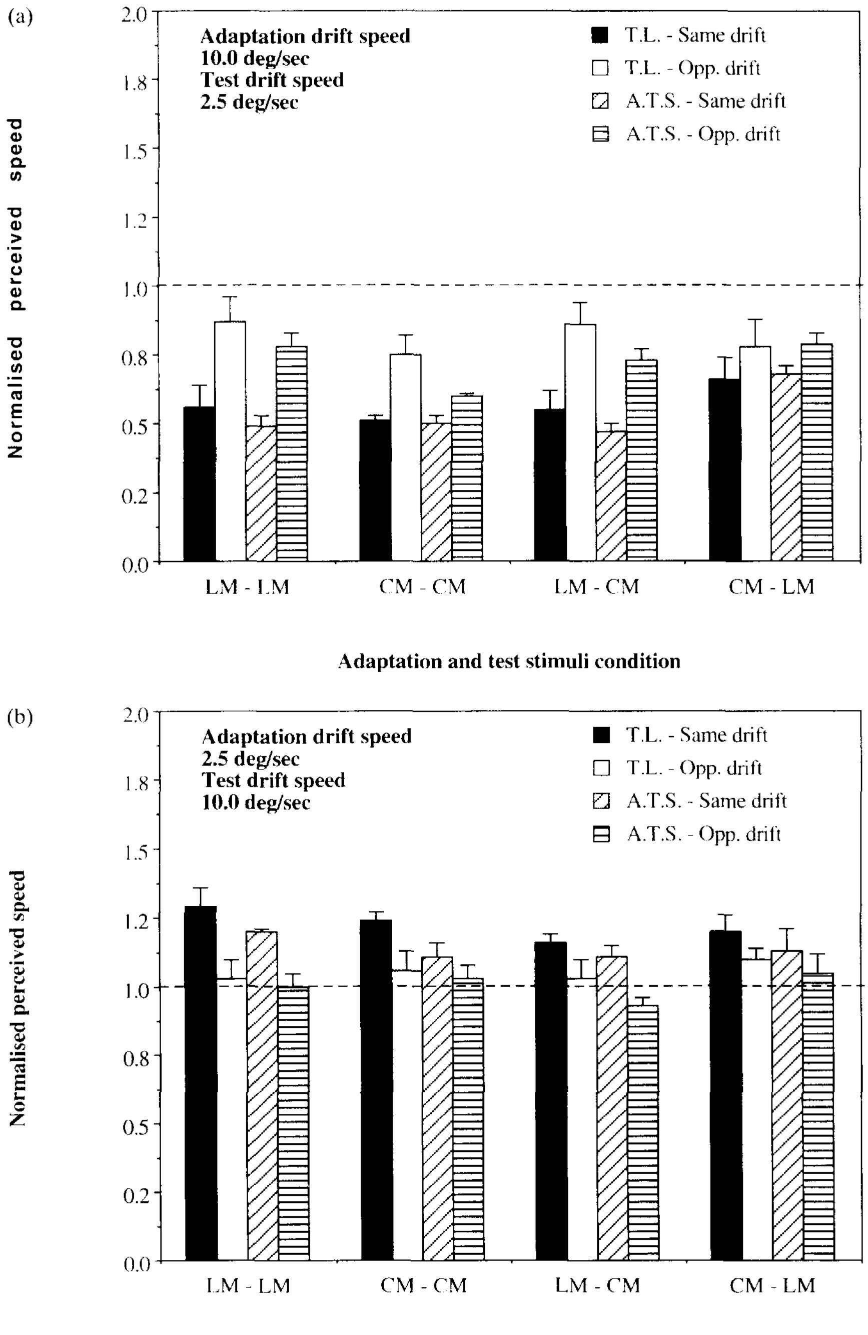


FIGURE 4. Histograms showing post-adaptation changes in perceived speed for two observers for motion stimuli containing high-pass spatial frequency filtered two-dimensional static noise carriers. Results are plotted separately for both combinations of drift direction of the adaptation and test stimuli (either same drift or opposite drift) and the modulation characteristics of each pair of stimuli (either LM or CM noise). The cut-off frequency of the high-pass (isotropic) filter applied to the carrier, prior to multiplication with or addition to the drifting 1 c/deg sinusoid, was 2 c/deg. The mean Michelson contrast of the filtered noise carrier was 0.5 (corresponding to a root-mean-sqaure contrast of about 0.35). The drift speeds of the adaptation and test stimuli were either 10.0 and 2.5 deg/sec, respectively (a) or 2.5 and 10.0 deg/sec, respectively (b) and all test stimuli were presented at approximately ten times their respective direction-identification threshold. The vertical line above each bar (where visible) represents ± 1 S.E.

distortion products, if indeed present, were responsible for the substantial post-adaptation changes in perceived speed observed in the present experiment.

Another type of artifact that may arise in CM noise patterns and potentially contaminate measures of second-order motion perception results from local clustering of noise elements of the same polarity in the carrier. Clusters of "light" or "dark" noise elements could introduce prominent low spatial frequencies in the carrier and give rise to consistent local first-order motion signals (in the same direction as the contrast modulation) even though the image is globally drift-balanced (Chubb &

Sperling, 1988). This may be especially problematic for static broadband noise carriers that are composed of relatively large noise elements. There is some evidence that local artifacts may mediate psychophysical performance for CM static noise, at least at threshold. For example, Smith and Ledgeway (1995, 1996) found that orientation and direction thresholds were similar for second-order motion stimuli containing static noise (particularly when composed of large noise elements), as they are for first-order motion. However, direction thresholds were consistently higher than orientation thresholds when the stimuli contained dynamic noise, or high-pass spatial frequency filtered noise (two manipulations which eliminate consistent local first-order artifacts) rather than static broadband noise. These results suggest that the mechanism that encodes second-order motion cannot specify direction at the threshold for detecting orientation and that local artifacts may mediate detection for patterns composed of static broadband noise. If such artifacts were indeed present in our second-order motion stimuli then it remains a possibility that the velocity aftereffects observed in the present experiment were due entirely to adaptation to local first-order motion artifacts.

An additional possibility is that the changes in perceived speed were due entirely to adaptation to the first-order motion energy that is present in all second-order motion stimuli. It is not the case that second-order motion stimuli contain no motion energy, only that motion energy is equal in opposite directions. Although some models include subtraction of opposite motion signals at an early stage, which would eliminate motion energy in our images, it is not certain that this occurs in the visual system. It is therefore conceivable that velocity aftereffects could occur as a result of adaptation to motion energy even when the image is drift-balanced. If this were the case then these aftereffects should not exhibit direction-specificity.

We obtained control data to investigate whether or not either local first-order motion artifacts or direction-non-specific adaptation was responsible for the velocity aftereffects found in the present experiment by measuring post-adaptation changes in perceived speed using an identical procedure, and similar stimuli, to those described previously (see Methods) with the following exceptions:

1. The noise element size was made as small as possible (1.5×1.5 arc min);
2. The carrier was composed of either dynamic noise or high-pass spatial frequency filtered noise, rather than static broadband noise, to minimize the probability of consistent groupings of noise elements with the same polarity; and
3. The effects of adaptation to motion in both the same and opposite directions to the test stimulus were investigated in order to establish whether changes in the perceived speeds of second-order motion stimuli following adaptation are direction-specific.

Data were collected at both high and low drift speeds and the results obtained using dynamic noise carriers are shown in Fig. 3 and those obtained using a high-pass filtered carrier with a cut-off frequency of 2 c/deg (one octave higher than the spatial frequency of the modulation signals) are shown in Fig. 4. In each figure histograms showing post-adaptation changes in perceived speed, for two observers (T.L. and A.T.S.), are plotted separately for each adaptation speed, drift direction of the adaptation and test stimuli (either same drift or opposite drift) and the modulation characteristics of each stimulus.

It is clear that substantial velocity aftereffects were found for stimuli containing either dynamic noise (Fig. 3) or high-pass filtered noise (Fig. 4) and for each adaptation and test speed combination examined these were very similar across all same- and cross-adaptation conditions. Importantly, the changes in perceived speed that occurred for adaptation and test stimuli drifting in the same direction closely resemble those in Figs 1 and 2. Same- and cross-adaptation resulted in robust decreases in perceived speed when the drift speed of the adaptation stimulus was greater than or equal to the test speed. Furthermore, when the adaptation speed was low, the test speed was high and the two patterns had the same direction of drift, adaptation produced modest but consistent increases in perceived speed. It is also apparent that post-adaptation changes in perceived speed were much less marked (or in some cases absent) when the adaptation and test stimuli had opposite directions of drift than when they had the same direction of drift.

Two main points arise from these results. Firstly, given that the basic pattern of the results found in the main experiment and control conditions was extremely similar, despite the fact that extensive measures were taken in the latter to eliminate the action of any local first-order (luminance) artifacts that could arise in the second-order images, we conclude that it is highly improbable that such artifacts, if present, could have been solely responsible for the robust post-adaptation changes in perceived speed observed. Secondly, the velocity aftereffects shown in Figs 3–4 exhibit some degree of direction-specificity in that much smaller changes in perceived speed were always found when the adaptation and test stimuli had opposite directions of drift. The implication of this result is that the changes in perceived speed found for all conditions in which the adaptation stimulus was a second-order motion pattern cannot be due simply to adaptation to the first-order motion energy present in that stimulus. If this were the case then adaptation would result in aftereffects of equal magnitude when the adaptation and test stimuli drifted in the same or opposite directions.

The present results also bear on models of speed perception. A number of current computational models [e.g. Harris (1980); Smith & Edgar (1994); Wright & Johnston (1985)] suggest that speed sensitivity could emerge by a process of comparing the activity within a relatively small number of broadly tuned temporal channels. Given the similarities between psychophysical measures of first-order and second-order speed processing, it seems likely that second-order speed may have a similar basis.

In summary, it is clear from the present study that the mechanisms underlying the processing of both first-order and second-order motion are susceptible to adaptation and that adaptation can give rise to substantial changes in the perceived speeds of moving images. When the two varieties of motion stimuli are equated for visibility not only are same- and cross-adaptation effects possible between such stimuli, but they produce post-adaptation increases and decreases in perceived speed that are comparable in terms of their magnitude. The present results therefore not only confirm previous reports that same- and cross-adaptation phenomena are possible between first-order and second-order motion stimuli (Holliday & Anderson, 1994; Ledgeway, 1994; Turano, 1991) but also extend these findings to changes in perceived speed. Furthermore, our control data demonstrate that first-order (luminance) artifacts that may arise from the use of second-order motion stimuli are likely to be too small to explain the velocity aftereffects that occur following adaptation to this variety of second-order motion.

REFERENCES

Adelson, E. H. & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*, 284–299.

Cavanagh, P. & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision, 4*, 103–129.

Chubb, C. & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, 5*, 1986–2007.

Derrington, A. M. (1987). Distortion products in geniculate X-cells: A physiological basis for masking by spatially modulated gratings? *Vision Research, 27*, 1377–1386.

Derrington, A. M. (1994). Analysis of the motion of contrast-modulated patterns. Motions. *Investigative Ophthalmology and Visual Science, 35 (Suppl.)*, 1406.

Derrington, A. M. & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research, 25*, 1869–1878.

Harris, M. G. (1980). Velocity sensitivity of the flicker to pattern sensitivity ratio in human vision. *Vision Research, 20*, 687–691.

Harris, L. R. & Smith, A. T. (1992). Motion defined by second-order characteristics does not evoke optokinetic nystagmus. *Visual Neuroscience, 9*, 565–570.

Holliday, I. E. & Anderson, S. J. (1994). Different processes underlie the detection of second-order motion at low and high temporal frequencies. *Proceedings of the Royal Society of London B, 257*, 165–173.

Johnston, A. & Clifford, C. W. G. (1995). Perceived motion of contrast-modulated gratings: Predictions of the multi-channel gradient model and the role of full-wave rectification. *Vision Research, 35*, 1771–1783.

Johnston, A., McOwan, P. W. & Buxton, H. (1992). A computational model of the analysis of some first-order and second-order motion patterns by simple and complex cells. *Proceedings of the Royal Society of London B, 250*, 297–306.

Ledgeway, T. (1994). Adaptation to second-order motion results in a motion aftereffect for directionally ambiguous test stimuli. *Vision Research, 34*, 2879–2889.

Ledgeway, T. & Smith, A. T. (1992). Adaptation to second-order motion: Direction-specific threshold elevation for direction-identification. *Perception, 21 (Suppl.)*, 44.

Ledgeway, T. & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research, 34*, 2727–2740.

Ledgeway, T. & Smith, A. T. (1995a). The perceived speed of second-order motion and its dependence on stimulus contrast. *Vision Research, 35*, 1421–1434.

Ledgeway, T. & Smith, A. T. (1995b). Effects of adaptation to second-order motion on perceived speed. *Investigative Ophthalmology and Visual Science, 36 (Suppl.)*, S53.

Marr, D. & Ullman, S. (1981). Directional selectivity and its use in early visual processing. *Proceedings of the Royal Society of London B, 211*, 151–180.

Mather, G. & West, S. (1993). Evidence for second-order motion detectors. *Vision Research, 33*, 1109–1112.

McCarthy, J. E. (1993). Directional adaptation effects with contrast modulated stimuli. *Vision Research, 33*, 2653–2662.

Nishida, S., Ashida, H. & Sato, T. (1994). Complete interocular transfer of motion aftereffect with flickering test. *Vision Research, 34*, 2707–2716.

Smith, A. T. (1985). Velocity coding: Evidence from perceived velocity shifts. *Vision Research, 25*, 1969–1976.

Smith, A. T. & Edgar, G. K. (1994). Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Research, 34*, 253–265.

Smith, A. T. & Hammond, P. (1986). Hemifield differences in perceived velocity. *Perception, 15*, 111–117.

Smith, A. T. & Ledgeway, T. (1995). Second-order motion: The carrier is crucial. *Perception, 24 (Suppl.)*, 28.

Smith, A. T. & Ledgeway, T. (1996). Separate detection of moving luminance and contrast modulations: Fact or artifact? *Vision Research, 37*, 45–62.

Stone, L. S. & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research, 32*, 1535–1549.

Stoner, G. R. & Albright, T. D. (1992). Motion coherency rules are form-cue invariant. *Vision Research, 32*, 465–475.

Taylor, M. M. & Creelman, C. D. (1967). PEST: Efficient estimates on probability functions. *The Journal of the Acoustical Society of America, 41*, 782–787.

Thompson, P. (1981). Velocity aftereffects: The effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli. *Vision Research, 21*, 337–345.

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research, 22*, 377–380.

Turano, K. (1991). Evidence for a common motion mechanism of luminance-modulated and contrast-modulated patterns: Selective adaptation. *Perception, 20*, 455–466.

Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics, 18*, 292–297.

Werkhoven, P., Sperling, G. & Chubb, C. (1993). The dimensionality of texture-defined motion: A single channel theory. *Vision Research, 33*, 463–485.

Wilson, H. R., Ferrera, V. P. & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9*, 79–97.

Witt, R., Conte, M. M., Waran, M. & Victor, J. D. (1994). Perceived velocity of Fourier and non-Fourier stimuli. *Investigative Ophthalmology and Visual Science, 35 (Suppl.)*, 1269.

Wright, M. J. & Johnston, A. (1985). Invariant tuning of motion aftereffect. *Vision Research, 25*, 1947–1955.

Zhou, Y. & Baker, C. L. (1993). A processing stream in mammalian visual cortex neurons for non-Fourier responses. *Science, 261*, 98–101.

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