



# Failure of direction identification for briefly presented second-order motion stimuli: evidence for weak direction selectivity of the mechanisms encoding motion

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## Abstract

We sought to investigate why the direction of second-order motion, unlike first-order motion, cannot be identified when the stimulus exposure duration is brief (<200 ms). In a series of experiments observers identified both the orientation (vertical or horizontal) and the direction (left, right, down or up) of a drifting sinusoidal modulation (0.93 c°) in either the luminance (first order) or the contrast (second order) of a two-dimensional noise carrier. All motion stimuli were equated for visibility, and the duration was varied using the method of constant stimuli. Performance was measured for second-order motion over a range of drift temporal frequencies (0.63–5.04 Hz) and for first-order motion stimuli composed of two, opposite drifting modulations in luminance of unequal modulation depth. Orientation-identification performance was nearly 100% correct for both first-order and second-order motion stimuli, even at the briefest stimulus duration tested (26.49 ms). Direction identification for first-order motion was also typically good with brief presentations, but was poor for second-order motion when the exposure duration was <~200 ms. Importantly increasing either the drift temporal frequency of second-order motion or the bidirectional nature of the first-order motion patterns produced comparable levels of performance for the two varieties of motion (i.e. the minimum duration required for reliable direction identification could be equated). As orientation-identification performance for the first-order and second-order motion stimuli was comparably good and minimally affected by duration, the marked differences on the direction-identification task must be specific to mechanisms that encode drift direction, rather than spatial structure. We propose that second-order motion detectors are much less selective for stimulus direction than first-order motion sensors, and thus are more susceptible to the deleterious effects of limiting stimulus duration (which introduces spurious motion in the opposite direction, particularly at low drift rates). Alternative explanations based on the delayed propagation of second-order motion signals or the temporal characteristics of the underlying motion mechanisms are not supported by our findings.

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**Keywords:** Second-order motion; First-order motion; Stimulus duration; Direction selectivity

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## 1. General introduction

Objects in the world principally differ from each other and their surroundings in terms of the intensity of light that they each reflect. Consequently whenever an object moves, or the observer moves, intensity variations within the retinal image corresponding to edges, boundaries and contours in the visual scene are also displaced. Movement conveyed by intensity differences

is termed “first-order motion” (Cavanagh & Mather, 1989) and has been studied extensively (see Smith & Snowden, 1994). First-order motion perception presumably is mediated by specialised neural mechanisms that extract the direction, and the rate, of movement within the retinal image. Several influential computational models of first-order motion utilise pairs of linear spatial and temporal filters to construct receptive fields oriented in space-time that respond maximally to first-order motion in a particular direction (Adelson & Bergen, 1985; Van Santen & Sperling, 1985; Watson & Ahumada, 1985). Models based on these principles can be conceptualised as detectors of “motion energy” (summed directional power) in the image; these detectors embody many of the properties of motion-sensitive

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neurones found in mammalian visual cortex (e.g. DeAngelis, Ohzawa, & Freeman, 1993a,b; Emerson, Bergen, & Adelson, 1992; Hubel & Wiesel, 1962).

Objects in the world can also differ from each other and from their surroundings in terms of their textural attributes (e.g. the mean size, contrast or orientation of surface markings). Even when in motion, such objects give rise to vivid impressions of movement, despite the absence of first-order motion (Badcock & Derrington, 1985; Chubb & Sperling, 1988; Ramachandran, Rao, & Vidyasagar, 1973). Motion conveyed in this manner is termed “second-order motion” (Cavanagh & Mather, 1989). The principles governing second-order motion processing have yet to be firmly established, but prevailing theories suggest that it is based on computational principles similar to those used for first-order motion (Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Johnston, McOwan, & Buxton, 1992). For example Wilson, Ferrera, and Yo (1992) propose that a specialised pathway extracts second-order motion by rectifying the outputs of spatial-frequency-selective filters, prior to conventional motion-energy analysis at a coarser spatial scale. A separate pathway encodes first-order motion, but the two converge to determine the resultant direction. The general processing scheme exemplified by this model is consistent with a broad range of psychophysical and electrophysiological evidence (see Baker, 1999; Smith, 1994; Sperling & Lu, 1998).

There are, however, important differences between the processing of first-order motion and second-order motion, especially with regard to the temporal properties of the putative motion-detecting mechanisms (Badcock & Derrington, 1989; Derrington & Badcock, 1985; Holliday & Anderson, 1994; Pantle & Turano, 1992). For example Derrington, Badcock, and Henning (1993) found that observers could not identify the drift direction of an abruptly presented second-order motion stimulus (a sinusoidal, contrast modulation or beat pattern) when the stimulus was presented for  $<\sim 200$  ms. For first-order motion (sinusoidal, luminance-defined gratings), performance was typically very good even at the briefest duration tested (22 ms). This finding has been subsequently confirmed (Cropper & Derrington, 1994, 1996) and is not simply an artifact due to a mismatch in the effective amplitudes of the first-order and second-order motion signals. Three alternative explanations of this phenomenon are discussed below.

*Processing-delay hypothesis:* It has been suggested (e.g. Yo & Wilson, 1992; Wilson & Kim, 1994) that second-order motion detection is inherently slow because of the additional processing required to extract the second-order image structure. In support of this proposal Wilson et al. (1992) found that the perceived direction of type II plaids (two-dimensional (2-d) patterns

containing both first-order and second-order motion) changes with stimulus duration. They postulated that perceived direction was initially governed by the first-order motion signals and was then also influenced by a delayed ( $\sim 60$  ms) second-order motion signal. There are, however, potential problems with this processing-delay hypothesis. First, similar changes in perceived direction with stimulus duration occur with type II plaids composed only of second-order motion components (Cropper, Badcock, & Hayes, 1994). Second, a pure delay does not explain why observers cannot, given sufficient time after the stimulus offset, determine drift direction for brief exposures ( $<200$  ms). A delay should not prevent the stimulus from eventually being processed to a level at which a decision can be made regarding its direction. It is doubtful, therefore, that a simple processing delay is responsible for the inability to identify second-order motion direction in brief displays.

*Low-pass temporal filtering hypothesis:* Derrington et al. (1993) proposed that second-order motion, unlike first-order motion, cannot be identified when the stimulus duration is brief because it is subjected to more severe low-pass temporal filtering by the visual system. Compared to first-order motion temporal acuity for second-order motion is typically poorer, and sensitivity declines much more rapidly as drift temporal frequency increases (Derrington, 1994; Holliday & Anderson, 1994; Smith & Ledgeway, 1998; but see Lu & Sperling, 1995). But this explanation may not be entirely satisfactory. Even when the drift temporal frequency was low (0.5 Hz), and the motion stimuli were suprathreshold, beats still needed to be presented for twice as long ( $\sim 150$  ms) as luminance-defined gratings to identify direction correctly on 75% of trials. Thus gross differences in the temporal sensitivity and/or acuity of the mechanisms that encode each variety of motion, may be insufficient to explain this pattern of results.

*Direction-selectivity hypothesis:* We propose an alternative explanation, that incorporates two factors known to influence greatly the ability to identify drift direction, at least with respect to first-order motion (e.g. Derrington & Goddard, 1989; Watson, Ahumada, & Farrell, 1986). First, a motion stimulus is directionally ambiguous when its presentation is sufficiently brief. This can be seen in the Fourier energy spectrum (a standard representation of the motion energy available in a stimulus) of a smoothly drifting sinusoidal waveform that is progressively restricted (windowed) in time. As duration decreases, spurious motion energy is introduced in the direction opposite to the actual sinusoid displacement, and gives rise to directional ambiguity (see Fig. 1a). For very brief presentations, a sinusoid nominally drifting say leftwards may actually contain substantial motion energy in the opposite direction

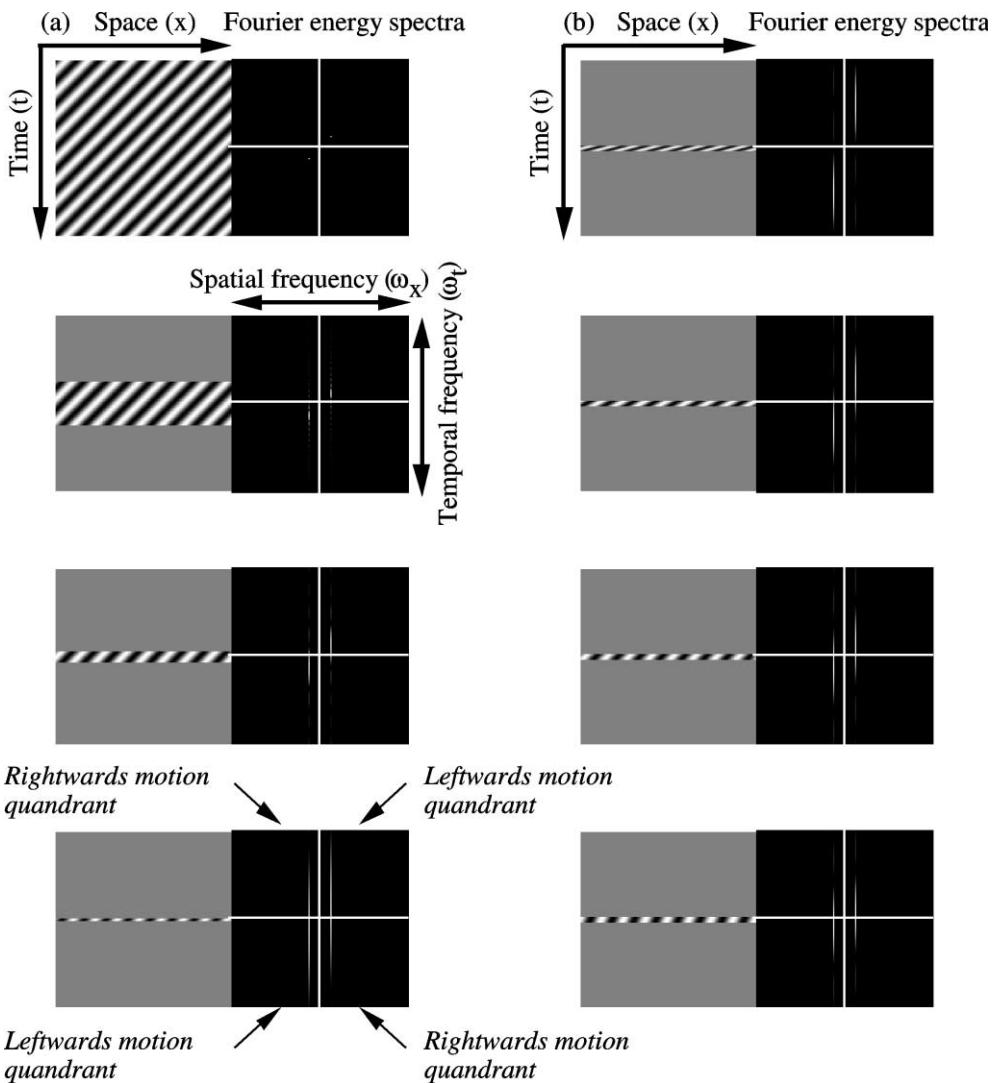


Fig. 1. Space-time ( $x$ - $t$ ) plots and Fourier energy spectra of a first-order (luminance-defined), sinusoidal grating drifting leftwards. Each  $x$ - $t$  plot is based on a  $128 \times 128$  pixel array and the spectral intensity values (representing power at each frequency) have been scaled to cover the available brightness range. In (a) the spatial frequency and the drift temporal frequency of the grating are both 8 c/image and it is presented within a rectangular temporal window with a duration of either 128, 32, 8 or 2 pixel rows (from the top to the bottom of the figure, respectively). The motion energy of the stimulus (an estimate of the information available for motion analysis) is smeared along the temporal frequency axis ( $\omega_t$ ) to an extent that is inversely related to its duration. For the briefest presentations shown, temporal frequency is smeared such that the stimulus nominally drifting leftwards actually contains substantial motion energy in the opposite direction (rightwards). In (b) the spatial frequency and duration of the grating are fixed at 8 c/image and 4 pixel rows, respectively, but drift temporal frequency varies (either 32, 16, 8, or 4 c/image from the top to the bottom of the figure, respectively). As drift temporal frequency decreases spectral bandwidth remains constant (on a linear scale), but systematically encroaches on quadrants representing motion in the opposite direction, resulting in significant motion energy in both directions. In principle second-order motion stimuli composed of sinusoidal modulations in contrast also exhibit the same properties, when their spectral characteristics are considered in the contrast, rather than the luminance, domain.

(rightwards), particularly when the drift temporal frequency is low (Fig. 1b). Second, the degree to which a motion detector responds differentially to movement in one direction, compared with other (e.g. the opposite) directions, must limit the ability of that mechanism, and ultimately the observer, to disambiguate the direction of a moving stimulus. This raises the possibility that second-order motion detectors cannot reliably signal the

direction of motion when the stimulus duration is brief, because they are less direction selective than first-order motion detectors.

There is evidence that second-order motion mechanisms may be less selective for direction than first-order motion mechanisms. It is well established that adaptation to second-order motion, unlike first-order motion, typically fails to evoke a compelling motion aftereffect in

stationary test patterns (see Culham et al., 1998). This may be indicative of little differential activation of detectors selective for opposite directions of motion. Although adaptation to second-order motion sometimes gives rise to substantial aftereffects when drifting or flickering test patterns are employed, these may simply amplify any relatively modest imbalance in the activity of adapted and unadapted motion detectors (Ledgeway, 1994). Consistent with this suggestion Nishida, Ledgeway, and Edwards (1997) found that adaptation to second-order motion tended to produce smaller direction-selective reductions in sensitivity to drifting test patterns than did first-order motion. Second-order motion also poorly drives both optokinetic nystagmus (OKN) andvection (Gurnsey, Fleet, & Potechin, 1998; Harris & Smith, 1992, 2000). In higher mammals OKN andvection are dependent primarily on direction-selective cortical mechanisms that generate robust and unambiguous estimates of overall image motion (Duffy & Wurtz, 1991a,b; Hoffmann, 1989). Second-order motion may be an impoverished drive for both OKN andvection because it is encoded by mechanisms that are only weakly selective for drift direction.

There is also some limited physiological evidence with a bearing on the issue of the direction selectivity of second-order motion detectors. In primate visual area MT, Albright (1992) found that responses to second-order motion exhibited greater bidirectionality (less direction selectivity) and were considerably weaker (by a factor of ~2) than those to first-order motion. Analogous observations have been made in primate MSTd (Churan & Ilg, 2001; Geesaman & Andersen, 1996), an area involved in the processing of large field, flow patterns (cf. OKN- andvection-inducing stimuli). Similarly, in areas 17 and 18 of feline cortex, Zhou and Baker (1994) found that the degree of direction selectivity exhibited by cells to each variety of motion was not significantly correlated. Indeed of the cells that exhibited a difference, most were less selective for second-order motion.

If the failure to identify the direction of second-order motion with brief exposures is due to a combination of spurious second-order motion energy (directional ambiguity) and relatively broad direction selectivity, as we have suggested, then it follows that: (1) Identification of the spatial orientation of first-order and second-order motion patterns should be comparably good and minimally affected by stimulus duration. (2) The minimum stimulus duration required to identify the direction of second-order motion should decrease as drift temporal frequency increases. (3) Regardless of the stimulus duration used, observers should require a greater imbalance in second-order motion energy, than first-order motion energy, between opposite directions to disambiguate the overall (net) direction of movement. (4) Increasing the directional ambiguity of first-order motion (by superimposing two, opposite drifting luminance-

defined gratings), should mimic the visual response to second-order motion and elicit similar performance. These predictions, of the direction-selectivity hypothesis, were tested in a series of experiments.

## 2. Experiment 1: Comparison of first-order motion and second-order motion stimuli equated for visibility and the presence of a carrier

### 2.1. Introduction

The principal objective, in Expt 1, was to investigate the ability to identify the direction of first-order and second-order motion under conditions comparable to those used previously (Derrington et al., 1993). Although these authors reported that even for very brief presentations the spatial structure (e.g. orientation) of beat patterns was clearly visible, and was not the factor limiting direction-identification performance, they did not formally collect data on this important issue. Accordingly, in the present experiment we also measured orientation identification as a function of stimulus duration. Orientation identification is a task well suited to assess the ability to extract the spatial structure of drifting patterns, as it is directly analogous to direction identification and cannot be performed on the basis of local (first-order) flicker cues present in second-order motion stimuli (Ledgeway & Smith, 1992; Smith, Hess, & Baker, 1994).

Second-order motion stimuli should ideally be “drift-balanced” (Chubb & Sperling, 1988), such that any first-order motion energy they contain is equal in opposite directions at each spatial and temporal scale. But this is not always the case. For example drifting beats (the sum of two, luminance-defined gratings of slightly different spatial frequency that move in opposite directions) are not strictly drift-balanced. As a result, perceived direction may be biased erroneously in the direction of the most visible first-order motion component (the carrier) (Cropper & Derrington, 1996; Derrington et al., 1993). Therefore, great care must be taken to minimise potentially confounding first-order motion cues. This can be achieved using a carrier composed of either static or dynamic random noise, such that the resultant second-order motion stimulus is drift-balanced. Furthermore, to make meaningful comparisons between first-order motion and second-order motion, stimuli should be equated for both the presence of the carrier (e.g. Ledgeway, 1994; Smith, Musselwhite, & Hammond, 1984) and the visual system’s relatively poor sensitivity to second-order motion (e.g. Smith et al., 1994). Consequently we employed drift-balanced, second-order motion stimuli (contrast-modulated noise) and first-order motion stimuli (luminance-modulated noise) that were comparable in visibility.

## 2.2. Methods

### 2.2.1. Observers

TL and RFH (the authors) participated in the experiment and each had normal or corrected-to-normal acuity.

### 2.2.2. Apparatus and stimuli

Motion stimuli were computer generated and displayed on a *NanoFlexScan 6600* monochrome monitor (frame refresh rate of 75.5 Hz) that was gamma corrected by internal look up tables. As an added precaution psychophysical procedures were used to confirm that any residual luminance nonlinearities were minimised (Ledgeway & Smith, 1994; Nishida et al., 1997). For precise control of luminance contrast the number of intensity levels available was increased to 12 bits using a video attenuator (Pelli & Zhang, 1991). Stimuli were time locked to the monitor refresh rate, were presented centrally and subtended  $5 \times 5^\circ$  at the viewing distance of 1.01 m. The mean luminance of the remainder of the display (which was homogeneous) was  $\sim 18 \text{ cd/m}^2$ . A central fixation spot was presented both immediately prior to and following each motion stimulus to maintain steady fixation.

First-order motion stimuli were composed of either a conventional luminance-defined sinusoidal grating (L), luminance-modulated static noise (LMSN) or luminance-modulated dynamic noise (LMDN). LMSN and LMDN were produced by adding a sinusoidal grating to a 1-bit, spatially 2-d, random noise carrier of Michelson contrast 0.15. Noise was generated by assigning individual screen pixels (1.17 min arc) to be either “white” or “black” with equal probability and in the case of LMDN a new stochastic sample was used for each separate image in the motion sequence. The spatial frequency of the luminance modulation was 0.93 c/ $^\circ$ , orientation was either horizontal or vertical and drift direction was either upwards, downwards, leftwards or rightwards, as appropriate. Second-order motion stimuli were composed of either contrast-modulated static noise (CMSN) or contrast-modulated dynamic noise (CMDN) and were produced by multiplication, rather than addition, of a drifting sinusoidal grating and noise.

The duration of the motion sequences could be one of 15 values, ranging from 26.49 to 397.35 ms (2–30 refreshes of the image) in equal steps. The temporal (and spatial) window within which each motion sequence was displayed was abrupt, so that the stimulus duration could be specified precisely. The modulation in luminance or contrast was always displaced through a total distance corresponding to 0.25 cycles of its spatial period during each presentation interval, irrespective of the stimulus duration. This was achieved by updating the phase of the modulation on each image refresh (1/75.5 s intervals) by an amount determined by the overall

stimulus duration (i.e.  $0.5\pi/[\text{number image refreshes} - 1]$  rad). Therefore both the “smoothness” of the motion and drift temporal frequency covaried with the stimulus duration, as was the case in the initial experiments of Derrington et al. (1993) that we sought to replicate (this issue will be addressed subsequently in Expts 2 and 3).

The first-order and second-order motion stimuli were presented at the same multiple of direction-identification threshold in order to equate suprathreshold visibility. Thresholds, individually measured for each observer using the method of constant stimuli, are shown in Fig. 2. The drift temporal frequency was 1.26 Hz (equal to the median of the stimuli when this varied with duration), and each motion stimulus was presented for 503.31 ms. Pilot studies revealed that this duration was sufficiently long to enable the drift direction of all stimuli to be readily discerned. Direction-identification thresholds for contrast modulated, but not luminance modulated, noise patterns were markedly higher ( $\sim 1.66$  times) than orientation thresholds, indicating that our second-order motion stimuli were not contaminated by measurable first-order motion artifacts. Although the principal cause of the separation of the two thresholds has been disputed (Benton & Johnston, 1997; but see Fig. 2), this difference in thresholds is a characteristic signature of second-order motion-detecting mechanisms, and it occurs over a wide range of drift rates (Smith & Ledgeway, 1997, 1998).<sup>1</sup> In the case of first-order motion stimuli the two thresholds are the same, except at very low temporal and high spatial frequencies (Green, 1983; Watson, Thompson, Murphy, & Nachmias, 1980).

### 2.2.3. Procedure

Performance was measured using the method of constant stimuli. On each trial observers were presented with a motion sequence, the duration of which was selected at random from a set of 15 values with the constraint that no value was repeated until each had been presented once over the previous 15 trials. Each sequence was immediately followed by a homogeneous blank field of the same mean luminance. The orientation of the drifting modulation could be either horizontal or vertical with equal probability, and drift direction (always orthogonal to the orientation) was also randomised. The initial phase of the modulation was randomised from trial to trial and the noise carrier, when present, was

<sup>1</sup> CMSN can sometimes give rise to local first-order luminance artifacts, due to clustering of noise elements with the same polarity, such that modulation-depth thresholds for identifying direction and orientation converge. However such artifacts are minimal, or absent, when there is no spatial variation in luminance within each noise element (Nishida et al., 1997; Smith & Ledgeway, 1997) as in this study.

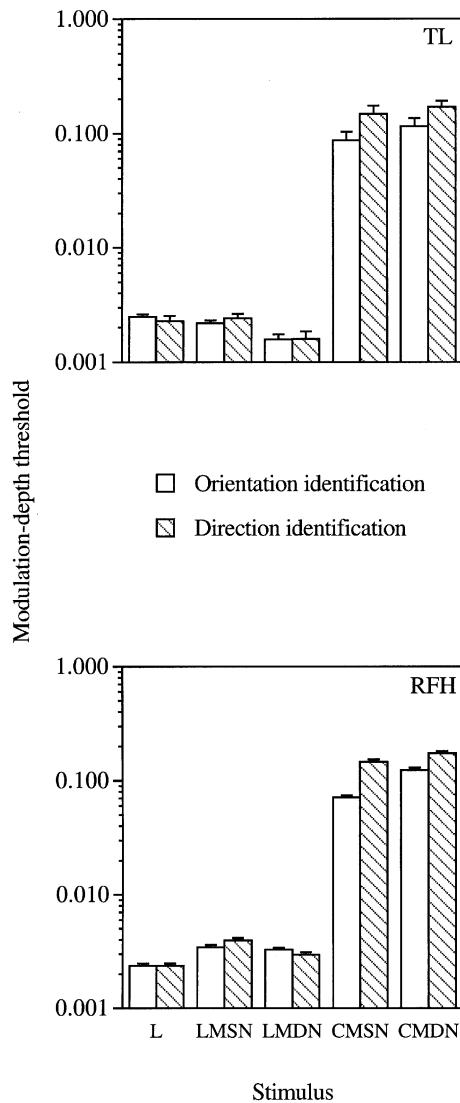


Fig. 2. Orientation-identification and direction-identification thresholds for two observers. Direction-identification thresholds were used to equate the visibility of the motion stimuli used in all experiments. First-order motion stimuli were either a conventional luminance-defined grating (L), luminance-modulated static noise (LMSN) or luminance-modulated dynamic noise (LMDN). Second-order motion stimuli were either contrast-modulated static noise (CMSN) or contrast-modulated dynamic noise (CMDN). The spatial frequency of the modulation was 0.93 c/° and it drifted smoothly at 1.26 Hz for 503.31 ms on each trial. The Michelson contrast of the 2-d noise carrier was 0.15. On each trial the orientation (either vertical or horizontal) and drift direction (either upwards, downwards, leftwards or rightwards) were randomized. The modulation depth, which was determined by the method of constant stimuli, was selected at random from a set of seven values. Observers identified both the orientation and the drift direction and completed 4 runs of 70 trials for each motion stimulus. Weibull (1951) functions were fitted to the data for each run of trials and the modulation depth producing 75% correct performance (threshold) was derived. The vertical line above each column represents +1 SEM based on variability between runs.

generated a new before each stimulus presentation. The observer identified both the orientation of the modulation and its drift direction. This dual-judgement task

logically ensures that direction identification cannot be better than orientation identification (as orientation could always be inferred from perceived direction). Observers completed 4 runs of 150 trials (10 at each of the 15 stimulus durations tested) for each motion stimulus (L, LMSN, LMDN, CMSN and CMDN) and the order in which runs were completed was randomised for each observer. Results are plotted separately for the orientation-identification and direction-identification tasks and are expressed as the percentage of trials on which the observers responded correctly to each motion stimulus as a function of its duration. Weibull (1951) functions were fitted to the data obtained for each run of trials, where this was possible, and the minimum duration corresponding to the 75% correct performance level and its SEM (based on variability between runs) were derived.

### 2.3. Results and discussion

#### 2.3.1. Orientation identification

Fig. 3 (top) shows the orientation-identification performance of observers TL and RFH as a function of duration for each of the first-order (L, LMSN and LMDN) and second-order (CMSN and CMDN) motion stimuli. Orientation-identification performance for all varieties of motion stimuli is similar and almost perfect (~100% correct) over most of the range of durations examined, with one exception: For the briefest duration, performance deteriorates, particularly for the CMDN motion stimulus. The fall off in performance at the briefest duration is perhaps unsurprising given that the nominal drift temporal frequency was maximal (18.88 Hz).<sup>2</sup> It is well established that absolute sensitivity to spatial orientation drops markedly as temporal frequency increases, especially for CMDN, even when a much longer (750 ms) stimulus duration is used (Smith & Ledgeway, 1998).

#### 2.3.2. Direction identification

For both observers direction identification (Fig. 3, bottom) exhibits the same pattern as orientation identification when first-order motion patterns were used. Performance is again close to 100% correct at all but the shortest duration tested, where it drops but remains above chance. Identifying the direction of second-order motion, however, shows a clear and robust dependence on duration. For the briefest presentations, performance

<sup>2</sup> Derrington et al. (1993) state that at the briefest stimulus duration tested in their study (22.22 ms corresponding to two images at the refresh rate of 90 Hz), during which the modulation in luminance or contrast was displaced through 0.25 spatial periods, the nominal drift temporal frequency was ~12 Hz. However this displacement, if sustained, would actually result in a drift temporal frequency of  $90 \times 0.25 = 22.5$  Hz.

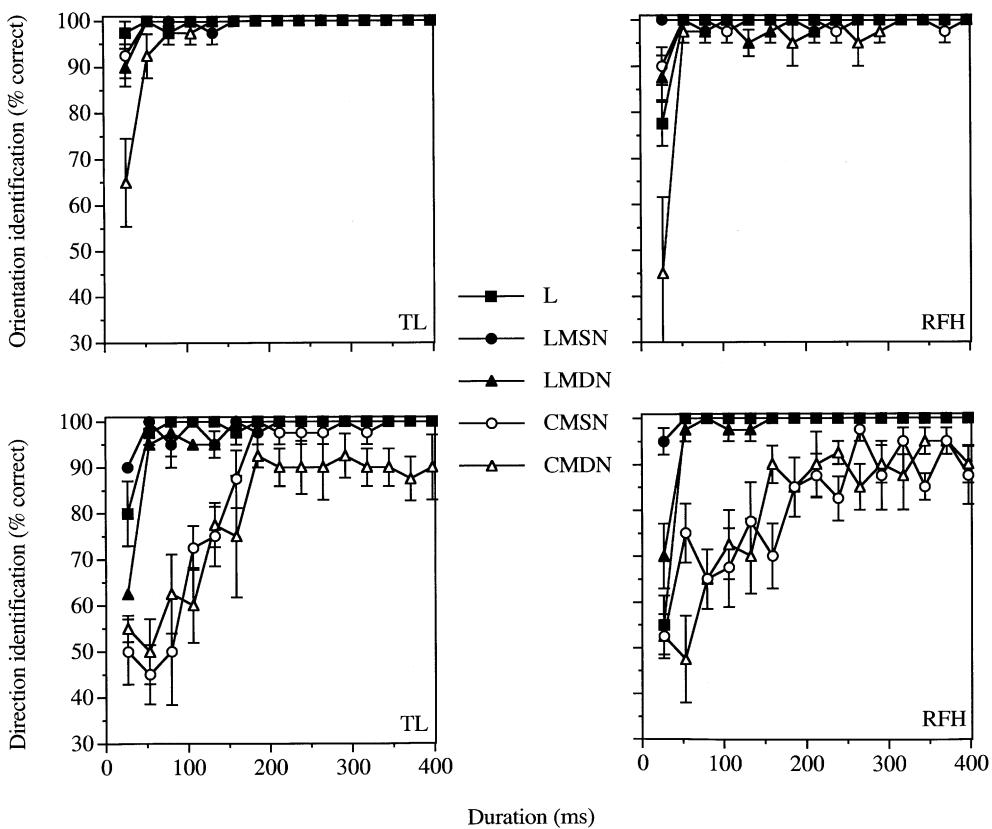


Fig. 3. Orientation-identification (top) and direction-identification (bottom) performance for comparable first-order (filled symbols) and second-order (open symbols) motion stimuli, as a function of stimulus duration for two observers. The modulation in either luminance (L, LMSN and LMDN) or contrast (CMSN and CMDN) had a spatial frequency of 0.93 c° and a drift temporal frequency that changed with duration such that each stimulus was displaced, as smoothly as was possible, through 0.25 spatial cycles during its presentation interval. All motion stimuli were presented at the same multiple of direction-identification threshold (5.9 and 5.8 times threshold for observers TL and RFH, respectively). Observers completed 4 runs of 150 trials (10 at each of the 15 stimulus duration tested) for each motion stimulus examined. The vertical lines above and below each data point represent  $\pm 1$  SEM based on variability between runs of trials.

is at chance and improves slowly with duration. The minimum durations required by observer TL to identify the direction of second-order motion were 120 ( $\pm 7$ ) and 174 ( $\pm 48$ ) ms for the CMSN and CMDN patterns, respectively. For RFH the corresponding values were 133 ( $\pm 32$ ) and 136 ( $\pm 8$ ) ms.

Thus even when first-order and second-order motion stimuli are matched for the presence of a salient noise carrier and gross differences in visibility, the ability to extract the direction of second-order motion is still considerably worse at durations  $< 100\text{--}200$  ms. Orientation-identification performance for these same classes of motion stimuli was similar, very good and affected little by duration, implying that the marked differences on the direction-identification task must be specific to mechanisms that encode drift direction rather than spatial structure. Extracting either the orientation or the direction of a second-order motion stimulus likely involves additional processing compared to first-order motion (Sutter, Beck, & Graham, 1989). Hence, it is unlikely that a delay incurred (e.g. Yo & Wilson, 1992) would selectively affect direction judgements so drasti-

cally. In addition, given that the temporal sensitivity functions for identifying either the orientation or the drift direction of contrast-defined patterns are qualitatively very similar (Smith & Ledgeway, 1998), putative differences in the shapes of these functions relative to those for first-order motion cannot account for the pattern of results found (Derrington et al., 1993). The results are, however, compatible with the direction-selectivity hypothesis. Within this scheme, orientation judgements will be relatively unaffected by the spurious motion energy present at short durations, provided that the stimulus spatial structure remains clearly visible.

### 3. Experiment 2: Varying stimulus duration with constant number and magnitude of spatial displacements

#### 3.1. Introduction

In Expt 1 decreasing duration also decreased the number of spatial displacements (number of samples per temporal period) and increased the magnitude of the

spatial displacement (jump size) on each positional update. In the limiting case, for the briefest stimulus duration studied (26.49 ms corresponding to two refreshes of the image), the modulation in luminance or contrast was displaced only once by 0.25 spatial periods midway through its presentation. Thus it was impossible to determine which of these factors was responsible for the pattern of results found for second-order motion. Previous studies (e.g. Burr, Ross, & Morrone, 1986; Nakayama & Silverman, 1985), at least in the context of conventional, luminance-defined, sinusoidal gratings, have shown that the number of displacements and the jump size on each positional update can influence both contrast sensitivity for the identification of drift direction and the perceived smoothness of the motion of suprathreshold stimuli. To investigate any possible confounding influence of these two factors on task performance, both the number of spatial displacements and the jump size were held constant in Expt 2.

### 3.2. Methods

Methods were identical to those used in Expt 1 with the following exceptions. The modulation in image lu-

minance or contrast was displaced only once, midway through the presentation interval, by 0.25 cycles of its spatial period, irrespective of the stimulus duration. This was achieved by presenting each stimulus (either L, LMSN, LMDN, CMSN or CMDN) in one spatial phase (determined randomly on each trial) for half the total stimulus duration, displacing the modulation abruptly by 0.25 spatial cycles in a given direction and presenting the stimulus in this second spatial phase for the remainder of its duration. This enabled motion sequences to be produced that differed in terms of total duration but were related by a simple temporal scaling factor (equivalent to an expansion of the time-scale of the briefest motion sequence used in Expt 1). Thus once again the nominal drift temporal frequency covaried with stimulus duration.

### 3.3. Results and discussion

#### 3.3.1. Orientation identification

Orientation-identification performance for both observers is again close to perfect for the first-order and second-order motion stimuli (Fig. 4, top) over much of the range of durations examined. At the briefest dura-

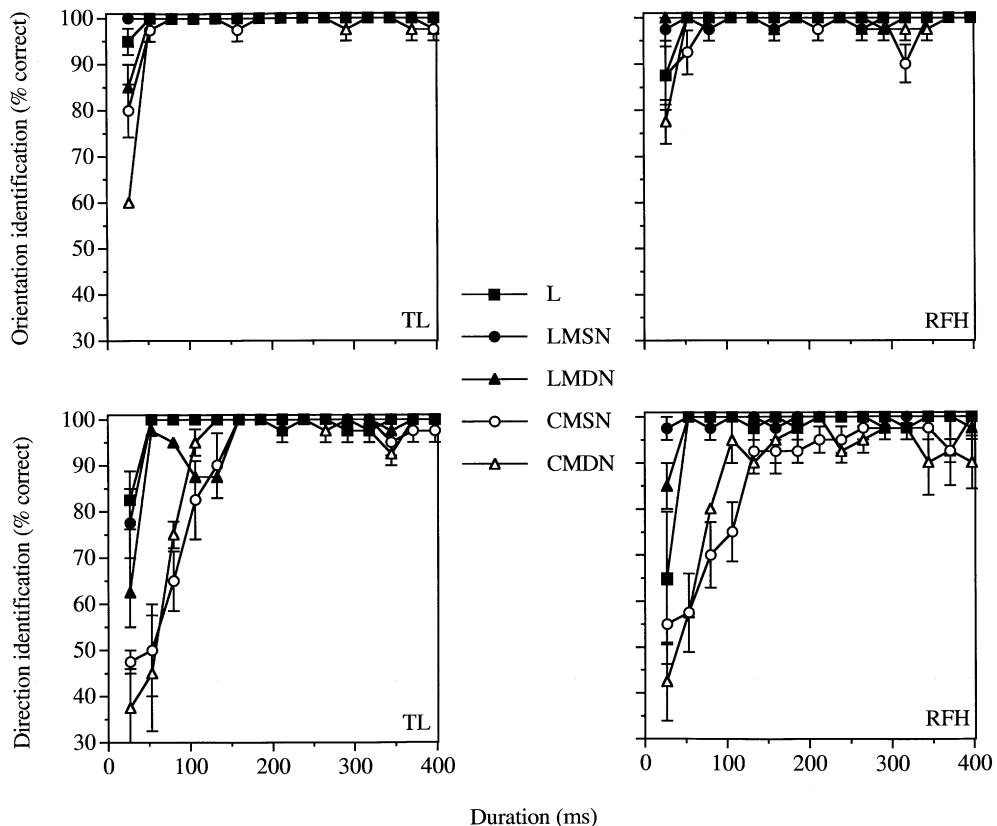


Fig. 4. Legend as for Fig. 3 with the exception that the number and the magnitude of the spatial displacement of the modulation in either luminance (L, LMSN and LMDN) or contrast (CMSN and CMDN) on each positional update were constant (i.e. "smoothness" of motion was constant). This was achieved by displacing the modulation signal only once, by 0.25 spatial periods, midway through its presentation irrespective of the stimulus duration. Thus the motion sequences used differed in terms of total duration but were related to each other by a simple temporal scaling factor.

tion performance declines, as in Expt 1, but equating the stimuli at each duration in terms of the number of spatial displacements and jump size had little effect on orientation identification.

### 3.3.2. Direction identification

For both observers the ability to identify the drift direction of the first-order motion patterns (L, LMSN and LMDN) is comparable and largely independent of stimulus duration (Fig. 4, bottom). Performance is reduced, but remains above chance, at the shortest duration and asymptotes at ~100% correct for longer durations. For the second-order motion patterns (CMSN and CMDN), however, drift direction cannot be accurately identified until the duration is ~100 ms. The minimum durations required by observer TL to identify the direction of second-order motion were 97 ( $\pm 8$ ) and 78 ( $\pm 2$ ) ms for the CMSN and CMDN patterns, respectively. For RFH the corresponding values were 91 ( $\pm 10$ ) and 74 ( $\pm 8$ ) ms. These values are somewhat smaller than those found in Expt 1.

The failure to identify the direction of second-order motion at brief durations in Expt 1, was not simply a consequence of either the reduced number of spatial displacements or the magnitude of the jump on each positional update. However when these two stimulus properties were held constant, in Expt 2, performance for both the CMSN and CMDN patterns improved. That is, correct identification of second-order motion direction was possible at shorter stimulus durations. The difference between the results of the two experiments presumably lies in the different methods used to displace the stimuli in each case. In Expt 2, unlike Expt 1, the motion stimuli were displaced only once midway through each presentation interval, irrespective of the stimulus duration. Thus the temporal transients associated with the abrupt stimulus onset and offset (which introduce spurious direction signals), were maximally equidistant in time from the stimulus displacement. This may have enabled the observers to identify the direction of second-order motion at briefer stimulus durations in Expt 2 than in Expt 1. This result is not easily accommodated by positing that either a pure processing delay (Yo & Wilson, 1992) or temporal sensitivity solely determine performance.

## 4. Experiment 3: Varying stimulus duration at each of a range of drift temporal frequencies

### 4.1. Introduction

In Expts 1 and 2 the nominal drift temporal frequency varied inversely with the stimulus duration and this may have confounded the magnitude of the effects found. As illustrated in Fig. 1, extending the duration of

a motion stimulus tends to reduce directional ambiguity, but simultaneously decreasing the drift rate exacerbates that ambiguity. Thus to isolate the effects of varying stimulus duration on the detection of first-order and second-order motion direction, it is necessary to keep drift temporal frequency constant. Using this approach, Derrington et al. (1993) found that the minimum duration required to identify the direction of luminance-defined gratings was ~80 ms when the drift rate was 0.5 Hz, but only 30 ms, or less, when it was 8 Hz. For drifting beat patterns, however, the results were less clear. Direction judgements appeared to be influenced by both the second-order motion (drifting contrast modulation) and the first-order motion (luminance components of the carrier) present in the stimulus. Consequently, they were unable to measure meaningfully the influence of stimulus duration on second-order motion, at different temporal frequencies.

In Expt 3, using drift-balanced motion stimuli, we investigated whether the minimum duration needed to identify the direction of second-order motion systematically decreases when drift temporal frequency is increased, as it does for first-order motion. If the direction-selectivity hypothesis is correct, stimulus manipulations that lead to reductions in directional ambiguity (e.g. an increase in drift rate), should improve direction identification. Indeed with a judicious choice of drift temporal frequencies (higher for second-order motion than first-order motion), it should be possible to produce comparable patterns of performance for the two types of motion.

### 4.2. Methods

Methods were identical to those used in Expt 1 with the following exceptions. We initially compared the ability to identify both the orientation and the direction of first-order motion (L, LMSN and LMDN) and second-order motion (CMSN and CMDN), when stimulus duration varied and drift temporal frequency was constant (1.26 Hz). In addition, using one variety of second-order motion stimulus (CMSN), performance was measured for a range of drift temporal frequencies (either 0.63, 1.26, 2.52 or 5.04 Hz).

### 4.3. Results and discussion

#### 4.3.1. Orientation and direction identification of motion stimuli drifting at 1.26 Hz

Orientation identification for the two observers (Fig. 5, top) exhibits the same pattern of performance as was found in Expts 1 and 2. Therefore the spatial structure of the first-order and second-order motion stimuli was readily discernible at all durations tested. On the direction-identification task (Fig. 5, bottom), for the first time in this study, performance for the first-order

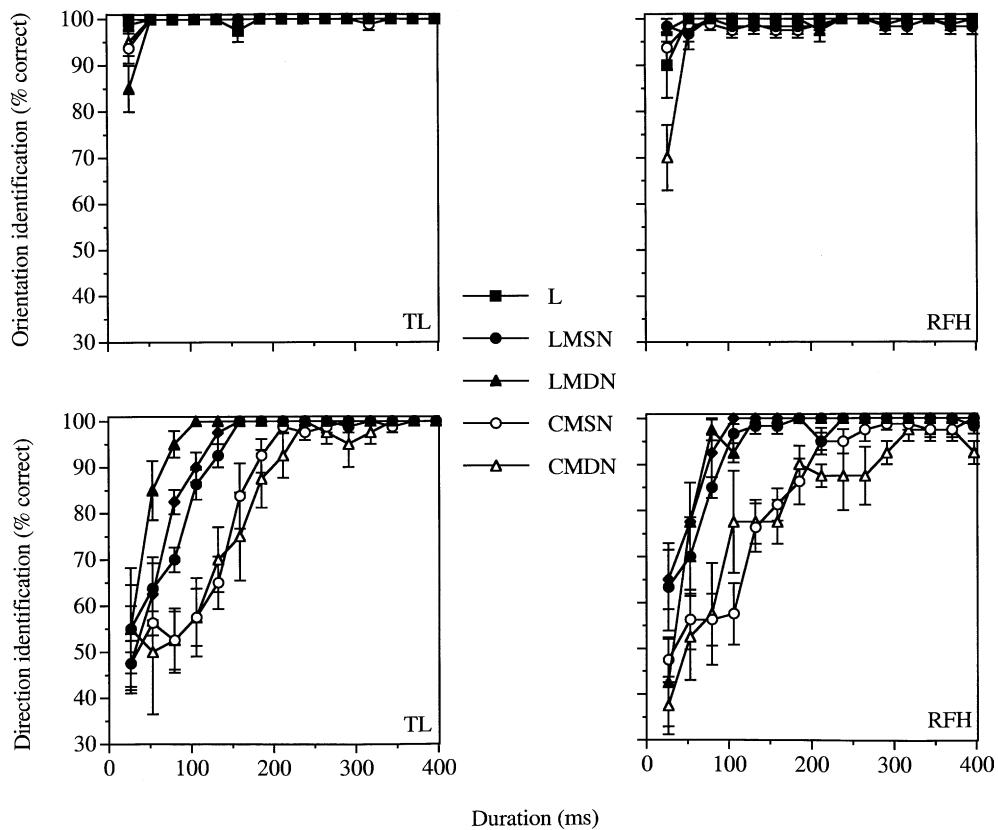


Fig. 5. Legend as for Fig. 3 with the exception that the drift temporal frequency of the modulation in either luminance (L, LMSN and LMDN) or contrast (CMSN and CMDN) was constant (1.26 Hz) and the stimulus duration was varied.

motion patterns (L, LMSN and LMDN) shows a distinct dependence on stimulus duration. To identify drift direction correctly on 75% of trials, observers TL and RFH required an average duration of 68 ( $\pm 6$ ) and 51 ( $\pm 3$ ) ms, respectively. Direction identification for the two varieties of second-order motion stimuli (CMSN and CMDN) is considerably worse than for the first-order motion patterns. TL and RFH required, on average, durations of 140 ( $\pm 7$ ) and 128 ( $\pm 13$ ) ms to achieve 75% correct performance. These values are similar to those found in Expt 1.

#### 4.3.2. Orientation and direction identification of second-order motion at each of a range of drift rates

Fig. 6 shows the results for orientation (top) and direction (bottom) identification of second-order motion (CMSN), at each of four drift temporal frequencies spanning a total range of three octaves. For both observers orientation identification is almost flawless at each stimulus duration tested, regardless of the drift temporal frequency used. In contrast, drift temporal frequency systematically influences the ability to identify second-order motion direction. The briefest duration at which accurate direction identification is possible, decreases as drift temporal frequency increases, with one exception: For observer RFH there is little difference

between the results obtained at the two highest temporal frequencies. The minimum durations required by observer TL to identify second-order motion direction at 0.63, 1.26, 2.52 and 5.04 Hz were 181 ( $\pm 3$ ), 136 ( $\pm 9$ ), 108 ( $\pm 14$ ) and 81 ( $\pm 5$ ) ms, respectively. For RFH the corresponding values were 202 ( $\pm 11$ ), 125 ( $\pm 17$ ), 96 ( $\pm 10$ ) and 99 ( $\pm 4$ ) ms, respectively. Therefore presenting second-order motion at a higher drift rate than first-order motion (cf. LMSN Fig. 5), results in similar levels of performance for the two types of motion.

The finding that the minimum stimulus duration required to identify second-order motion direction varies with drift temporal frequency, may be problematic for the processing-delay hypothesis (Yo & Wilson, 1992). This theory assumes that second-order motion is subject to a pure, and presumably invariant, processing delay. Also the fact that direction identification improves, rather than deteriorates, as temporal frequency increases, does not support the low-pass temporal filtering hypothesis (Derrington et al., 1993). The results, however, are entirely consistent with the direction-selectivity hypothesis. Brief displays and low drift rates introduce directional ambiguity, that cannot be as readily resolved by second-order motion detectors, as first-order motion detectors, because of their broader direction selectivity. In accordance with this proposal, but not originally

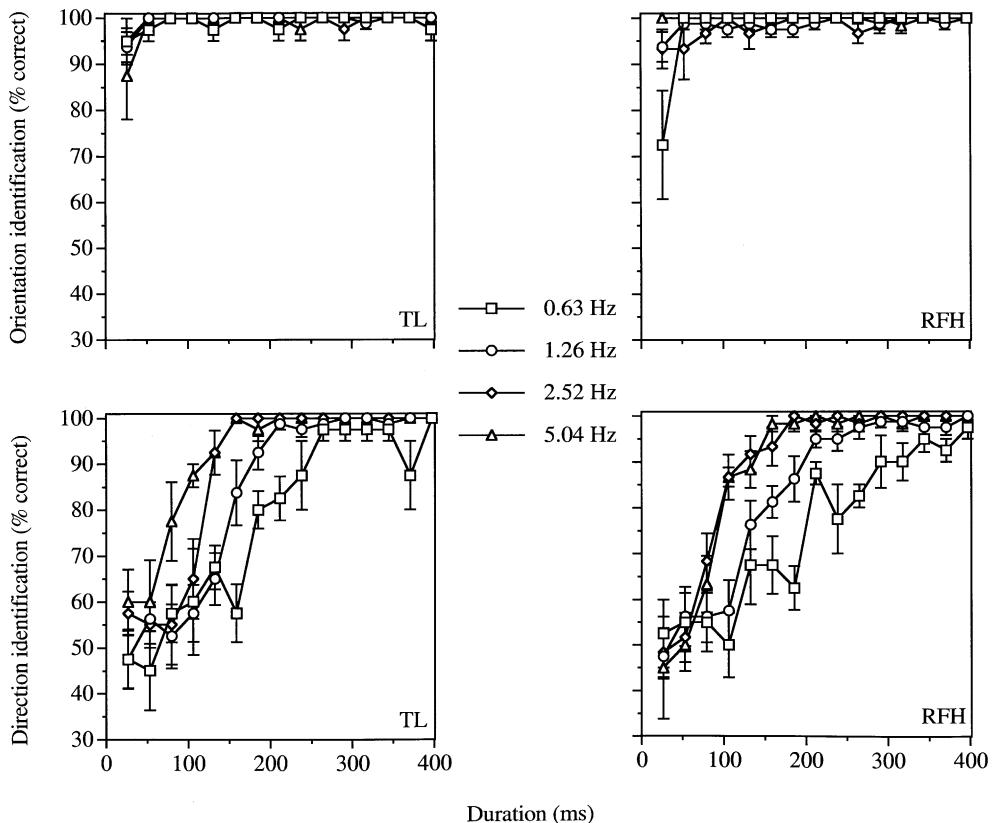


Fig. 6. Orientation-identification (top) and direction-identification (bottom) performance for second-order motion (CMSN) as a function of stimulus duration, at each of a range of drift temporal frequencies (either 0.63, 1.26, 2.52 or 5.04 Hz indicated by the different symbols). The contrast modulation had a spatial frequency of 0.93 c° and the modulation depth was either 5.9 (observer TL) or 5.8 (observer RFH) times the threshold for identifying the direction of motion at 1.26 Hz, as it was in all previous figures. In absolute terms these values correspond to modulate depths of 0.86 (TL) and 0.85 (RFH) and the stimuli were readily visible at all drift temporal frequencies tested. Observers completed at least 4 runs of 150 trials (10 at each of the 15 stimulus durations tested) for each drift temporal frequency and the vertical lines above and below each data point represent  $\pm 1$  SEM based on variability between runs of trials.

considered in these terms, Cropper and Derrington (1994, 1996) found that the lower threshold of motion (LTM—the minimum drift temporal frequency producing 75% correct direction identification), was  $\sim 3\text{--}4$  times higher for beat patterns than luminance-defined gratings. Moreover, the LTM decreased as stimulus duration increased at a similar rate in each case.

### 5. Experiment 4: The minimum modulation depth difference required between two, opposite drifting sinusoids to bias perceived direction at each of a range of stimulus durations

#### 5.1. Introduction

Several studies have employed motion displays, in which the relative modulation depths of two, or more, superimposed drifting sinusoids (typically modulations in either image luminance or contrast) are varied (e.g. Derrington & Goddard, 1989; Ledgeway, 1994; Stone,

Watson, & Mulligan, 1990; von Grünau, Bertone, & Pakneshan, 1998). This has been done to affect the balance of activity between motion-detecting mechanisms selective for different directions of drift and influence the resultant perceived direction of motion. If the mechanisms that respond to second-order motion are less selective for direction, than those that analyse first-order motion, they should require a greater imbalance in the motion energy present in each direction to disambiguate the overall (net) direction of movement. This prediction was tested, in Expt 4, by systematically varying the modulation depths of two, superimposed sinusoids drifting in opposite directions (either both first-order or both second-order), in an antagonistic (see-saw) manner. The minimum imbalance needed to identify reliably the direction of the component with the higher modulation depth, should serve as an index of the direction selectivity of the underlying mechanisms. Of course it is not necessary to assume that detectors tuned to opposite directions are in strict opponency (i.e. that explicit response subtraction occurs). The visual system

could implement some other decision rule (e.g. selecting the direction producing the largest output) based on relative activity to determine the net drift (Van Santen & Sperling, 1985).

## 5.2. Methods

Methods were similar to those used previously, but with the following exceptions. First-order motion stimuli were composed of LMSN and second-order motion stimuli of CMSN (although the generality of the basic result to L, LMDN and CMDN was confirmed in a control experiment). The motion stimuli were directionally ambiguous. LMSN was produced by summing two, vertically oriented, luminance-defined sinusoidal gratings of the same spatial (0.93 c°) and temporal (1.26 Hz) frequency, drifting in opposite directions with 2-d noise. CMSN was produced by multiplying two sinusoidal gratings with noise. The overall modulation depths of the first-order motion and second-order motion stimuli were constant and equated in terms of multiples of threshold. However the relative modulation depths of the opposite moving sinusoidal components could be manipulated in an antagonistic fashion. For example if the modulation depth of the leftwards drifting component increased by 10%, the rightwards component decreased by 10% accordingly. In this manner it was possible to induce a percept of net drift, in the direction of the component with the higher modulation depth.

Performance was measured separately at each of a number of stimulus durations. These ranged from a maximum of 503.31 ms to a minimum that was determined, independently for each observer and variety of motion stimulus, as that duration for which a robust psychometric function could be obtained. For LMSN the briefest duration tested was either 105.96 (TL) or 172.19 ms (RFH) and for CMSN it was either 172.19 (TL) or 238.41 ms (RFH). In addition performance for L, LMDN and CMDN was measured at the longest stimulus duration (503.31 ms).

On each trial observers were presented with a bidirectional motion stimulus, selected at random from a set of 11 (5 in which the component with the higher modulation depth drifted leftwards, 5 in which it drifted rightwards and 1 in which the modulation depth in each direction was equal). The observer indicated the overall perceived direction of motion. Weibull (1951) functions were fitted to the data. The relative modulation depth of the leftwards drifting component which gave rise to “leftwards” responses on 75% of trials and that of the rightwards drifting component which produced “rightwards” responses on 75% of trials were calculated. These two values were averaged to derive a relative modulation-depth threshold (expressed as a percentage of the overall stimulus modulation depth) and a SEM

(based on variability between runs) for each condition examined.

## 5.3. Results and discussion

### 5.3.1. Comparison of thresholds for L, LMSN, LMDN, CMSN and CMDN at a duration of 503 ms

In Fig. 7 (top) the relative modulation-depth threshold is plotted as a function of the stimulus duration separately for each observer. At the longest duration tested thresholds for the three varieties of first-order motion stimuli (L, LMSN and LMDN) are almost identical and are, on average, 52.58 (TL) and 52.14% (RFH). For the second-order motion stimuli (CMSN and CMDN) thresholds are also comparable, but are considerably higher than those for the first-order motion patterns. Averaged across the CMSN and CMDN stimuli the relative modulation-depth thresholds are 55.93 (TL) and 55.50% (RFH). Thus to determine the overall direction of first-order motion, either leftwards or rightwards, the modulation depth of the component drifting in that direction had to be at least ~1.10 times that of the component drifting in the opposite direction. For second-order motion the corresponding value is ~1.26. Therefore, even at this relatively long stimulus duration (longer than that required for errorless direction identification in Expts 1–3), performance for second-order motion is worse than for first-order motion.

### 5.3.2. The effects of reducing stimulus duration on relative modulation-depth thresholds

For the two observers thresholds for second-order motion (CMSN) are higher than those for first-order motion (LMSN), over the entire range of durations tested. As the stimulus duration decreases relative modulation-depth thresholds initially change very little for both varieties of motion, but increase rapidly at the briefest durations tested. Importantly the stimulus duration at which thresholds first begin to rise markedly, is longer for second-order motion than first-order motion. For example in the case of CMSN, thresholds for observer TL are approximately constant for stimulus durations >238 ms and are, on average, 56.62%. At the briefest duration tested the threshold for TL reaches a maximum of 71.63%, indicating that a modulation-depth ratio of ~2.5 is needed to identify the direction of the component with the greater modulation depth. For RFH a similar pattern of results is evident, but the effects are slightly less marked and thresholds are marginally lower. For the first-order motion stimulus (LMSN) thresholds change little over most of the durations tested (53.32% on average for the two observers), but increase, at least for observer TL, at the briefest duration to 64.79% (a ratio of ~1.8 between the modulation depths in opposite directions).

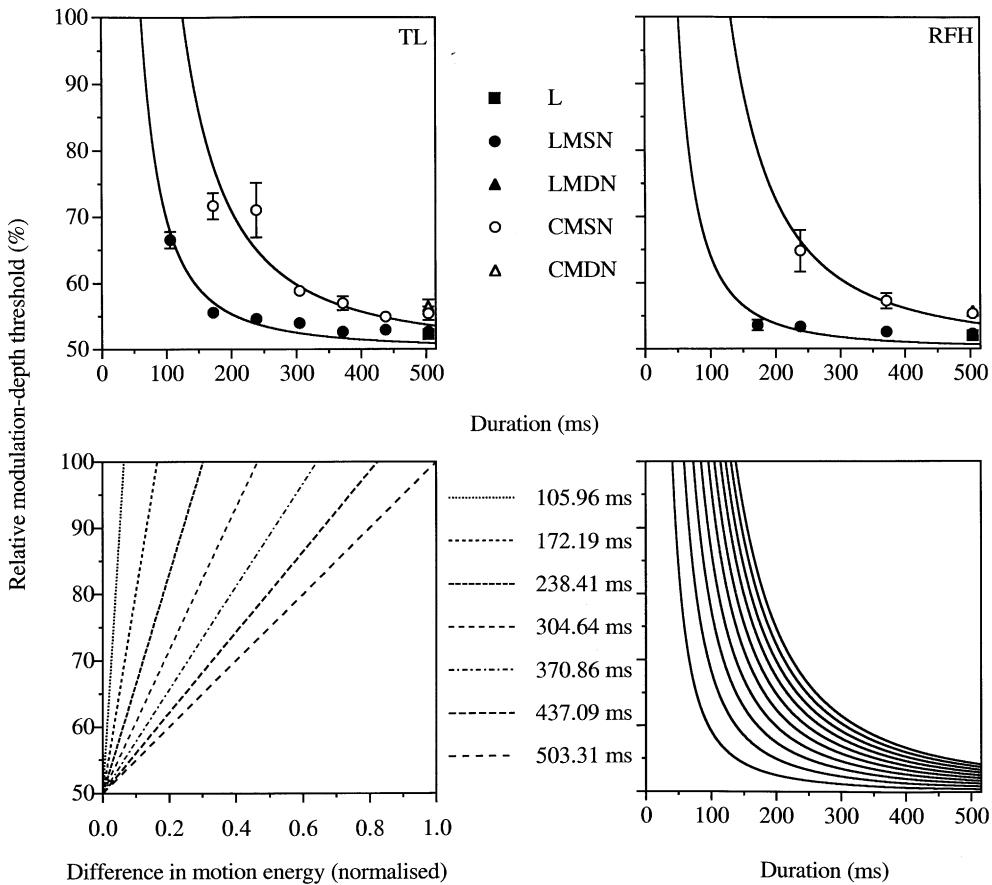


Fig. 7. The minimum differences in signal strength needed between two, opposite drifting modulations ( $0.93\text{ c}^{\circ}$  and  $1.26\text{ Hz}$ ) in either luminance (filled symbols) or contrast (open symbols) to elicit a reliable percept of net drift (top). These are expressed as a relative modulation-depth threshold (indicating the amplitude of the component with the higher modulation depth as a percentage of the total stimulus modulation depth). The overall modulation depths of the first-order motion and second-order motion stimuli were constant and equated. Thresholds were determined using the method of constant stimuli in which the relative modulation depths of the opposite drifting sinusoids were manipulated in an antagonistic (see-saw) fashion, to bias perceived direction either leftwards or rightwards. Each threshold is based on at least 4 runs of 110 trials (10 at each of 11 relative modulation depths chosen to bracket the threshold) and the vertical lines above and below each data point represent  $\pm 1\text{ SEM}$  based on variability between runs. The continuous lines represent the best-fitting curves to the data for which the difference in motion energy between the leftwards and rightwards directions is constant. The plot at the bottom left illustrates the relationship between relative modulation depth and the net difference in motion energy (range normalised to unity) between opposite directions for each of a range of stimulus durations (indicated by the different line styles). In the bottom right plot the continuous lines represent a family of curves. For each curve the normalised difference in motion energy is constant and ranges from 0.01 to 0.1 in steps of 0.01, as indicated by the translation of the curves both upwards and rightwards.

The results clearly support the direction-selectivity hypothesis. Thresholds for first-order motion were lower, affected less by decreasing stimulus duration and could be measured at much shorter exposures than for second-order motion. This suggests that the additional directional ambiguity that occurs as stimulus duration decreases (which will effectively reduce any inequality between opposite directions produced by a difference in modulation depth), had a greater impact on the mechanisms that encode contrast-defined motion than luminance-defined motion. Neither a processing delay specific to second-order motion, nor gross differences in temporal sensitivity or acuity to each type of motion (given that drift temporal frequency was constant and the stimuli were equally visible), could account for the pattern of results found.

### 5.3.3. The relationship between the relative modulation-depth threshold and the net motion energy

Fig. 7 (bottom left) was derived by taking Fourier transforms of image sequences analogous to those actually presented. Each motion sequence was represented as a  $256 \times 256$  pixel  $x-t$  plot and the relative modulation depth was varied from 50% to 100% in 5% steps. Second-order images were subjected to a pointwise non-linearity (e.g. full-wave rectification) prior to computing the transforms, to make explicit the second-order motion energy (summed power over all frequencies) in each drift direction was computed and the net difference calculated. Previous studies have used variants of this technique to estimate the net motion energy available for first-order and second-order motion detection (Boulton

& Baker, 1993; Dosher, Landy, & Sperling, 1989; Mather & Tunley, 1995a,b; Nishida & Sato, 1992).

As the net differences in motion energy scaled uniformly with the square of the overall modulation depths of the stimuli, and for second-order motion patterns depended on the form of the nonlinearity applied to the images, the range was normalised to unity. This procedure is not unreasonable in that the first-order and second-order motion stimuli used in the experiment were also normalised, in terms of multiples of direction-identification threshold. The assumption that first-order and second-order patterns give rise to neural signals of comparable magnitude under these conditions is well supported (e.g. Ledgeway & Smith, 1995). This produced an identical linear relationship between the relative modulation-depth threshold and the difference in motion energy, at each duration, for all varieties of motion stimuli used. The slope of this function increases as the duration decreases (due to the smearing of the distribution of motion energy across the two directions), as expected.

Fig. 7 (bottom right) illustrates a family of continuous curves. Each curve depicts how relative modulation-depth thresholds should vary with stimulus duration, if the mechanisms that analyse motion require a consistent minimum difference in energy between opposite directions to disambiguate the drift direction. The (normalised) difference in motion energy is constant for each curve, but increases (from 0.01 to 0.1 in steps of 0.01) as the curves shift systematically both upwards and rightwards across the page. Similarly the continuous lines shown in Fig. 7 (top) through each observer's data are the best-fitting curves for the LMSN and CMSN patterns for which the (normalised) difference in motion energy (the only free parameter used to derive each fit) is constant across all durations. The curves capture the variation in relative modulation-depth threshold with stimulus duration well and the  $r^2$  values of the fits were, on average, 0.91. For observer TL the difference in motion energy, derived from the curve fitting procedure, was 0.085 for CMSN and 0.022 for LMSN.<sup>3</sup> For observer RFH the corresponding values were 0.091 and 0.015, respectively. This analysis provides further support for the direction-selectivity hypothesis. Second-order motion detectors, compared with first-order motion

detectors, exhibit broader direction selectivity and consequently require a greater (by a factor of ~4) difference in motion energy between opposite directions to discern the net direction of image motion. Importantly the fitted curves also predict that when the relative modulation depth is 100% (equivalent to a single sinusoidal component drifting at 1.26 Hz), the briefest duration at which the direction can be identified should be longer for CMSN (~124 ms) than LMSN (~58 ms). It is apparent from Fig. 5 that this is indeed the case.

## 6. Experiment 5: Varying the stimulus duration of first-order motion patterns composed of two, opposite drifting sinusoids with unequal modulation depths

Another prediction of the direction-selectivity hypothesis is that any first-motion stimulus which reduces the inequality between detectors of opposite directions of motion, to an extent comparable to that of second-order motion sensors, should exhibit a similar dependence on stimulus duration. One method by which this could be achieved is to present bidirectional, first-order motion patterns composed of two, opposite drifting sinusoidal components and vary the stimulus duration at each of a range of relative modulation depths. The smaller the imbalance in modulation depth (and hence motion energy), the smaller will be the difference in activity between detectors sensitive to each direction. Consequently as the modulation depth difference is reduced, the minimum stimulus duration needed to identify the dominant direction of drift should systematically increase, and approach that obtained with second-order motion. This is important because in Expt 3, using a different technique, a corresponding similarity in direction-identification performance for the two varieties of motion was produced. This prediction was tested in the present experiment.

### 6.1. Methods

Methods were similar to those used in Expt 3 with the following exceptions. First-order motion stimuli were composed of LMSN and were produced by summing two sinusoidal gratings (each 0.93 c° and 1.26 Hz) of the same orientation (either vertical or horizontal) drifting in opposite directions with 2-d noise. In an analogous manner to Expt 4, the overall modulation depths of the LMSN stimuli were constant and identical, with respect to multiples of direction-identification threshold. However the relative modulation depths of the opposite moving sinusoidal components were unequal. The relative modulation depth of the component with the higher amplitude was either 60%, 70% or 80%, so that the component drifting in the other direction was always above its own absolute threshold for direction-

<sup>3</sup> Additional observations revealed that even when the overall modulation depth of the LMSN patterns was reduced from 5.9 to 2.95 times direction-identification threshold, relative modulation-depth thresholds measured for TL over a range of stimulus durations were best fit ( $r^2 = 0.98$ ) by a curve for which the normalised difference in motion energy was 0.021 (taking account of the fact that a 2-fold reduction in the overall modulation depth produces a 4-fold increase in the slopes of the linear functions depicted in Fig. 7, bottom left). This lends support for an analysis of the present results in terms of the motion energy difference between opposite directions rather than say the energy ratio (e.g. Stromeier, Kronauer, Madsen, & Klein, 1984).

identification when presented in isolation. For each relative modulation-depth condition, orientation-identification and direction-identification performance were measured as function of stimulus duration. To decide whether a direction response was correct or incorrect, we treated the stimulus as if it were moving in the same direction as the higher modulation-depth component (either upwards, downwards, leftwards or rightwards), as this determined the overall perceived direction of drift.

## 6.2. Results and discussion

### 6.2.1. Orientation identification

Fig. 8 (top) shows orientation-identification performance for the two observers. LMSN patterns had a relative modulation depth ranging from 60% to 100% and CMSN stimuli had a relative modulation depth of 100%. (Stimuli with a relative modulation depth of 100% consist of a single, sinusoidal component drifting at 1.26 Hz and the data shown have been replotted from Fig. 5 (top) for comparison purposes.) Performance for all stimuli is largely independent of stimulus duration

and is similar to that found in Expts 1–3. When the relative modulation depth of the LMSN patterns is low (e.g. 60%), performance deteriorates at the shortest durations tested, but is still above chance. Therefore the spatial structure of the patterns was readily visible and did not compromise the ability to extract the drift direction.

### 6.3. Direction identification

Direction-identification performance (Fig. 8, bottom) for the two observers exhibits a distinct dependence both on the stimulus duration and the relative modulation depth of the LMSN patterns. Performance is at chance at the briefest durations and gradually improves with increasing stimulus duration until it eventually stabilises close to 100% correct. The shortest stimulus duration at which accurate direction identification for the LMSN stimuli is possible, varies systematically with the relative modulation depth of the component drifting in that direction. As the relative modulation depth of this component decreases, and the motion energy in opposite directions becomes more similar, observers

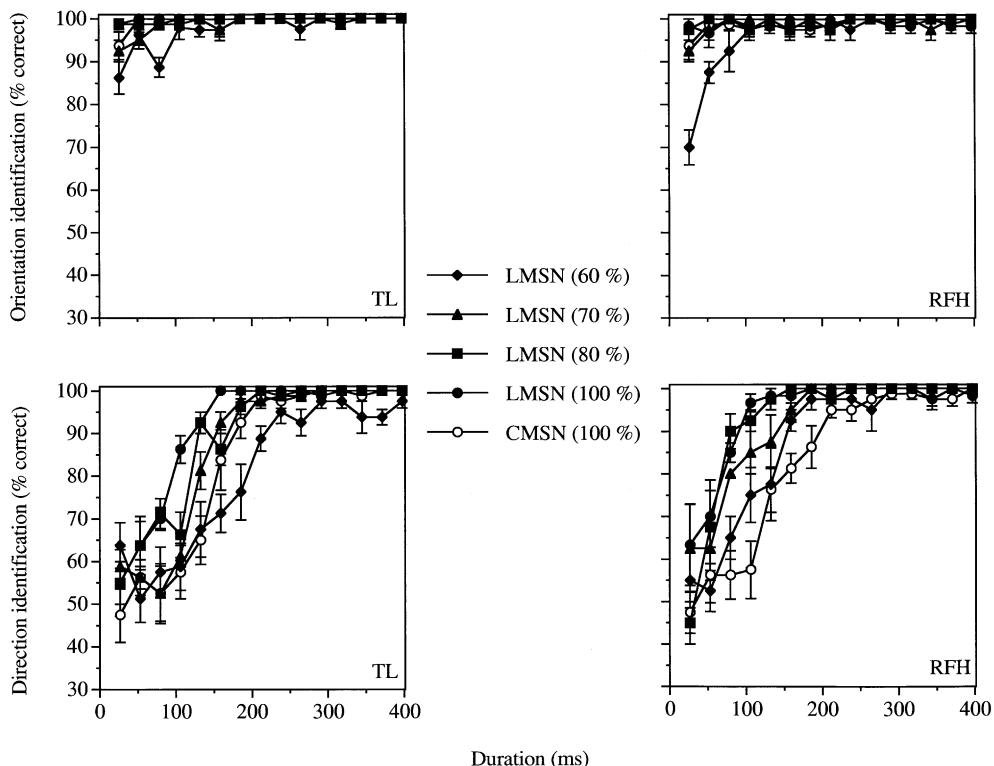


Fig. 8. Legend as for Fig. 5 with the exception that first-order motion stimuli (LMSN) were composed of two, opposite drifting sinusoidal components ( $0.93\text{ c}^\circ$  and  $1.26\text{ Hz}$ ) of unequal modulation depth. The overall (absolute) modulation depth of the patterns was constant and identical to that used previously, with respect to multiples of direction-identification threshold. The relative modulation depth (expressed as a percentage of the overall modulation depth) of the component with the higher luminance contrast was either 60%, 70% or 80% (indicated by the different filled symbols). To classify a direction response as either correct or incorrect each stimulus was treated as though it were drifting in the same direction as the higher modulation-depth component, as this determined the perceived motion direction. Performance for LMSN and CMSN patterns with a relative modulation depth equivalent to 100% (composed of a single, drifting sinusoidal modulation) is also replotted from Fig. 5 for comparison.

require a longer stimulus duration to achieve an equivalent level of performance. To achieve 75% correct performance using first-order motion patterns with relative modulation depths of 60%, 70%, 80% and 100%, the minimum stimulus durations were 155 ( $\pm 17$ ), 122 ( $\pm 8$ ), 88 ( $\pm 11$ ) and 80 ( $\pm 6$ ) ms for observer TL. For observer RFH the corresponding durations were 110 ( $\pm 9$ ), 66 ( $\pm 12$ ), 57 ( $\pm 8$ ) and 52 ( $\pm 6$ ) ms, respectively. For second-order motion with a relative modulation depth of 100% the values for TL and RFH were 136 ( $\pm 9$ ) and 125 ( $\pm 17$ ) ms, respectively.

Thus introducing directional ambiguity into luminance-defined motion patterns, can produce direction-identification performance that is quantitatively similar to that found with second-order motion. That this is even possible casts further doubt on the both the processing-delay hypothesis (Wilson et al., 1992) and the low-pass temporal filtering hypothesis (Derrington et al., 1993) of second-order motion processing. It is interesting to compare (in Fig. 9) the stimulus durations at which direction identification reached 75% correct in the present experiment with those obtained in Expt 3, when drift temporal frequency was also 1.26 Hz, and the relative modulation-depth thresholds measured at each duration in Expt 4. The continuous curves shown in the figure are identical to those shown in Fig. 7 (top) for each observer and variety of motion (i.e. the curve fits have not been adjusted). The consistency between the results of the three experiments is striking and all conform very closely to the model curves. These depict how performance should depend on stimulus duration, if motion mechanisms require a constant minimum difference in energy between opposite directions to determine the overall net drift. This provides compelling evidence that the mechanisms that respond to second-order motion are less selective for drift direction, and invariably require a greater disparity in the effective motion energy available in opposite directions, than those responsive to first-order motion.

Although the essence of the model depicted in Fig. 9 (i.e. comparing motion energy in opposite directions to derive the net drift direction) may be able to accommodate the essentially qualitative results of Expts 1 and 2, no formal attempt was made to do this for the following reasons. In the first two experiments the nominal drift temporal frequency of the motion patterns was not constant, but increased over a 29-fold range (from  $\sim 0.65$  to  $\sim 18.88$  Hz) as the stimulus duration decreased. Under these conditions the temporal sensitivity and acuity limits of motion-detecting mechanisms will inevitably constrain performance and there will be a concomitant deterioration in the ability to encode motion at high drift rates. It seems likely, therefore, that the higher drift temporal frequencies present at the shortest durations tested may have superficially extended the apparent minimum duration required to identify drift direction,

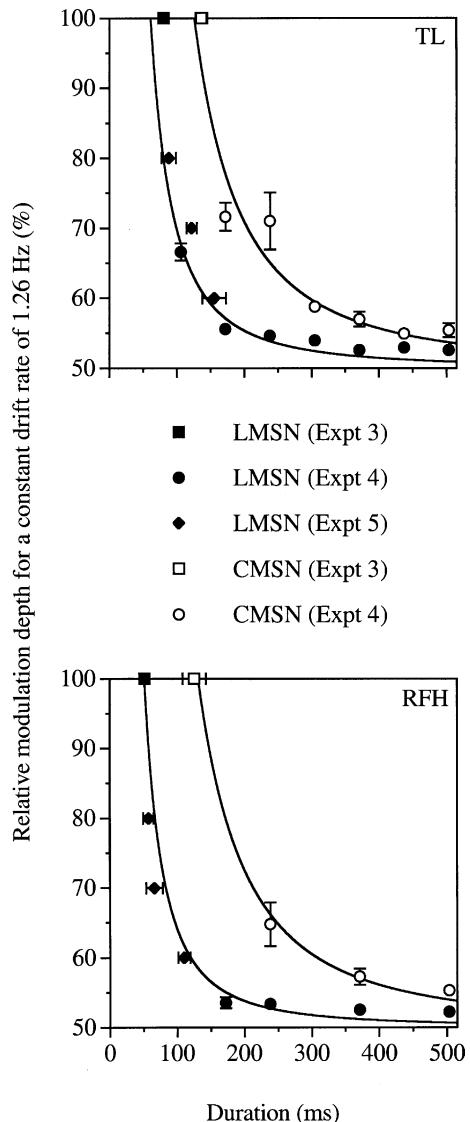


Fig. 9. Comparison of the minimum stimulus durations at which the drift direction could be accurately identified in Expts 3 (when drift temporal frequency was 1.26 Hz) and 5, with the relative modulation-depth thresholds measured at each duration in Expt 4. Data shown are for motion stimuli containing static noise only (LMSN and CMSN as indicated by the filled and open symbols, respectively) and are plotted separately for the two observers. The continuous curves in each plot are identical to those shown in Fig. 7 (top) and depict the patterns of performance expected if motion mechanisms require a constant minimum difference in motion energy, regardless of stimulus duration, between opposite directions to disambiguate the resultant drift. The vertical lines above and below each circular data point represent  $\pm 1$  SEM, based on variability between runs of trials, for the relative modulation-depth thresholds obtained in Expt 4. Similarly the horizontal lines to the left and right of each square and diamond data point represent  $\pm 1$  SEM for the stimulus durations derived in Expts 3 and 5.

especially for contrast-modulated noise patterns for which temporal resolution may be particularly poor. However in its present form the simple motion energy difference model we have considered utilises all of the potential motion information available in the stimulus regardless of temporal frequency. So, for example, very

high temporal frequencies near the acuity limit are given equal weight to spurious low temporal frequencies (introduced by the finite temporal window) moving in the opposite direction (cf. Fig. 1). However this potential weakness of the model is unproblematic for the experimental conditions where the drift temporal frequency was constant, low (1.26 Hz as in Fig. 9) and close to the region of maximal temporal sensitivity for both first-order motion and second-order motion. Although a more complete model would undoubtedly need to take account of the temporal limits of vision, these are still very much under debate in the case of second-order motion and first-order motion patterns containing noise carriers (Derrington, 1994; Gorea, Wardak, & Lorenzi, 2000; Holliday & Anderson, 1994; Lu & Sperling, 1995; Schofield & Georgeson, 2000; Smith & Ledgeway, 1998).

## 7. General discussion

The principal aim of this study was to investigate why the direction of second-order motion, unlike first-order motion, cannot be identified when the stimulus exposure duration is brief (<200 ms). Previous studies have attempted to explain this, and related phenomena, by postulating that second-order motion extraction is subject to either processing delays (e.g. Wilson et al., 1992) or sluggish temporal responses (Derrington et al., 1993). However neither of these theories is entirely satisfactory and they neglect both the spurious motion signals introduced by the temporal window within which any finite motion stimulus is presented and the direction selectivity of motion-detecting mechanisms. We suggested that the sensors that encode second-order motion may be simply less selective for stimulus direction than first-order motion detectors, and thus are more susceptible to the deleterious effects of limiting stimulus duration. Although previous studies (see Section 1) offer some limited and indirect support for this proposal, the results of all five experiments in the present study are in excellent agreement with its predictions and present considerable difficulties for the alternative explanations.

The results clearly support models that advocate that first-order motion and second-order motion are, at least initially, each detected by separate (distinct) mechanisms (e.g. Badcock & Derrington, 1985, 1989; Chubb & Sperling, 1988; Wilson et al., 1992; Zhou & Baker, 1993). The fact that there are robust and large differences in the processing of the two varieties of motion in human vision may pose particular problems for alternative models proposing that they are encoded by common (the same) direction-selective mechanisms (Johnston et al., 1992).

If first-order motion and second-order motion are initially detected by separate motion mechanisms, they

are likely to be subsequently combined at some stage in the visual system. This is supported by phenomena such as the transfer of aftereffects between first-order and second-order motion patterns at suprathreshold stimulus levels (e.g. Ledgeway, 1994; Nishida & Sato, 1995) and the phenomenological coherence of plaid patterns composed of first-order and second-order motion components (Stoner & Albright, 1992). Indeed Wilson et al. (1992) have tentatively identified, in primates, area MT as the possible neural substrate where this pooling of motion signals occurs. One would expect the mechanisms mediating this pooling process to be influenced by the fidelity of the inputs they receive from motion sensors responsive to either first-order motion or second-order motion. If the ability of second-order motion detectors to respond differentially to motion in different directions is relatively impoverished, then this would explain why neurones sensitive to both varieties of motion typically exhibit, as a population, poorer selectivity to the drift of second-order motion (Albright, 1992; Churan & Ilg, 2001; Geesaman & Andersen, 1996; Zhou & Baker, 1994). However electrophysiological studies have yet to identify cells that respond only to second-order motion and so the properties of the neurones feeding any subsequent pooling process are unknown. If such cells do exist, as predicted by most current motion models, then in light of the present results it would seem crucial to compare their direction selectivity to neurones that respond only to first-order motion (taking account of differences in absolute sensitivity and the presence of the carrier).

The results also have a bearing on studies that have examined the precision with which observers can make fine judgements of second-order motion direction. For example Ledgeway (1999) showed that under optimal conditions with a long stimulus duration (1.1 s), observers could reliably discriminate a 4–5° difference in the directions of two, random-dot patterns in which the dots were defined by contrast differences with respect to the background. Direction-discrimination thresholds for first order, luminance-defined dots can be as low as 1.5° under comparable conditions (Watamaniuk, Sekuler, & Williams, 1989). Similarly Donnelly, Bowd, and Patterson (1997) showed that thresholds for rigidly moving patterns composed of dots defined by binocular disparity (cyclopean second-order motion) were ~2.5 times higher (3.4°) than those for luminance-defined dots (1.4°). Interestingly when a fixed proportion of the dots (“signal” dots) moved in a consistent direction and the remainder (“noise” dots) were displaced randomly over a 360° range, discrimination thresholds were similar, but only when the percentage of signal dots in the first-order motion patterns was ~5 times lower (and the noise proportionally higher) than in the second-order motion stimuli. This indicates that the precision with which observers are able to determine the overall direction of

second-order motion is considerably worse than first-order motion, unless the latter is degraded by the presence of substantial directional noise (spurious motion signals). These results are in good agreement with those of the present study. They also suggest that the mechanisms that encode second-order motion are less selective for direction, and moreover not just with regard to opposite directions, than those that analyse first-order motion.

The existence of mechanisms poorly tuned for direction may also have an impact on the interpretation of some phenomena that have been attributed to the operation of slow, attention-based processes. Visual search times for identifying a second-order motion target (a patch of contrast-modulated grating or noise) among spatial distractors that all have the opposite drift to the target, are longer overall and increase more steeply with the number of items present (e.g. 76 ms/item) than those for first-order motion (e.g. 9.5 ms/item). This has been taken to indicate that the attentional demands for extracting the direction of second-order motion are greater than those for first-order motion (Ashida & Osaka, 1998; Seiffert & Cavanagh, 1999). However the onset of the patterns (which is abrupt to allow precise measurement of response latencies) will inevitably introduce spurious motion (directional ambiguity) into the display (cf. Fig. 1). This will have an adverse effect on the ability to rapidly extract and compare the directions of the target and distractors, especially when they contain second-order motion and the drift rate is low (Seiffert & Cavanagh, 1999). Furthermore if second-order motion detectors are less direction selective than first-order motion detectors, then second-order motion stimuli are in some sense (to the visual system) always more directionally ambiguous. Thus the second-order motion target and distractors may be less dissimilar perceptually and require a slower, more attention-demanding search (Duncan & Humphreys, 1989, 1992).

That the direction-selective properties of motion detectors could determine visual search efficiency has not been considered previously and may account for other latency-dependent differences reported (Allen & Derrington, 2000). If this is the case then some of the discrepancies should diminish when either the drift temporal frequency of second-order motion is increased, or the directional ambiguity of first-order motion patterns is increased. These possibilities remain to be tested, but it is clear that the results of the present study have important implications for a wide range of motion tasks.

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## 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.
- Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science*, 255, 1141–1143.
- Allen, H. A., & Derrington, A. M. (2000). Slow discrimination of contrast-defined expansion patterns. *Vision Research*, 40, 735–744.
- Ashida, H., & Osaka, N. (1998). Second-order motion does not pop-out. *Perception*, 27(Suppl.), 181.
- Badcock, D. R., & Derrington, A. M. (1985). Detecting the displacement of periodic patterns. *Vision Research*, 25, 1253–1258.
- Badcock, D. R., & Derrington, A. M. (1989). Detecting the displacement of spatial beats: No role for distortion products? *Vision Research*, 29, 731–739.
- Baker, C. L. (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology*, 9, 461–466.
- Benton, C. P., & Johnston, A. (1997). First-order motion from contrast modulated noise? *Vision Research*, 37, 3073–3078.
- Boulton, J. C., & Baker, C. L. (1993). Different parameters control motion perception above and below a critical density. *Vision Research*, 33, 1803–1811.
- Burr, D. C., Ross, J., & Morrone, M. C. (1986). Sampled and smooth motion. *Vision Research*, 26, 643–652.
- 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.
- Churam, J., & Ilg, U. J. (2001). Processing of second-order motion stimuli in primate middle temporal area and medial superior temporal area. *Journal of the Optical Society of America A*, 18, 2297–2306.
- Cropper, S. J., Badcock, D. R., & Hayes, A. (1994). On the role of second-role signals in the perceived direction of motion of type II plaid patterns. *Vision Research*, 34, 2609–2612.
- Cropper, S. J., & Derrington, A. M. (1994). Motion of chromatic stimuli: First-order or second-order? *Vision Research*, 34, 49–58.
- Cropper, S. J., & Derrington, A. M. (1996). Detection and motion detection in chromatic and luminance beats. *Journal of the Optical Society of America A*, 13, 401–407.
- Culham, J. C., Nishida, S., Ledgeway, T., Cavanagh, P., von Grünau, M. W., Kwas, M., Alais, D., & Raymond, J. E. (1998). Higher order effects. In G. Mather, F. Verstraten, & S. Anstis (Eds.), *The motion after-effect: A modern perspective* (pp. 85–124). Cambridge: MIT Press.
- DeAngelis, G. C., Ohzawa, I., & Freeman, R. D. (1993a). Spatiotemporal organization of simple-cell receptive fields in the cat's striate cortex. I. General characteristics and postnatal development. *Journal of Neurophysiology*, 69, 1091–1117.
- DeAngelis, G. C., Ohzawa, I., & Freeman, R. D. (1993b). Spatiotemporal organization of simple-cell receptive fields in the cat's striate cortex. II. Linearity of temporal and spatial summation. *Journal of Neurophysiology*, 69, 1118–1135.
- Derrington, A. M. (1994). Analysis of the motion of contrast-modulated patterns. *Investigative Ophthalmology and Visual Science*, 35(Suppl.), 1406.
- Derrington, A. M., & Badcock, D. R. (1985). Separate detectors for simple and complex patterns? *Vision Research*, 25, 1869–1878.
- Derrington, A. M., Badcock, D. R., & Henning, G. B. (1993). Discriminating the direction of second-order motion at short stimulus durations. *Vision Research*, 33, 1785–1794.
- Derrington, A. M., & Goddard, P. A. (1989). Failure of motion discrimination at high contrasts: Evidence for saturation. *Vision Research*, 29, 1767–1776.

- Donnelly, M., Bowd, C., & Patterson, R. (1997). Direction discrimination of cyclopean (stereoscopic) and luminance motion. *Vision Research*, 37, 2041–2046.
- Dosher, B. A., Landy, M. S., & Sperling, G. (1989). Kinetic depth effect from optic flow—I. 3D shape from Fourier motion. *Vision Research*, 29, 1789–1813.
- Duffy, C. J., & Wurtz, R. H. (1991a). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology*, 65, 1329–1345.
- Duffy, C. J., & Wurtz, R. H. (1991b). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology*, 65, 1346–1359.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96, 433–458.
- Duncan, J., & Humphreys, G. W. (1992). Beyond the search surface: Visual search and attentional engagement. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 578–588.
- Emerson, R. C., Bergen, J. R., & Adelson, E. H. (1992). Directionally selective complex cells and the computation of motion energy in cat visual cortex. *Vision Research*, 32, 203–218.
- Geesaman, B. J., & Andersen, R. A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *Journal of Neuroscience*, 16, 4716–4732.
- Gorea, A., Wardak, C., & Lorenzi, C. (2000). Visual sensitivity to temporal modulations of temporal noise. *Vision Research*, 40, 3817–3822.
- Green, M. (1983). Contrast detection and direction discrimination of drifting gratings. *Vision Research*, 23, 281–289.
- Gurnsey, R., Fleet, D., & Potechin, C. (1998). Second-order motion contribute tovection. *Vision Research*, 38, 2801–2816.
- Harris, L. R., & Smith, A. T. (1992). Motion defined by second-order characteristics does not evoke optokinetic nystagmus. *Visual Neuroscience*, 9, 565–570.
- Harris, L. R., & Smith, A. T. (2000). Interactions between first- and second-order motion revealed by optokinetic nystagmus. *Experimental Brain Research*, 130, 67–72.
- Hoffmann, K.-P. (1989). Control of the optokinetic reflex by the nucleus of the optic tract in primates. *Progress in Brain Research*, 80, 173–182.
- 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.
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology (London)*, 160, 106–154.
- 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. (1999). Discrimination of the speed and direction of global second-order motion in stochastic displays. *Vision Research*, 39, 3710–3720.
- 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. (1995). The perceived speed of second-order motion and its dependence on stimulus contrast. *Vision Research*, 35, 1421–1434.
- Lu, Z.-L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, 35, 2697–2722.
- Mather, G., & Tunley, H. (1995a). Temporal filtering enhances direction discrimination in random-dot patterns. *Vision Research*, 35, 2105–2116.
- Mather, G., & Tunley, H. (1995b). Motion detection in interleaved random dot patterns: evidence for a rectifying nonlinearity preceding motion analysis. *Vision Research*, 35, 2117–2125.
- Nakayama, K., & Silverman, G. H. (1985). Detection and discrimination of sinusoidal grating displacements. *Journal of the Optical Society of America A*, 2, 267–274.
- Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system. *Vision Research*, 37, 2685–2698.
- Nishida, S., & Sato, T. (1992). Positive motion after-effect induced by bandpass-filtered random-dot kinematograms. *Vision Research*, 32, 1635–1646.
- Nishida, S., & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, 35, 477–490.
- Pantle, A., & Turano, K. (1992). Visual resolution of motion ambiguity with periodic luminance- and contrast-domain stimuli. *Vision Research*, 32, 2093–2106.
- Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, 31, 1337–1350.
- Ramachandran, V. S., Rao, V. M., & Vidyasagar, T. R. (1973). Apparent movement with subjective contours. *Vision Research*, 13, 1399–1401.
- Seiffert, A. E., & Cavanagh, P. (1999). Serial search for texture-defined motion. *Investigative Ophthalmology and Visual Science*, 40(Suppl.), 4241.
- Schofield, A. J., & Georgeson, M. A. (2000). The temporal properties of first- and second-order vision. *Vision Research*, 40, 2475–2487.
- Smith, A. T. (1994). The detection of second-order motion. In A. T. Smith, & R. J. Snowden (Eds.), *Visual detection of motion* (pp. 145–176). London: Academic Press.
- Smith, A. T., & Hess, R. F., & Baker, C. L. (1994). Direction identification thresholds for second-order motion in central and peripheral vision. *Journal of the Optical Society of America A*, 11, 506–514.
- Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: Fact or artifact? *Vision Research*, 37, 45–62.
- Smith, A. T., & Ledgeway, T. (1998). Sensitivity to second-order motion as a function of temporal frequency and eccentricity. *Vision Research*, 38, 403–410.
- Smith, A. T., & Snowden, R. J. (Eds.) (1994). *Visual detection of motion*. London: Academic press.
- Smith, A. T., Musselwhite, M. J., & Hammond, P. (1984). The influence of background motion on the motion aftereffect. *Vision Research*, 24, 1075–1082.
- Sperling, G., & Lu, Z.-L. (1998). A systems analysis of visual motion perception. In T. Watanabe (Ed.), *High-level motion processing* (pp. 153–183). London: The MIT Press.
- Stone, L. S., Watson, A. B., & Mulligan, J. B. (1990). Effect of contrast on the perceived direction of a moving plaid. *Vision Research*, 30, 1049–1067.
- Stoner, G. R., & Albright, T. D. (1992). Motion coherency rules are from-cue invariant. *Vision Research*, 32, 465–475.
- Stromeyer, C. F., Kronauer, R. E., Madsen, J. C., & Klein, S. A. (1984). Opponent-movement mechanisms in human vision. *Journal of the Optical Society of America A*, 1, 876–884.
- Sutter, A., Beck, J., & Graham, N. (1989). Contrast and spatial variables in texture segregation: testing a simple spatial-frequency channels model. *Perception and Psychophysics*, 46, 312–332.
- Van Santen, J. P. H., & Sperling, G. (1985). Elaborated reichardt detectors. *Journal of the Optical Society of America A*, 2, 300–321.
- von Grünau, M. W., Bertone, A., & Pakneshan, P. (1998). Attentional selection of motion states. *Spatial Vision*, 11, 329–347.

- Watamaniuk, S. N. J., Sekuler, R., & Williams, D. W. (1989). Direction perception in complex dynamic displays: the integration of direction information. *Vision Research*, 29, 47–59.
- Watson, A. B., & Ahumada, A. J. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, 2, 322–341.
- Watson, A. B., Ahumada, A. J., & Farrell, J. E. (1986). Window of visibility: A psychophysical theory of fidelity in time-sampled visual motion displays. *Journal of the Optical Society of America A*, 3, 300–307.
- Watson, A. B., Thompson, P. G., Murphy, B. J., & Nachmias, J. (1980). Summation and discrimination of gratings moving in opposite directions. *Vision Research*, 20, 341–347.
- Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, 18, 292–297.
- Wilson, H. R., & Kim, J. (1994). Perceived motion in the vector sum direction. *Vision Research*, 34, 1835–1842.
- Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, 9, 79–97.
- Yo, C., & Wilson, H. R. (1992). Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. *Vision Research*, 32, 135–147.
- Zhou, Y.-X., & Baker, C. L. (1993). A processing stream in mammalian visual cortex neurons for non-Fourier responses. *Science*, 261, 98–101.
- Zhou, Y.-X., & Baker, C. L. (1994). Envelope-responsive neurones in areas 17 and 18 of cat. *Journal of Neurophysiology*, 72, 2134–2150.