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Choice reaction times for identifying the direction of first-order motion and different varieties of second-order motion

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Abstract

This study sought to quantify the temporal properties of the human visual system by measuring forced-choice reaction times for discriminating the drift direction of first-order motion (luminance-modulated noise) and a variety of second-order motion patterns (modulations of either the contrast, polarity, orientation or spatial length of a noise carrier) over a range of stimulus modulation depths. In general, reaction times for all types of second-order motion were slower than those for first-order motion. Specifically, reaction times were similar for modulations of image contrast, polarity and orientation but were markedly slower for modulations of spatial length. There was also a tendency for reaction times to decrease as stimulus modulation depth increased. The rate of this decrease was shallowest for first-order, luminance-defined patterns. For second-order motion reaction times decreased at a similar rate for contrast, polarity and orientation but this decrease was steepest for spatial length. However, when equated in terms of visibility (multiples of direction-discrimination threshold), the rate at which reaction times decreased as modulation depth increased became comparable for patterns defined by luminance, contrast, polarity and orientation. For patterns defined by spatial length, performance could not be equated in this manner. These findings demonstrate that the time taken to encode the direction of each pattern is not an invariant response metric. The results are consistent with psychophysical and electrophysiological evidence for longer response latencies for second-order motion and may reflect the additional processing stages (e.g. filter–rectify–filter) required for its extraction.

Keywords: Reaction times; First-order motion; Second-order motion; Modulation depth

1. Introduction

The temporal responses of the mammalian visual system are heavily dependent on stimulus contrast. For example, it has long been accepted that the response amplitude (firing-rate) of visual cortex neurons increases as stimulus contrast increases (e.g. Ikeda & Wright, 1974; Maffei & Fiorentini, 1973; Movshon & Tolhurst, 1975) and there is evidence to suggest that saccade latencies also decrease with increasing stimulus contrast (Ludwig, Gilchrist, & McSorley, 2004). Psychophysically, reaction times for detecting the presence of a stimulus also decrease as stimulus contrast increases (e.g. Ejima & Ohtami, 1987; Harwerth & Levi, 1978; Murray & Plainis, 2003; Plainis & Murray, 2000) and this phenomenon is most readily apparent when performance is measured over a wide contrast range that extends to near-threshold levels.

Psychophysical (behavioural) reaction time paradigms have been employed previously to illustrate the operation of physiologically-distinct mechanisms for encoding motion defined by different stimulus properties. Burr et al. (1993) for example measured reaction times for detecting the onset of luminance-defined and chromatically-defined gratings and found that, at low (0.25 deg/s) and intermediate (1 deg/s) speeds, reaction times for detecting the onset of motion decreased at different rates for luminance and chromatic gratings as stimulus contrast increased. At low stimulus contrasts, reaction times for detecting the motion onset of chromatic gratings were

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markedly slower than those for detecting the onset of luminance-defined motion. In addition, reaction times for detecting the motion onset of chromatic gratings decreased more rapidly with increasing stimulus contrast than those for luminance gratings. Burr, Fiorentini, and Morrone (1993) interpreted their results in the context of evidence that the temporal response of the visual system is slower to chromatic stimuli than to luminance stimuli (e.g. Burr & Morrone, 1993). However it is worth noting that due to the nature of the task employed, this paradigm is likely to tap the properties of mechanisms sensitive to temporal change, rather than motion specific responses *per se*.

Analogously, there is evidence that the temporal resolution of the mechanism/s that encodes texture-defined (second-order) motion is markedly inferior to that which encodes luminance-defined (first-order) motion. Whereas observers are able to discriminate the direction of first-order motion at very brief stimulus exposure durations (26.49 ms), they are unable to discriminate the direction of second-order motion (contrast-modulations and spatial beat patterns) at stimulus exposure durations of $\leqslant\sim 200$ ms (Derrington, Badcock, & Henning, 1993; Ledgeway & Hess, 2002). In addition, 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; Hutchinson & Ledgeway, 2006; Smith & Ledgeway, 1998). The temporal sluggishness of the visual system to second-order motion has been attributed to the additional processing (e.g. filter–rectify–filter) required in order to extract the second-order image structure (Wilson & Kim, 1994; Yo & Wilson, 1992). Although this hypothesis is not in itself sufficient to explain all the instances where second-order motion perception is inferior, if second-order motion perception is 'slower' than first-order motion perception, it follows that reaction times for detecting second-order motion should be slower than those for detecting first-order motion.

Ellemberg et al. (2003) have compared VEP responses and psychophysical reaction times to the onset of first-order (luminance-modulated static noise) and second-order (contrast-modulated static noise) motion. Their task consisted of an extended stationary phase in which a static grating was presented on-screen (3.5–5.5 s), after which the grating was made to drift abruptly rightwards at 6 deg/s for 140 ms, followed by another stationary phase and so on. The observers' task was to respond as soon as they detected the onset of motion. Results were averaged across all eight adult observers who took part in the study and it was found that VEP latencies for second-order motion were longer than for first-order motion. The P1 peak was on average 69 ms slower for second-order than for first-order motion and the N2 peak was around 73 ms later for second-order motion. Psychophysically, observers were around 104 ms slower at reporting the onset of second-order motion than the onset of first-order motion. This study is important in that it distinguishes the temporal mechanisms underlying the simple detection of first-order and second-order motion onset, but the paradigm employed does not necessarily selectively probe motion mechanisms *per se.* When the grating moved, it always moved to the right and as such observers were not required to make an objective judgement based on motion direction (i.e. a 'simple' rather than a 'choice' reaction time task was employed). Thus, in principle, observers could have performed the task by detecting that there had been a temporal change in the stimulus. Interestingly, although there were differences between reaction times for first-order and second-order motion, the group-averaged reaction times only decreased very slightly, if at all, as stimulus contrast increased. Rather, they remained at around 400 ms for first-order motion and around 500 ms for second-order motion, irrespective of the modulation depth of the stimulus. It may be that motion onset detection for these particular stimuli is relatively immune to changes in stimulus modulation depth, at least over the range of values tested for which a reaction time measure was obtainable (0.0325, 0.125, 0.25, 0.5 and 1 for first-order motion and 0.25, 0.5 and 1 for second-order motion). Consequently, there is a need to re-examine this issue using a task that is designed specifically to measure behavioural response latencies based on judgements of motion direction, over a wider range of modulation depths.

On a more general note, the study of second-order motion has mainly concentrated on how contrast-modulated noise patterns are encoded by the human visual system and the findings of this work have been taken to represent the operation of a generic second-order motion-encoding system. However, it has been suggested that there may be some degree of inhomogeneity concerning how different kinds of second-order motion are processed (Hutchinson & Ledgeway, 2006; Lu & Sperling, 2001b; Petersik, 1995). In addition Kingdom, Prins, and Hayes (2003) have presented evidence using static second-order patterns that also suggests that the human visual system employs mechanisms that may be selective to stimulus type. Thus there is a growing realisation that in order make valid generalisations concerning the encoding of second-order motion by the visual system, studies need to compare performance for different varieties of second-order motion stimuli on the same tasks (e.g. Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2005; Schofield, Ledgeway, & Hutchinson, 2007).

Therefore, the aims of the present study were to extend the reaction time experiments of Ellemberg et al. (2003) by: (1) Enabling a more precise investigation of motion mechanisms, rather than temporal mechanisms, by measuring forced-choice reaction times for discriminating drift direction. (2) Comparing performance for different types of second-order motion stimuli. (3) Investigating reaction time responses over a wider range of modulation depths, and (4) examining different stimulus parameters (i.e. a speed other than 6 deg/s and using dynamic, rather than static, noise as a carrier). If reaction times to correctly identify the direction of second-order motion (regardless of how it is defined) are consistently slower overall than those for first-order motion, this would suggest that the former requires more elaborate processing (and hence more time) to encode its direction, as proposed by most current models. Furthermore any similarities or gross differences in the patterns of performance found for the different varieties of second-order motion, should provide important information concerning whether or not they are likely to be encoded using the same computational strategies. Finally if reaction times for each type of pattern can be shown to depend on the modulation depth at which performance is measured, this would suggest that the time needed to extract motion direction is not simply a fixed parameter.

2. Experiment 1: Reaction times for discriminating the direction of first-order and different types of second-order motion

Experiment 1 measured reaction times for discriminating the direction of first-order (luminance-modulated dynamic noise) and four types of second-order (contrast-modulated, polarity-modulated, orientation-modulated and spatial length-modulated dynamic noise) motion as a function stimulus modulation depth.

2.1. Methods

2.1.1. Observers

Six observers took part in the study. CVH is an author and is an experienced psychophysical observer with motion stimuli of the kind used in the present study. JD, CC, LKS, RWD and SH were all naïve observers. All had normal or corrected-to-normal visual acuity and had no history of any visual disorders.

2.1.2. Apparatus and stimuli

Stimuli were generated using a *Macintosh G4* and presented on a *Sony Trinitron monitor* with a refresh rate of 75 Hz using custom software written in the C programming language. For precise control of luminance contrast the number of intensity levels available was increased from 8 to 14 bits using a Bits++ attenuator (*Cambridge Research Systems*). The mean luminance of the display was 58.4 cd/m^2. Images were viewed binocularly and in darkness at a distance of 138.7 cm. One screen pixel subtended 2.3 arc min of visual angle resulting in a display that subtended 8 degrees vertically and 8 degrees horizontally. To ensure that the second-order motion stimuli did not contain any luminance artifacts, the monitor was carefully gamma-corrected using a photometer and look-up-tables (LUT). As an additional precaution, the adequacy of the gamma-correction was also checked psychophysically for each observer using a sensitive motion-nulling task (Gurnsey, Fleet, & Potechin, 1998; Ledgeway & Smith, 1994; Lu & Sperling, 2001a; Scott-Samuel & Georgeson, 1999).

Stimuli were vertically-oriented, 1 c/deg, first-order or second-order motion patterns drifting either leftwards or rightwards at a temporal frequency of 1 Hz. All stimuli contained a dynamic visual noise carrier to allow direct comparisons between the results for each stimulus type. For all motion patterns the noise had a (mean) Michelson contrast of 0.25 and each noise pixel element subtended 2.3 arc min. The noise was replaced with a new stochastic sample (or its elements were subjected to luminance reversal in the case of polarity-modulated dynamic noise, as described below) each time the position of the drifting waveform was updated, at a rate of 37.5 Hz.

First-order motion patterns were luminance-modulated dynamic noise and were constructed by adding a drifting sinusoidal luminance grating to a field of spatially two-dimensional (2-d) noise. Second-order motion patterns were either contrast-modulated, polarity-modulated, orientation-modulated or spatial length-modulated dynamic noise. For contrast-modulated patterns, a drifting sinusoidal luminance grating was multiplied by 2-d noise. For patterns defined by polarity, a sinusoidal modulation determined the probability that individual 2-d noise elements would reverse their luminance polarity over time. Since the probability of the reversal varied sinusoidally, the result was a travelling wave of flicker that produced a moving grating of smoothly drifting bars composed of flickering dots. Such a stimulus can be described as second-order because the space-time averaged luminance of the flicker is constant across all parts of the pattern (Stoner & Albright, 1992). For patterns defined by orientation, a sinusoidal modulation determined the local orientation of the striped elements within the noise. Orientation-modulated patterns have been employed previously by Kingdom et al. (2003) to investigate spatial vision, but those used in the present experiment were based on the motion stimuli recently described by Schofield et al. (2007). These were constructed by generating a spatially one-dimensional (1-d), horizontally-oriented, dynamic noise carrier and shifting each column of pixels in the vertical (y) dimension by an amount and direction (either upwards or downwards) that was determined by the following equation:

$$y = \frac{\tan(\frac{m\pi}{4}) \times \sin(2\pi[fx + \omega t])}{\sin(2\pi f)} \tag{1}$$

where m is the depth of the sinusoidal orientation modulation (see Eq. (3) below), f is spatial frequency and ω is temporal frequency. This resulted in a motion sequence in which the local orientation of the dynamic noise was modulated over space and time. For patterns defined by spatial length, a sinusoidal modulation determined the vertical length of flickering bars (Hutchinson & Ledgeway, 2006). Stimulus examples are shown in Fig. 1.

The strength or modulation depth (m) of each stimulus (with the exception of orientation-modulated dynamic noise) was determined by the following general equation:

$$M = (A_{\max} - A_{\min})/(A_{\max} + A_{\min}) \tag{2}$$

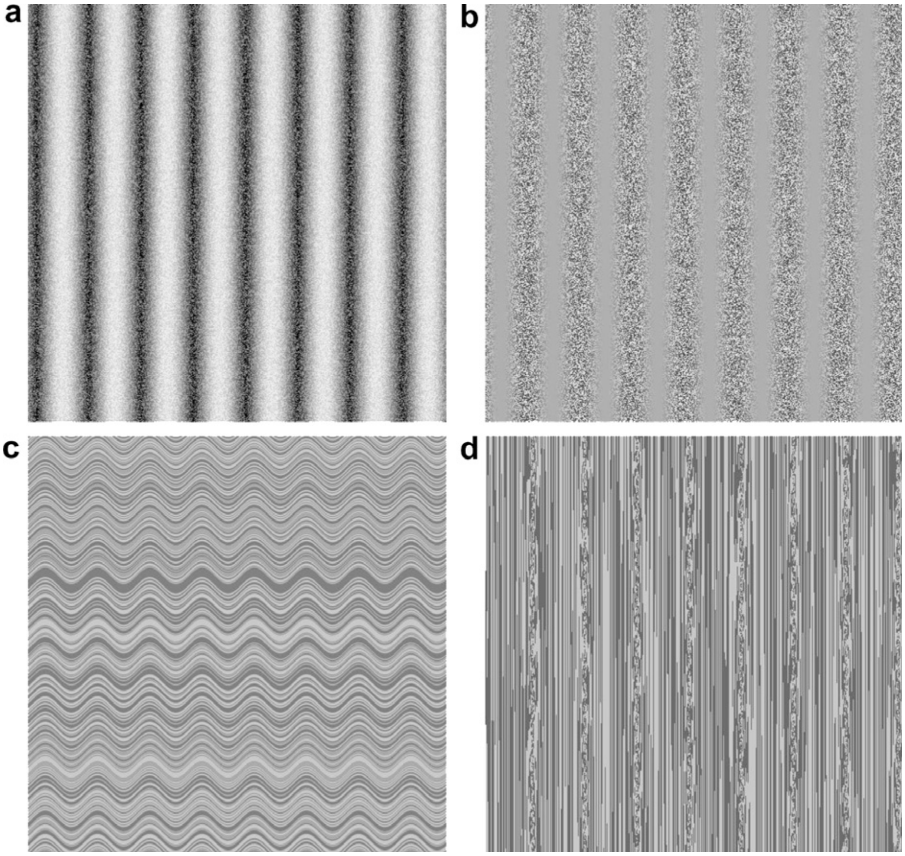

Fig. 1. Examples of the first-order and second-order motion patterns represented as space (x)–space (y) plots. Shown are (a) luminance-modulated dynamic noise, (b) contrast-modulated dynamic noise, (c) orientation-modulated dynamic noise and (d) spatial length-modulated dynamic noise. Note that polarity-modulated dynamic noise cannot be depicted in this figure, as its sinusoidal spatial structure is defined by the polarity reversal of individual pixel elements over time (i.e. "white" pixels flipping to "black" and vice-versa). This produces a grating of smoothly drifting bars composed of flickering dots.

where $A_{\max}$ and $A_{\min}$ represent the maximum and minimum values of each stimulus type. For luminance-modulated dynamic noise, $A_{\max}$ and $A_{\min}$ refer to the maximum and the minimum luminances, respectively, averaged over adjacent noise elements with opposite polarity in the image. For contrast-modulated dynamic noise, $A_{\max}$ and $A_{\min}$ refer to the maximum and the minimum local Michelson contrasts in the image computed over adjacent noise elements with opposite polarity. For polarity-modulated dynamic noise, $A_{\max}$ and $A_{\min}$ refer to the maximum and the minimum probability that each pixel would reverse its luminance polarity. For spatial length-modulated dynamic noise, $A_{\max}$ and $A_{\min}$ refer to the maximum and the minimum bar height expressed as a percentage of the full image height.

For orientation-modulated dynamic noise the modulation depth could be varied within the range 0–1 according to following equation:

$$m = (O_{\max} - O_{\min})/90 \tag{3}$$

where $O_{\max}$ and $O_{\min}$ refer to the maximum and the minimum local orientations in the image computed relative to a reference orientation of 90 deg (corresponding to horizontal).

The modulation depths used in the experiment were chosen on the basis of pilot studies to bracket the range of values that would be expected to support reliable direction-identification performance for each motion stimulus. For luminance-modulated dynamic noise a set of nine modulation depths were used (spaced equally on a logarithmic scale such that consecutive members of the set differed by a factor of 2) that spanned the range 0.0039–0.7071. For modulations of contrast, polarity and orientation a set of nine modulation depths (each differing from its neighbour by a factor of 1.41) ranging from 0.0625 to 1 were employed. For spatial length five modulation depths were tested ranging from 0.7711 to 1 (consecutive values differed by a factor of 1.09).

2.2. Procedure

A single-interval binary forced-choice task was employed. Trials were self-paced and observers initiated each trial by pressing the spacebar. On each trial, observers were presented with a fixation cross. After a 1000 ms delay a drifting grating was then presented on-screen for 500 ms. The drift direction of the grating was chosen to be either leftwards or rightwards on each trial with equal probability. After the presentation of the stimulus, observers were required to respond, as quickly and accurately as possible with a key press. Their task was to judge the direction of the grating's motion. Feedback was given after trials in which the observer responded incorrectly. The observer then initiated the next trial by pressing the space bar and following a 1000 ms inter-trial interval another motion stimulus was presented, and so on.

Reaction times for discriminating the direction of each motion pattern were measured over a range of stimulus modulation depths using the method of constant stimuli. Each modulation depth was presented twenty-five times in each run of trials and the order of presentation was randomised. Each run of trials took ~10 min to complete and observers completed 1–3 runs per sitting. Observers were also encouraged to take regular breaks between consecutive runs which, together with an inter-trial interval that was at least twice as long as the duration of each motion stimulus, served to minimise any potential contrast adaptation effects from prolonged viewing. Each observer completed a minimum of six runs of trials for each condition and the order of testing was also randomised. The mean reaction time was computed for each stimulus modulation depth *within* each run of trials. These means were used to calculate the grand mean and SEM *across* each run of trials for each motion type and stimulus modulation depth. Similar to previous studies (e.g. Murray & Plainis, 2003; Plainis & Murray, 2000) only reaction times within a particular range were included in the analysis. Although this is common practice there is little consensus in the literature regarding the precise range that should be used. However severe truncation of data sets is known to introduce bias, because extreme but valid reaction times may be excluded (e.g. Ulrich & Miller, 1994). In the present study, reaction times that were less than 50 ms or greater than 2000 ms were excluded. Excluded responses were subsequently re-tested by re-randomising the order of trials within that run. More than 98.7% of all measured responses fell within the range 200–1000 ms.

2.3. Results

Fig. 2 shows reaction times for first-order (luminance-modulated dynamic noise) and second-order (contrast-modulated, polarity-modulated, orientation-modulated and spatial length-modulated dynamic noise) motion as a function of stimulus modulation depth. Reaction times were calculated for correct responses only (as is conventional) and are plotted for stimulus modulation depths where observers achieved at least 70% correct performance and above. Although all observers were tested at the same modulation depths, a failure to meet the 70% accuracy criterion for some conditions means that the range of modulation depths for which reaction time data are shown in Fig. 2 is not necessarily the same all observers.

The data for each motion type were fitted with the following equation:

$$y = a + \frac{k}{m} \tag{4}$$

where a is the asymptotic reaction time and k is the slope parameter describing the rate of decrease in reaction time with increasing stimulus modulation depth (m). When plotted on log–log axes, a determines the degree to which the fitted curve flattens (decelerates), if at all, at relatively high values of m. Previous studies (e.g. Murray & Plainis, 2003; Plainis & Murray, 2000) have shown that, at least in the context of first-order stationary patterns, this equation provides a robust and satisfactory description of reaction times vs. modulation depth curves under a wide range of stimulus conditions (e.g. luminance, spatial frequency). Indeed from Eq. (4) it follows that if the data were re-plotted in terms of $1/m$, the resulting slope, k, would be linear, a result we have confirmed for all of the motion stimuli used in the present experiment. The values of a, k, and R^2 are given in Appendix A.[1]

The first thing to note is that there are some differences between the results of the six observers. For example reaction times were uniformly longer overall for CVH and SH than the remaining observers. For the second-order motion stimuli CVH could perform the task at lower modulation depths than the naïve observers, and SH could not reliably discriminate the direction of spatial length-modulated dynamic noise even at the maximum modulation depth tested. In addition the slope of the modulation depth response to the second-order conditions is somewhat steeper for CVH than all the other observers.

Despite these individual differences it is readily apparent that the results of all observers exhibit a number of consistent features. First, observers were able to reliably discriminate the direction of first-order motion at much lower modulation depths than second-order motion and, for a given modulation depth, reaction times for discriminating the direction of first-order motion were markedly faster than those for discriminating the direction of any of the second-order motion patterns. Second, reaction times for discriminating the direction of contrast-modulated, polarity-modulated and orientation-modulated dynamic noise (second-order motion) were largely equivalent. However, if anything, reaction times for contrast-modulated dynamic noise were usually marginally faster than those for polarity-modulated or orientation-modulated dynamic noise (except for observer SH where responding was fastest to orientation modulations). In addition, observers were able to reliably discriminate their direction across a similar range of modulation depths (i.e. they exhibited similar sensitivity). Reaction times for discriminating the direction of spatial

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[1] For spatial length, although the fit parameters are given for each observer, these values are not particularly reliable given the limited range over which performance could be reliably measured.

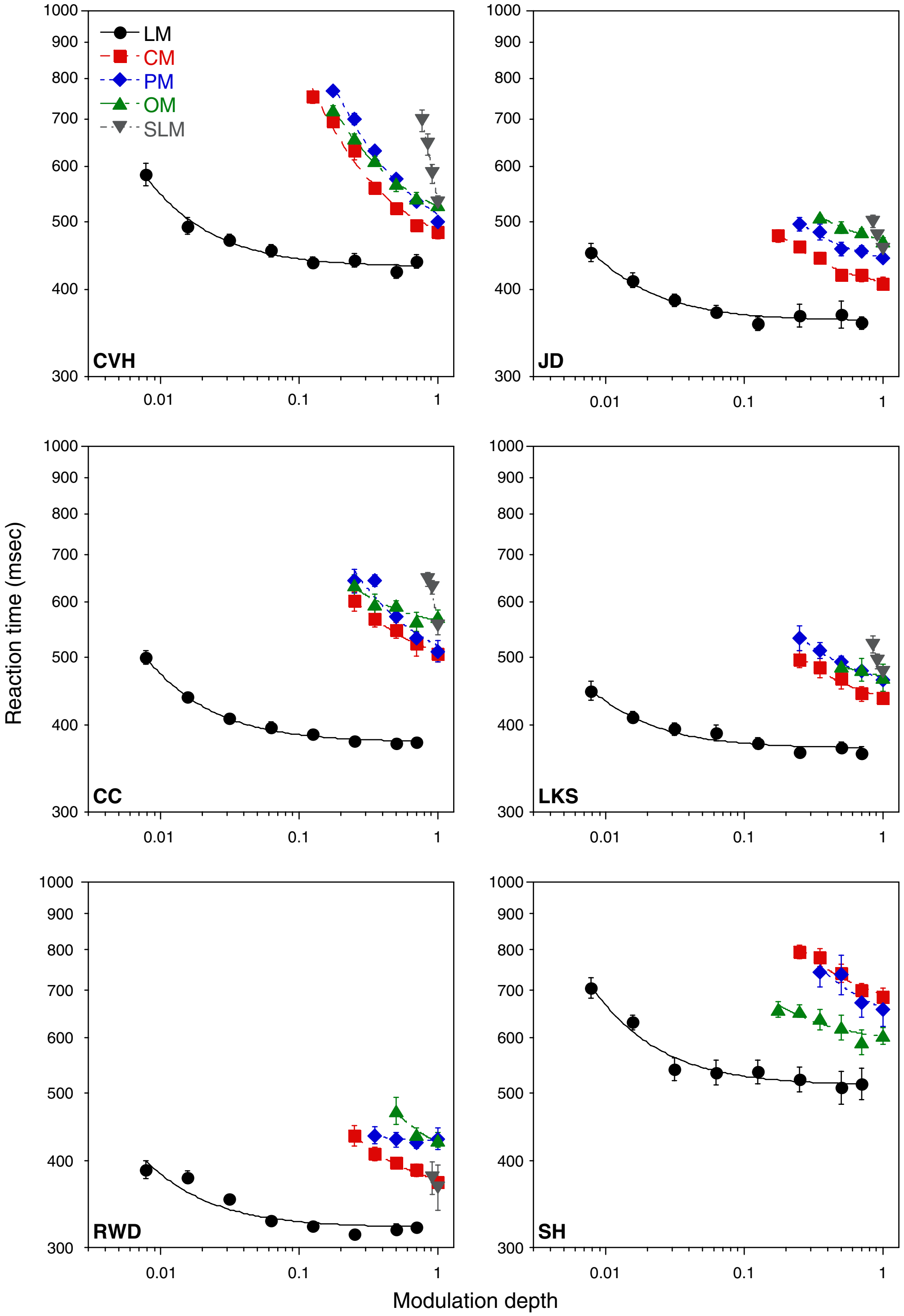

Fig. 2. Reaction times (symbols) for observers CVH, JD, CC, LKS, RWD and SH for determining the drift direction of first-order (LM: luminance-modulated dynamic noise) and four second-order (CM: contrast-modulated, PM: polarity-modulated, OM: orientation-modulated and SLM: spatial length-modulated dynamic noise) motion patterns as a function of stimulus modulation depth. Error bars represent ±1 SEM. Lines represent the best fitting curves determined by Eq (4).

length-modulated dynamic noise (second-order motion) were typically slowest. Moreover, observers were only able to reliably discriminate the direction of spatial length-modulated dynamic noise at modulation depths of around 0.8 and above.

Another important characteristic of the results shown in Fig. 2 is that as stimulus modulation depth increased, reaction times decreased. This was the case for all the motion patterns employed and reaction times were, on average, ~20% faster at the highest compared with the lowest modulation depth tested for each stimulus. However first-order motion exhibited the shallowest slope and reaction times were approximately constant for modulation depths $>\sim0.02$. For each observer, reaction times for contrast-modulated, polarity-modulated and orientation-modulated dynamic noise patterns decreased as stimulus modulation depth increased at approximately the same rate and the slope of this decrease was markedly steeper than that for first-order motion. For conditions where the direction of spatial length-modulated dynamic noise could be reliably discriminated, the decrease in reaction times as a function of stimulus modulation depth was most pronounced.

The findings of studies that use reaction time as a measure of behavioural responses are sometimes confounded by what is commonly referred to as the speed-accuracy trade-off. This refers to the trade-off between how fast a task can be performed and how accurate that performance is. If performance is affected by the speed-accuracy trade-off then the task can either be performed slowly with few errors or quickly with more errors. If the pattern of results shown in Fig. 2 reflects a speed-accuracy trade-off, then percent correct performance should be relatively low for the fastest reaction times and higher for slowest reaction times. To address this issue, in Fig. 3 reaction times have been plotted as a function of percent correct direction-discrimination performance (accuracy). It is readily apparent that the results were not indicative of a speed-accuracy trade-off. Rather than becoming less accurate as reaction times decreased, percent correct performance either increased as reaction times decreased or remained relatively constant.

3. Experiment 2: Reaction times for discriminating the drift direction of 'equivalent' first-order and second-order motion patterns

3.1. Introduction

The results of Experiment 1 have shown that over the same range of modulation depths, reaction times were different for different types of motion stimuli. Reaction times were fastest for first-order motion (luminance-modulated dynamic noise). For second-order motion, reaction times for contrast-modulated, polarity-modulated and orientation-modulated dynamic noise were similar and those for spatial length-modulated dynamic noise were slowest. One crucial point worth noting however is that the times taken to respond to the direction of first-order and second-order motion do not appear to be fixed parameters since they both depend on the physical modulation depths of the stimuli that are presented. Indeed, a first-order stimulus with a relatively low modulation depth can elicit exactly the same reaction time as a second-order stimulus with a relatively high modulation depth (i.e. it is possible to select pairs of modulation depths giving equivalent performance). This may reflect differential sensitivity to the two types of motion. For example, direction-discrimination thresholds for the first-order and second-order motion patterns used in Experiment 1 differ markedly, in that sensitivity to second-order motion is considerably lower than sensitivity to first-order motion (e.g. Hutchinson & Ledgeway, 2006; Schofield et al., 2007; Smith, Hess, & Baker, 1994). Indeed, if equated in terms of stimulus visibility, reaction times for discriminating the drift direction of the different motion patterns may become similar. That is, the reaction time vs. modulation depth function for the different stimuli may simply be related by a scaling factor equivalent to shifting the curves horizontally along the modulation depth axes of Fig. 2.

As such, in Experiment 2 direction-discrimination thresholds were measured for each of the motion patterns. These thresholds were subsequently used to equate each motion pattern in terms of visibility/sensitivity in that they were presented at equal multiples of direction-discrimination threshold.

3.2. Methods

3.2.1. Observers

The observers who took part in Experiment 1 also took part in Experiment 2.

3.2.2. Apparatus and stimuli

The apparatus and stimuli were identical to those employed in Experiment 1.

3.3. Procedure

3.3.1. Direction-discrimination thresholds

The modulation depth of the grating was varied from trial to trial according to a modified 1-up 3-down staircase designed to converge on the modulation-depth corresponding to 79.4% correct performance (Levitt, 1971; Wetherill & Levitt, 1965). At the beginning of each run of trials the modulation depth of the test grating was initially set to a suprathreshold level (typically ~6 dB above threshold) and the initial staircase step size was chosen to be half this value. On subsequent reversals the step size was halved and testing was terminated after a total of 16 reversals. Threshold estimates were taken as the mean of the last four reversals in each staircase. Each observer completed a minimum of eight runs of trials (i.e. 8 staircases) for each condition and the order of testing was randomised. The mean threshold and SEM were then calculated for each stimulus type.

3.3.2. Reaction times

Reaction times for discriminating the direction of each motion pattern were measured at threshold, 1.5, 3, and 6 times threshold, sensitivity permitting, using the method of constant stimuli. In a manner identical to that employed in Experiment 1, each modulation depth was presented twenty-five times in each run of trials and the order of presentation was randomised. Each observer completed a minimum of eight runs of trials for each condition and the

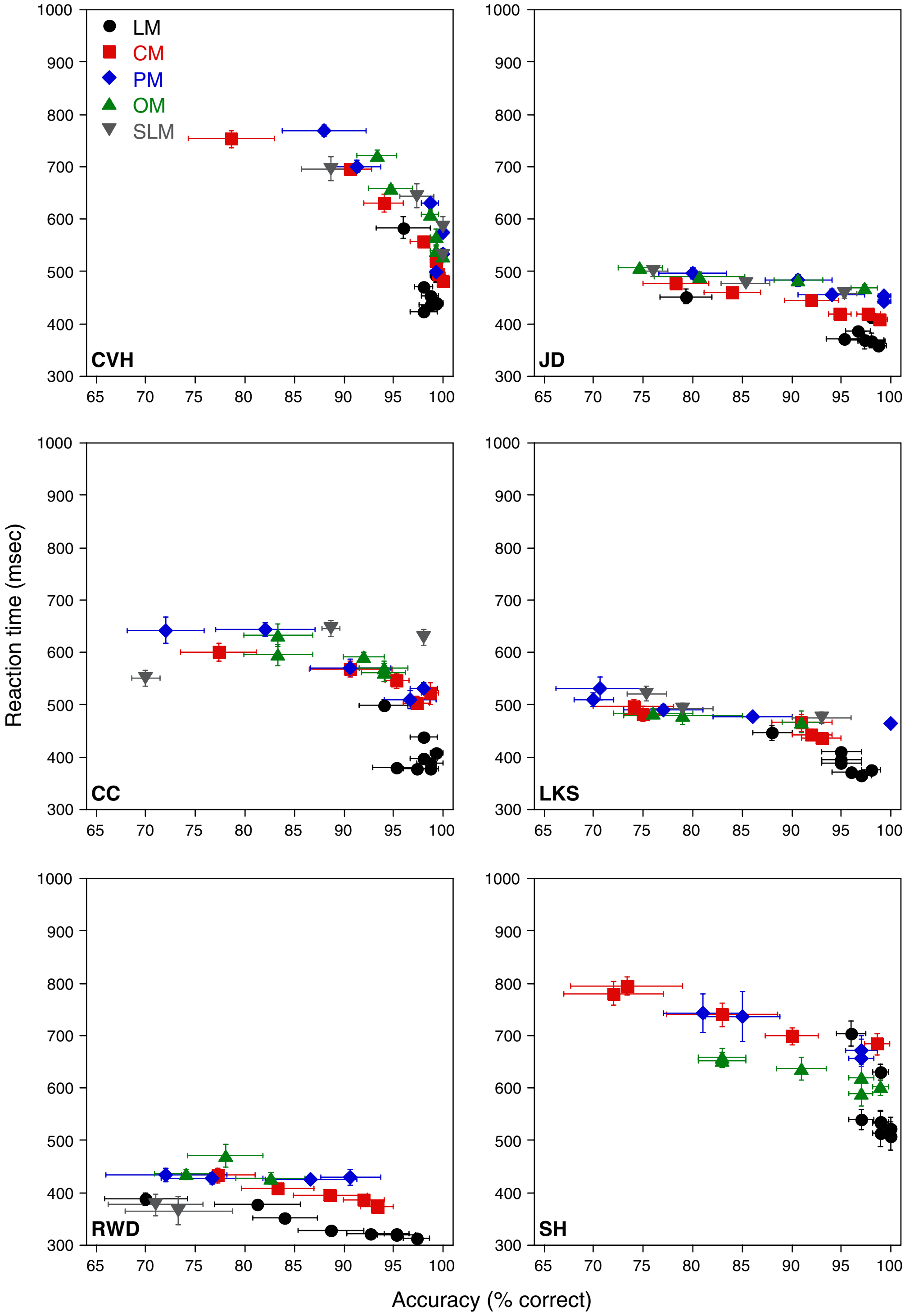

Fig. 3. Reaction times vs. accuracy (percent correct) observers CVH, JD, CC, LKS, RWD and SH for each motion pattern. Error bars represent ±1 SEM.

order of testing was also randomised. The mean correct reaction time and SEM were then calculated for each condition.

3.4. Results

Modulation-depth thresholds for discriminating the drift direction of each motion pattern are shown in Fig. 4. In agreement with previous findings (e.g. Hutchinson & Ledgeway, 2006; Schofield et al., 2007; Smith et al., 1994), direction-discrimination thresholds for first-order motion (luminance-modulated dynamic noise) were markedly lower than those for second-order motion. For second-order motion, thresholds for contrast-modulated, polarity-modulated and orientation-modulated dynamic noise were similar. Finally, thresholds for spatial length

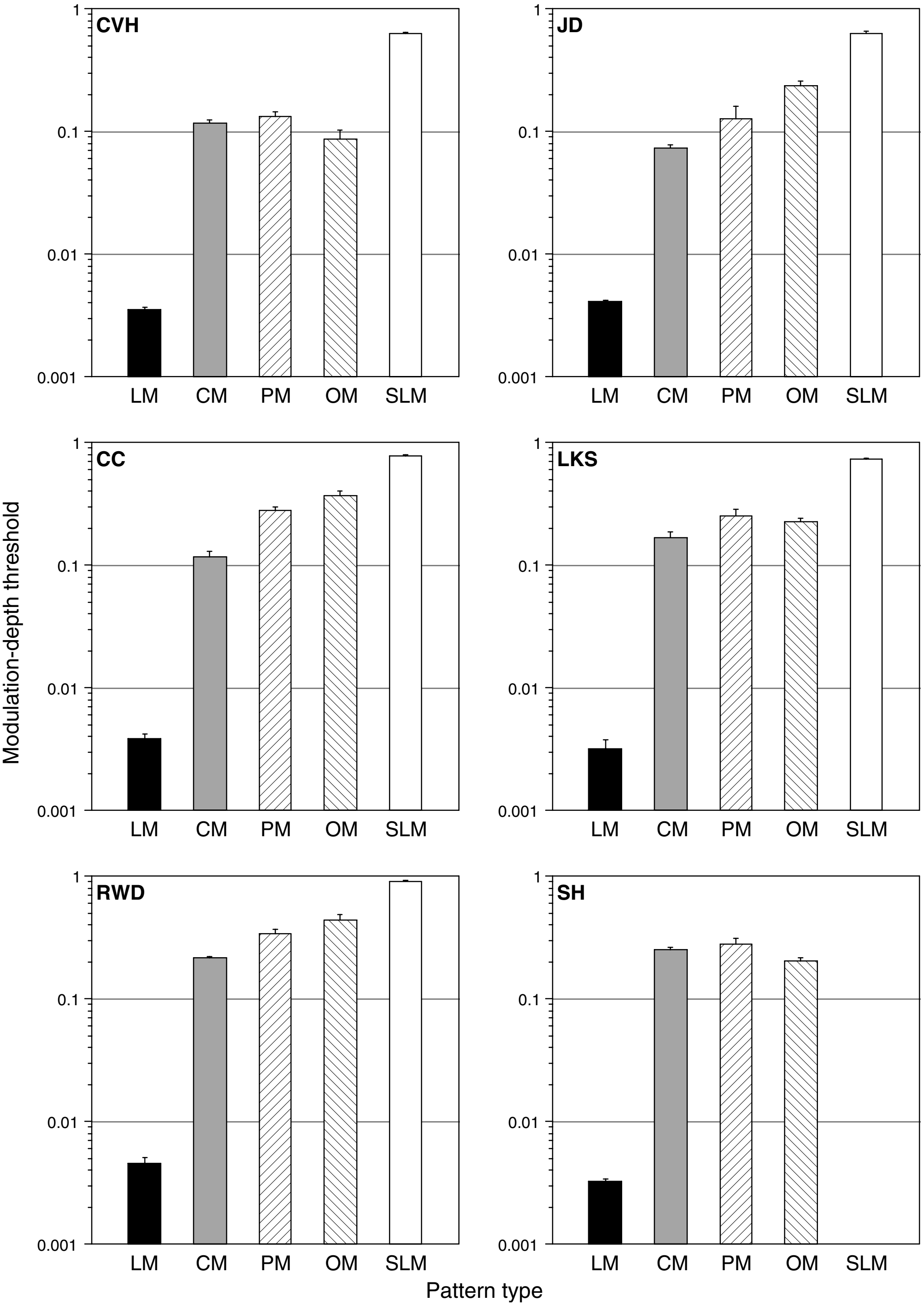

Fig. 4. Modulation depth thresholds (corresponding to 79.4% correct performance) for observers CVH, JD, CC, LKS, RWD, and SH for determining the drift direction of first-order (LM) and four second-order (LM, CM, PM, OM, and SLM) motion patterns. Error bars represent +1 SEM. Note that for observer SH a threshold could not be measured for the SLM stimulus (even at unity modulation depth performance did not consistently exceed 79.4% correct).

were markedly higher than those for the other types of second-order motion pattern. Indeed for observer SH a reliable threshold could not be measured for this stimulus because even at unity modulation depth, performance did not consistently exceed 79.4% correct.

Fig. 5 shows reaction times for each motion pattern as a function of stimulus modulation depth expressed in terms of multiples of direction-discrimination threshold. The data have been fitted with an almost identical equation to Eq. (4) as follows:

$$y = a + \frac{k}{t} \quad (5)$$

where a is the asymptotic reaction time, k is the slope and t is threshold multiple. The values of a, k, and R^2 are given

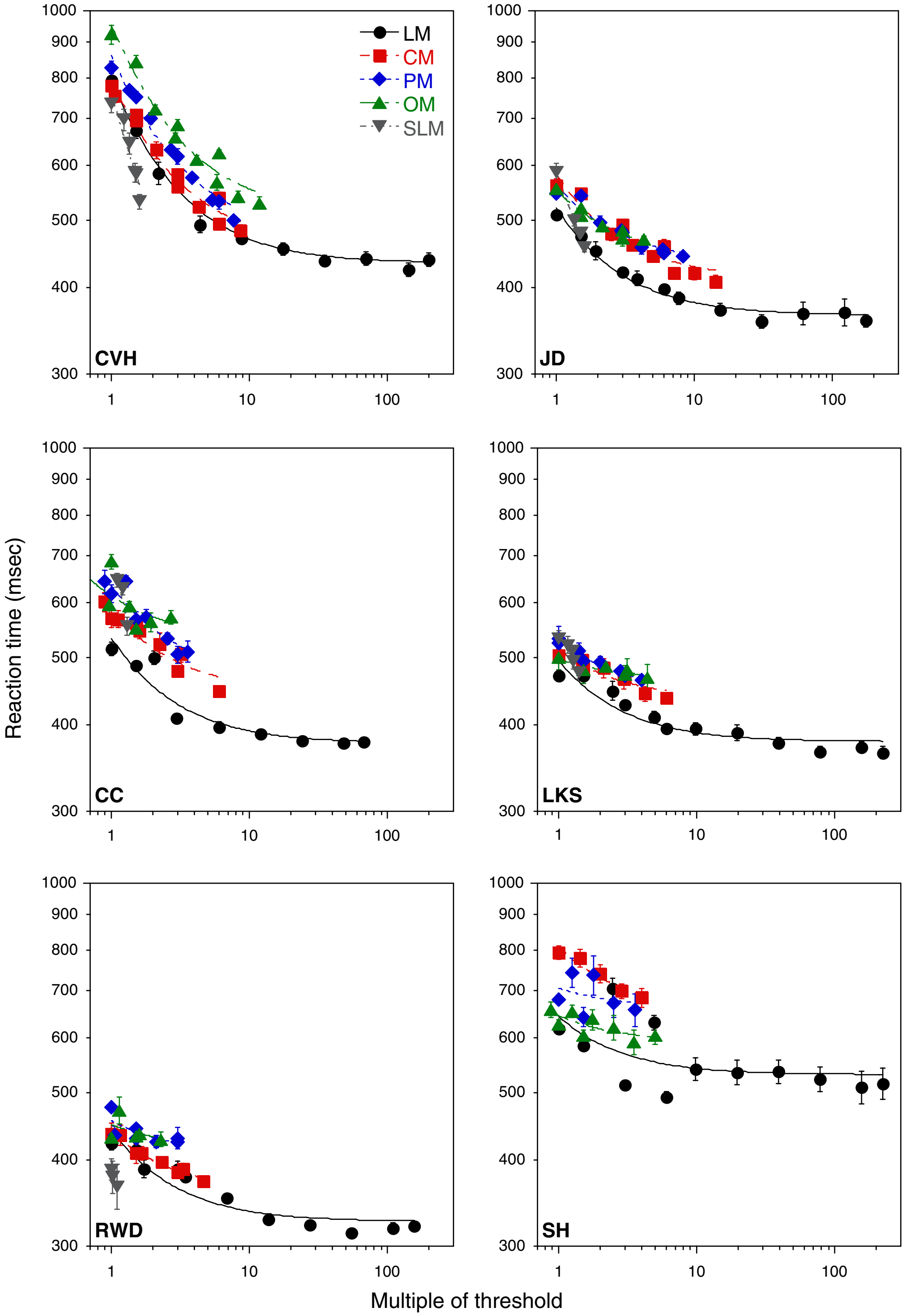

Fig. 5. Reaction times (symbols) for observers CVH, JD, CC, LKS, RWD, and SH for discriminating the drift direction of each motion pattern when equated in terms of multiples of direction-discrimination threshold. Error bars represent ±1SEM. Lines represent the best fitting curves determined by Eq. (5).

for each observer in Appendix B.[2] To give a more reliable fit (i.e. more data points), data from Experiment 1 have also been rescaled as multiples of threshold and included in Fig. 5 along with the additional data points measured in Experiment 2.

When equated in terms of visibility and expressed as multiple of threshold, reaction times for all motion patterns, spatial length excepted, decreased at approximately the same rate as stimulus visibility increased. The rate of

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[2] Again, although the fit parameters for spatial length are given for each observer in Appendix B, they are not particularly reliable.

decrease for these motion patterns resulted in similar slopes (see values of k in Appendix B). In terms of sensitivity, at a given multiple of threshold, reaction times were generally still faster for luminance-modulated (first-order) dynamic noise patterns than for either contrast-, polarity- or orientation-modulated dynamic noise. For these latter three patterns, reaction times were more similar at each multiple of threshold (notwithstanding potential errors in scaling) than when they were compared at the same absolute (physical) modulation depth (see Fig. 2). As regards spatial length-modulated noise, slopes remained extremely steep.

3.5. Discussion

This study sought to probe directly the temporal response characteristics of the mechanisms that encode motion direction in human vision, by measuring forced-choice reaction times for discriminating the direction of 1 c/deg sinusoidal patterns drifting at 1 Hz. Performance for first-order motion (luminance-modulated dynamic noise) and for several varieties of second-order motion (contrast-modulated, polarity-modulated, orientation-modulated and spatial length-modulated dynamic noise) were compared over a wide range of modulation depths. Comparing responses to different types of second-order motion stimuli on the same task is important, because the precise principles governing its perception are still the subject of much debate. Previous research in this area has tended to focus, almost exclusively, on moving contrast variations. Yet contrast is only one of many potential second-order cues that can differentiate moving objects from their backgrounds. This approach relies heavily on the assumption that different varieties of second-order motion are likely to be processed in a homogenous manner by the visual system, but there is little evidence that this is actually the case.

The results showed that at the same physical modulation depths (Fig. 2, Experiment 1), reaction times for discriminating the direction of first-order motion (luminance-modulated dynamic noise) were markedly faster than those for discriminating the direction of any of the second-order motion patterns. This finding is consistent with current models of motion that propose that the extraction of second-order spatiotemporal information requires one or more additional processing stages (and hence more time) than the encoding of first-order motion (e.g. Wilson, Ferrera, & Yo, 1992). In addition, observers were able to reliably discriminate the direction of first-order motion at much lower modulation depths than second-order motion. For second-order motion, reaction times were typically slowest for spatial length-modulated dynamic noise and absolute sensitivity was poorest. In addition for all the motion patterns tested reaction times tended to decrease as stimulus modulation depth increased demonstrating that, at least under the conditions of the current study, the time taken to encode the direction of each pattern is not an invariant response metric. The rate at which reaction times decreased as stimulus modulation depth increased was shallowest for first-order motion (luminance-modulated dynamic noise) and this effect was chiefly restricted to modulation depths $\leqslant\sim 0.02$. As Ellemberg et al. (2003) did not test first-order motion patterns at modulation depths less than 0.0325, this could explain why the reaction times in their motion onset task showed much less dependence on modulation depth. For the second-order motion patterns employed in the current study, reaction time vs. modulation depth slopes were similar for contrast-modulated, polarity-modulated and orientation-modulated dynamic noise but for spatial length-modulated dynamic noise slopes were typically much steeper.

Although the observers generally exhibited qualitatively similar patterns of results, there were nonetheless some individual differences in terms of the overall magnitude of the reaction times, the range of modulation depths over which performance could be measured for each variety of motion, the steepness of the functions relating reaction times to modulation depth and absolute sensitivity. At least some of these differences may be largely superficial or incidental (e.g. uniform differences in overall reaction time magnitude), but others may be attributable in part to the degree of experience each observer had with the stimuli used this study. For example, even though all observers were given extensive practice trials prior to formal data collection, none of the naïve observers had previously taken part in experiments utilising these particular stimuli. On the other hand observer CVH has participated in numerous psychophysical experiments with first-order and second-order motion for several years. It may not be unreasonable to assume that CVH's results were affected by perceptual learning, as changes in task performance are known to accompany persistent exposure to particular stimulus attributes (e.g. see Fahle & Poggio, 2002). This emphasises the importance of reporting each individual's results separately, as averaging the data of different observers across conditions in this study would have obscured these variations in performance.

It is possible that the reaction time data presented here may indirectly reflect the operation of contrast gain control in the neural mechanisms that encode first-order and second-order motion. Contrast gain control is evident at all levels of visual processing, from the retina to visual cortex (Sclar, 1987; Sclar, Maunsell, & Lennie, 1990; Shapley & Victor, 1978, 1981) and has been explicitly included in models of second-order motion perception (e.g. Wilson et al., 1992). In Experiment 1 of the present study, for a given increase in stimulus modulation depth, reaction times decreased much more rapidly for second-order motion than for first-order motion (although reaction times were still much slower for second-order motion). Therefore the rate at which reaction times varied as a function of stimulus modulation depth may, all other things being equal, reflect differences in the contrast gain of the mechanisms that encode the two classes of motion. For example, the visual system may "boost" the second-order signal to make it more detectable, hence the steepness of the slopes for second-order motion compared to those for first-order motion in Fig. 2. Cells sensitive to second-order motion have been found at many levels of visual cortex including A17/18, V1 and MT Zhou & Baker, 1993), Albright, 1992) and the contrast response functions (CRFs) of visual cortex neurons show a more rapid increase in neural firing-rate as stimulus modulation depth increases for second-order motion than for first-order motion. Furthermore, whereas cell responses saturate at high modulation depths for first-order motion, those for second-order motion are invariably monotonic (see Ledgeway, Zhan, Johnson, Song, & Baker, 2005).

In terms of the physiological mechanisms that could mediate the behavioural effects reported in the present study, there is evidence that the temporal phase-lag (response latency) of neural responses to luminance-defined stimuli decreases as stimulus contrast increases. This has been demonstrated in the retina (Shapley & Victor, 1978), the lateral geniculate nucleus (Maunsell et al., 1999) and in motion-sensitive cells in striate visual cortex (Albrecht, 1995). That stimulus modulation depth has a qualitatively similar effect on both neural and behavioural response latencies suggests that both phenomena may share a common underlying physiological basis. However how the phase-lag of neural responses to second-order motion stimuli varies with stimulus contrast has yet to be investigated but may shed light on this interesting issue.

An important additional aspect of this study was to determine if differences in reaction times to different varieties of motion could be accounted for simply on the basis of differences in sensitivity. Indeed, when equated in terms of multiples of direction-discrimination threshold, slopes for luminance-modulated, contrast-modulated, polarity-modulated and orientation-modulated dynamic noise became much more similar (Fig. 5). However, despite being equated, reaction times for discriminating the direction of luminance-modulated noise (first-order motion) remained faster than those for contrast-modulated noise (second-order motion), a finding in agreement with Ellemberg et al. (2003). This similarity in the results of the two studies despite considerable methodological differences (e.g. in terms of the range of modulation depths studied, drift temporal frequency, the use of dynamic vs. static noise carriers and a discrimination vs. detection task) suggests that this phenomenon is robust and reflects a fundamental difference in the processing of luminance-defined and contrast-defined motion. Polarity-modulated and orientation-modulated noise (second-order motion) showed an equivalent pattern of results to those found for contrast-modulated noise. Even when equated in terms of direction-discrimination threshold, reaction times for spatial length-modulated noise decreased much more rapidly than for any of the other motion patterns. Furthermore absolute sensitivity for this particular variety of motion was lowest overall and gave rise to the most marked differences in reaction time performance between the different observers. This pattern of results suggests that it may be encoded by a different mechanism. For example, it has been proposed (Cavanagh, 1992; Hutchinson & Ledgeway, 2006; Lu & Sperling, 1995, 2001b) that some second-order motion patterns (e.g. those defined by motion-from-motion, dynamic stereo depth and interocular luminance modulations) may be encoded using a high-level, attentive, feature-based strategy, the defining characteristics of which are extremely poor sensitivity and severely low-pass temporal tuning. Both these characteristics are also true of spatial length-modulated noise undergoing motion (Hutchinson & Ledgeway, 2006). In the context of the present findings, another characteristic of an attentive, feature-based motion system may be that using multiples of threshold as a metric to equate stimulus visibility does not necessarily guarantee equivalent patterns of performance.

In terms of further research, there is evidence that behavioural response times also decrease as the spatial frequency (Ludwig et al., 2004; Manahilov, Calvert, & Simpson, 2003; Murray & Plainis, 2003) or speed (Burr et al., 1993) of a stimulus increases. Under these conditions reaction times are also dependent on stimulus type. Manahilov et al. (2003) for example measured reaction times at near-threshold contrast levels for stationary first-order and second-order stimuli of 0.5 and 7 c/deg. At a spatial frequency of 0.5 c/deg, reaction times were slower for second-order stimuli than for first-order stimuli. However at 7 c/deg, reaction times were similar for the two types of pattern. In addition, Burr et al. (1993) measured reaction times for detecting the onset of luminance gratings and chromatic gratings as a function of speed. At low speeds ($\leqslant\sim 2$ deg/s), reaction times were slower for detecting the onset of chromatic gratings than luminance gratings. However at speeds greater than ~2 deg/s reaction times for the two types of pattern were equivalent. How reaction times for discriminating the drift direction of the motion patterns employed in the present study vary under these conditions would provide further insights into the temporal dynamics of the mechanisms that encode these types of motion.

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Appendix A

The values of *a*, *k*, and R^2 for each observer and motion pattern derived from fitting a curve based on Eq. (4) to the data of Experiment 1

Parameters	LM	CM	PM	OM	SLM
Observer CVH					
a	430.47 (±3.38)	444.74 (±11.29)	454.07 (±11.12)	483.53 (±3.80)	−26.97 (±24.99)
k	1.16 (±0.06)	41.06 (±2.65)	58.17 (±3.43)	42.73 (±1.17)	560.62 (±21.74)
R^2	0.98	0.98	0.99	0.99	0.99
Observer JD					
a	360.67 (±2.41)	394.68 (±4.27)	425.55 (±5.26)	450.85 (±4.79)	231.39 (±3.35)
k	0.73 (±0.05)	15.23 (±1.32)	18.16 (±2.11)	20.02 (±2.47)	226.08 (±3.06)
R^2	0.98	0.97	0.96	0.97	0.99
Observer CC					
a	377.58 (±1.07)	477.20 (±4.64)	471.19 (±26.17)	541.68 (±10.25)	87.39 (±206.65)
k	0.95 (±0.02)	31.41 (±1.86)	48.15 (±10.51)	21.60 (±4.11)	477.51 (±188.55)
R^2	0.99	0.99	0.88	0.90	0.87
Observer LKS					
a	370.15 (±2.61)	417.87 (±6.59)	444.18 (±2.94)	453.50 (±9.60)	231.55 (±28.28)
k	0.62 (±0.05)	20.85 (±2.65)	22.50 (±1.18)	15.92 (±6.29)	242.18 (±25.80)
R^2	0.96	0.95	0.99	0.87	0.99
Observer RWD					
a	320.55 (±4.89)	356.48 (±3.22)	422.82 (±4.82)	379.33 (±17.57)	−7.68 (±31.87)[a]
k	0.62 (±0.09)	19.08 (±1.29)	3.47 (±2.49)	44.25 (±11.50)	542.78 (±28.12)
R^2	0.88	0.99	0.49	0.94	0.99
Observer SH					
a	512.08 (±5.86)	651.55 (±16.00)	608.34 (±29.73)	586.84 (±9.80)	—[b]
k	1.54 (±0.11)	39.17 (±6.43)	51.67 (±15.35)	14.21 (±3.02)	—
R^2	0.97	0.93	0.85	0.85	—

[a] Only 2 data points available.

[b] No data available (observer failed to achieve criterion level of performance).

Appendix B

The values of *a*, *k*, and R^2 for each observer and motion pattern derived from fitting a curve based on Eq. (5) to the data of Experiment 2

Parameters	LM	CM	PM	OM	SLM
Observer CVH					
a	433.50 (±6.40)	457.72 (±10.77)	473.43 (±12.15)	509.78 (±14.46)	230.22 (±73.45)
k	358.15 (±0.06)	335.69 (±19.58)	389.12 (±23.54)	443.51 (±31.99)	528.37 (±96.06)
R^2	0.98	0.97	0.97	0.96	0.88
Observer JD					
a	364.81 (±2.97)	411.23 (±8.53)	432.67 (±6.87)	439.35 (±5.19)	252.75 (±8.37)
k	155.01 (±7.38)	169.48 (±19.60)	128.58 (±14.45)	112.75 (±8.92)	332.70 (±11.08)
R^2	0.98	0.90	0.92	0.97	0.99
Observer CC					
a	375.88 (±9.37)	444.95 (±12.08)	465.09 (±19.069)	530.29 (±38.60)	87.39 (±206.65)
k	156.58 (±20.73)	141.03 (±17.44)	168.70 (±27.11)	81.97 (±42.93)	622.27 (±245.71)
R^2	0.89	0.90	0.84	0.42	0.87

Appendix B (*continued*)

Parameters	LM	CM	PM	OM	SLM
Observer LKS					
a	377.97 (±5.24)	434.58 (±7.87)	444.84 (±4.36)	463.57 (±4.91)	346.34 (±43.33)
k	115.62 (±13.50)	77.73 (±14.29)	83.49 (±6.59)	33.37 (±8.68)	191.59 (±51.67)
R^2	0.88	0.83	0.96	0.79	0.82
Observer RWD					
a	325.57 (±5.96)	358.95 (±3.49)	405.91 (±14.14)	414.49 (±31.29)	189.53 (±71.74)
k	114.66 (±13.94)	79.59 (±5.71)	48.96 (±20.81)	34.40 (±41.85)	193.82 (±74.18)
R^2	0.88	0.97	0.53	0.18	0.87
Observer SH					
a	529.96 (±20.83)	651.55 (±16.00)	659.29 (±51.22)	589.56 (±13.85)	—[a]
k	112.46 (±53.66)	157.66 (±25.87)	46.59 (±77.32)	54.31 (±19.66)	—
R^2	0.31	0.93	0.08	0.56	—

[a] No data available (observer failed to achieve criterion level of performance).

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