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Second-order optic flow processing

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Abstract

Optic flow—large-field rotational and radial motion—is processed as efficiently as translational motion for first-order (luminance-defined) stimuli. However, it has been suggested recently that the same pattern does not hold for second-order (e.g. contrast-defined) stimuli. We used random dot kinematogram (RDK) stimuli to determine whether global processing of optic flow is as efficient as processing of global translational motion for both first- and second-order stimuli. For first-order stimuli, we found that coherence thresholds for radial and rotational motion were equivalent to thresholds for translational motion, supporting previous findings. For second-order stimuli we found, firstly, that given sufficient contrast, second-order optic flow can be processed as efficiently as first-order optic flow and, secondly, that rotational and translational second-order motion are processed with equal efficiency. This contradicts the suggestion that there is a loss of efficiency between integration of second-order global motion and second-order optic flow. The third interesting finding was that the processing of radial second-order motion appears to suffer from a deficit that is dependent upon both the contrast and spatial extent of the stimulus. Further experiments discounted the possibility that the observed deficit is caused by a centrifugal or centripetal bias, but demonstrated that a longer temporal integration period for radial second-order motion is responsible for the observed difference. For durations of ~850 ms, all three types of motion are processed with equal efficiency.

Keywords: Global; Motion; Optic flow; Complex motion; MST

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1. Introduction

Humans are able to derive heading precisely from sparse or discontinuous flow fields and can use extra-retinal information from corollary eye movements to derive heading in the absence of depth information (Warren & Hannon, 1988, 1990). It is likely that the human visual system incorporates mechanisms specifically for the detection of optic flow—radial, rotational or spiral motion patterns. Early psychophysical experiments used adaptation to reveal mechanisms for the detection of radial and rotational motion (Regan & Beverley, 1978, 1985). Extraction of these motion patterns is extremely important as they are caused by movement of the individual ('optic flow') or by external objects moving in three dimensions (Koenderink, 1986).

One of the current models of optic flow analysis argues that optic flow is decomposed into three cardinal components, namely translational, radial and rotational motion (Burr, Badcock, & Ross, 2001; Morrone, Burr, Di Pietro, & Stefanelli, 1999 *but see also* Meese & Anderson, 2002; Snowden & Milne, 1996). There is physiological evidence that translational motion is computed in area MT (Movshon, Adelson, Gizzi, & Newsome, 1985) while radial and rotational motions are first seen in the response properties of cells in MSTd (Duffy & Wurtz, 1991a, 1991b; Tanaka, Fukada, & Saito, 1989; Tanaka & Saito, 1989). Thus, according to this view, optic flow stimuli are processed serially, starting in the striate cortex with the analysis of motion in local parts of the field by cells with small

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receptive fields. This local motion information is globally integrated in area MT by cells with larger receptive fields, which compute global translational motion. Finally, global radial and rotational motion is encoded by MSTd cells with much larger receptive fields based on their MT input.

Previous research (Bertone & Faubert, 2003; Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006) has shown that there is no sensitivity difference between translational and radial/rotational first-order (luminance-defined) motion. This has been interpreted as showing that there is no loss of efficiency between MT and MST processing. In the following experiments we reassessed this claim using large- and small-field random dot kinematogram (RDK) stimuli that require a global motion analysis (Morgan & Ward, 1980; Siegel & Andersen, 1988; Williams & Sekuler, 1984).

In addition to detection of motion defined by variations in luminance ('first-order' motion), the visual system is also capable of detecting motion defined by 'second-order' characteristics such as variations in contrast, flicker or texture (Cavanagh & Mather, 1989; Chubb & Sperling, 1988). The ability to detect this type of motion may be especially important for detecting camouflaged prey or predators (Derrington & Henning, 1993) or for maintaining position in water by detecting the movement of suspended particles (Orger, Smear, Anstis, & Baier, 2000). Second-order motion could be detected by the first-order motion system if the signal was subjected to an early non-linear transduction in luminance that produced distortion products in the neural representation of the image (Derrington, 1987; MacLeod, Williams, & Makous, 1992). However, psychophysical and physiological evidence suggests that the two types of motion are initially analysed separately and in parallel and subsequently combined (pooled, integrated or compared) at a later stage of processing (Albright, 1992; Edwards & Badcock, 1995; Geesaman & Andersen, 1996; Nishida, Ledgeway, & Edwards, 1997; Scott-Samuel & Georgeson, 1999; Wilson, Ferrera, & Yo, 1992). However, the nature of this combination process and whether or not it is mandatory are currently indeterminate.

Several studies point to a role for second-order motion in optic flow analysis. Bertone and Faubert (2003) found that observers could discriminate the direction of second-order optic flow, but they showed a difference in sensitivity between translational and radial/rotational flow patterns which they interpreted as a loss of efficiency in second-order processing between MT (translation) and MST (radial and rotation). Vection, the illusion of self-motion caused by large-field motion, can be induced by purely second-order stimuli, although the resulting sensation is weak (Gurnsey, Fleet, & Potechin, 1998), suggesting a diminished second-order contribution to optic flow. Second-order motion in the periphery appears to show a centrifugal bias, i.e. it is easier to detect if it is moving away from the fovea (Dumoulin, Baker, & Hess, 2001). Second-order motion can also be used to derive heading, but only if the motion does not involve decomposition of the flow field into separate components (Hanada & Ejima, 2000). On the other hand, Allen and Derrington (2000) argued against any second order contribution to optic flow analysis after finding slow responses to multiple-aperture 'beat' stimuli.

Our questions, therefore, relate to the role of second order motion in optic flow. Unlike previous attempts, we use a stimulus that requires the global extraction of motion direction (Morgan & Ward, 1980; Siegel & Andersen, 1988; Williams & Sekuler, 1984) to assess whether second-order motion makes a contribution to optic flow and, if so, whether there is any difference in the relative sensitivities of second-order translational and rotational/radial motion that could reflect a loss of processing efficiency between MT and MST.

Global motion analysis (including optic flow) has been argued to be a two-stage process (Morrone, Burr, & Vaina, 1995). The first stage involves the contrast-dependent detection of local motion in different parts of the field and contrast is temporally summated up to 300 ms, whereas the second stage involves the combination of these local motions and integrates motion information for up to 3 s (Burr & Santoro, 2001). The first stage has been linked to cells with small receptive fields in area V1 that undertake a contrast-energy analysis and encode local motions (Movshon & Newsome, 1996). The second stage has been linked to the cells in area MT whose receptive fields are larger and where V1 inputs are combined (Movshon et al., 1985; Rodman & Albright, 1989). The responses of MT cells are relatively contrast-insensitive but depend crucially on the signal-to-noise ratio, or the global motion coherence level. To answer the questions outlined above, we used RDK stimuli and measured coherence thresholds for global motion as a function of the contrast (or modulation depth in the case of second-order motion). This technique enabled us to assess the possible origin of any differences in sensitivity to different types of motion (Simmers, Ledgeway, & Hess, 2005, 2003, 2006).

We measured coherence thresholds as a function of stimulus contrast for detection of first- and second-order translational, radial and rotational global motion in normal observers. The results of Experiment 1 show that second-order motion, if given sufficient contrast, can reach levels of performance equivalent to first-order motion, suggesting that the primary difference between the two processing streams is due to the sensitivity of low-level (i.e. V1) detectors. For first-order stimuli, with either small or large spatial extents, thresholds for both types of optic flow are equivalent to translational motion thresholds across a large range of contrasts, as has been shown previously (Simmers et al., 2006). For second-order stimuli, thresholds for rotational motion are equivalent to translational motion thresholds, although radial motion thresholds are consistently higher and show a greater loss at low contrasts, especially with large field stimuli. These results are different from those of Bertone and Faubert (2003) who found an impairment of both rotational *and* radial motion processing of second-order stimuli. Experiment 2 shows that the impairment in radial thresholds is not due to an asymmetry in detection of second-order expansion and contraction. Experiment 3 used much larger stimuli to better isolate MST mechanisms and showed a much greater radial impairment, which was confined to low contrasts. Previous work has suggested that second-order motion detectors in the periphery favour centrifugal motion (Dumoulin et al., 2001). Experiment 4 discounted the possibility that this impairment is caused by an asymmetry in detection of second-order expansion and contraction. Experiment 5 shows that a longer temporal integration period for radial second-order motion is responsible for the observed difference. The contrast-dependent nature of this impairment suggests a low-level explanation.

2. Experiment 1

2.1. Observers

The observers consisted of one of the authors (CAS) and five experienced observers naïve to the purposes of the experiment. All observers had normal acuity or wore their prescribed correction. Viewing was monocular and observers were randomly assigned to use either their left or right eye (the other eye was occluded using a patch). Average age of the observers was 29.17 years (SD of 4.96 years).

2.2. Apparatus and stimuli

Random dot kinematograms (RDKs) were generated by custom software on an *Apple Macintosh G4* and displayed on a 22 in. *Mitsubishi Diamond Pro 2070SB* CRT monitor. The resolution of the screen was 1078 × 768 pixels and the frame rate was 75 Hz. The display was gamma corrected with the use of internal look-up tables, by a psychophysical technique described elsewhere (Ledgeway & Smith, 1994).

The RDKs were "movies" composed of eight consecutively presented frames and each frame was presented for 53 ms. The total presentation duration was therefore 427 ms. The RDKs contained 50 non-overlapping dots (radius 0.235°), which were presented in a circular window with a diameter that subtended 12° of visual angle from the viewing distance of 93 cm. This resulted in an average dot density of 0.44 dots/deg^2. A circular portion of the display centred at fixation (radius 0.7°) was occluded (i.e. set to mean luminance) to prevent the sudden appearance or disappearance of dots at fixation acting as a potential cue to global motion direction in the radial stimuli. A pilot study demonstrated that observers could use this cue and this resulted in artificially low thresholds for radial motion. Inclusion of a foveal occlusion zone eliminated this advantage.

All of the dots were displaced 0.3° on each frame. If a dot exceeded the boundary of the display area it was wrapped around to reappear at the opposite edge of the stimulus area. The direction in which the dots were displaced depended upon the condition and whether a dot was assigned to be a "signal dot" or "noise dot". In the *translational* condition, signal dots were displaced vertically upwards or downwards. In the *radial* condition, signal dots were displaced outwards or inwards. In the *rotational* condition, signal dots were displaced clockwise or anticlockwise. Noise dots were always displaced in a random direction. On each frame, dots were randomly reassigned to be either a noise dot or signal dot, so that subjects could not complete the task by tracking a single dot.

The background of the stimulus presentation area was composed of two-dimensional, static, binary noise with a Michelson contrast of 0.1. Each noise element was assigned a single luminance value (randomly chosen to be either "black" or "white" with equal probability) and was composed of a single screen pixel to avoid potential luminance artefacts (Smith & Ledgeway, 1997). A different stochastic noise sample was used for every motion sequence that was generated. The remainder of the display was set to the mean luminance of the monitor (~40 cd/m^2). Each dot was a circular region (radius 0.235°) of noise elements and either the mean luminance (in the case of first-order stimuli) or mean contrast (in the case of second-order stimuli) of the noise within the dot could be increased relative to that of the noise in the background. The 'modulation depth' of the dots refers to this increase in luminance or contrast. In first-order stimuli the modulation depth is defined as:

$$\text{Modulation depth} = (\text{DL}_{\text{mean}} - \text{BL}_{\text{mean}})/(\text{DL}_{\text{mean}} + \text{BL}_{\text{mean}}),$$

where DL_{mean} and BL_{mean} refer to the mean dot luminance and background luminance, respectively. Whilst in second-order stimuli the modulation depth is defined as:

$$\text{Modulation depth} = (\text{DC}_{\text{mean}} - \text{BC}_{\text{mean}})/(\text{DC}_{\text{mean}} + \text{BC}_{\text{mean}}),$$

where DC_{mean} and BC_{mean} refer to the mean dot contrast and background contrast, respectively.

In line with previous studies that have used comparable radial and rotational RDK stimuli (e.g. Burr & Santoro, 2001; Simmers et al., 2006), the magnitude of the dot displacement was always constant across space (i.e. did not vary with distance from the origin as it would for a strictly rigid radial or rotational flow field) so that performance could be directly compared with the translational RDK stimuli. Indeed many studies suggest that neurons in MSTd are relatively insensitive to the presence or absence of speed gradients within the receptive field (Orban, Lagae, Raiguel, Xiao, & Maes, 1995; Tanaka et al., 1989; but see also Duffy & Wurtz, 1997).

2.3. Procedure

A single-interval 2AFC staircase procedure was used to obtain observers' global motion thresholds for each of a range of dot modulation depths (visibility levels). The trials all began with presentation of a fixation cross in the centre of the display, which was replaced by an RDK stimulus.

The task of the subject was to identify the global motion direction (up/down, outward/inward or clockwise/anti-clockwise according to the condition) and respond with a button press. Initially, all dots were displaced in the 'signal' direction. An adaptive 1-up, 3-down staircase procedure (Edwards & Badcock, 1995) was used to vary the percentage of signal dots in order to converge on the observers' motion coherence threshold, which was defined as the stimulus coherence (minimum number of signal dots) supporting 79% correct performance. The step size of the staircase was initially set to eight signal dots and this was subsequently halved for each reversal (change in staircase direction), so that after the third reversal the step size was reduced to a single dot. The staircase terminated after eight reversals and the threshold value was calculated as the mean of the last six reversals. Thresholds were obtained for all three motion types (translational, radial and rotational) and stimulus types (first-order and second-order) at each of a range of modulation depths. Observers repeated each condition five times and the reported thresholds are the mean of these five staircases.

2.4. Results

The mean motion coherence threshold (averaged across the observers as a group) and standard error were calculated for each dot modulation depth condition that was tested. As in previous studies using this technique (Simmers et al., 2005, Simmers, Ledgeway, Hess, & McGraw, 2003, 2006), the individual and group data were well fitted by a curve of the form $y = ax^b + c$. Fitting this type of function allows us to decouple the effects of low- and high-level motion processes. For example, if any observed differences are primarily due to effects occurring in low-level, first-stage processing (i.e. V1) then we would expect a strong contrast-dependence and the function relating coherence sensitivity and stimulus contrast would be horizontally displaced along the contrast axis. If, on the other hand, deficits are due to higher-level (i.e. MT or MST) processing differences (stage 2) then we would expect a strong dependence on motion coherence and as a result the function would be displaced vertically along the motion coherence (or motion integration) axis.

At low modulation depths, thresholds are limited by the efficiency with which early stages of the visual system could summate local contrast. Above a certain modulation depth, motion coherence thresholds are approximately constant, limited by the efficiency with which later global motion mechanisms can integrate the local motions (Morrone et al., 1995). Table 1 presents the values of a,b and c for the three types of motion and the corresponding r^2 values for these fits.

The data are presented graphically in Fig. 1. First-order coherence thresholds (Fig. 1, top) are minimal and constant for a wide range of contrasts but increase sharply for the lowest contrasts tested. There appears to be no difference in the results for the different types of motion for first-order stimuli, which is in accordance with previous findings using this method (Simmers et al., 2006). The coherence thresholds for second-order motion (Fig. 1, bottom) are generally higher than for first-order motion at

Table 1
Model parameters obtained for the different conditions

Stimulus class	Motion type	a	b	c	r^2
First-order	Translational	4.87e−4	−2.24	6.91	0.95
	Radial	2.77e−5	−2.86	7.72	0.96
	Rotational	4.9e−5	−2.71	6.67	0.97
Second-order	Translational	0.59	−4.21	7.28	0.98
	Radial	0.45	−4.9	9.01	0.98
	Rotational	0.47	−4.61	6.84	0.99

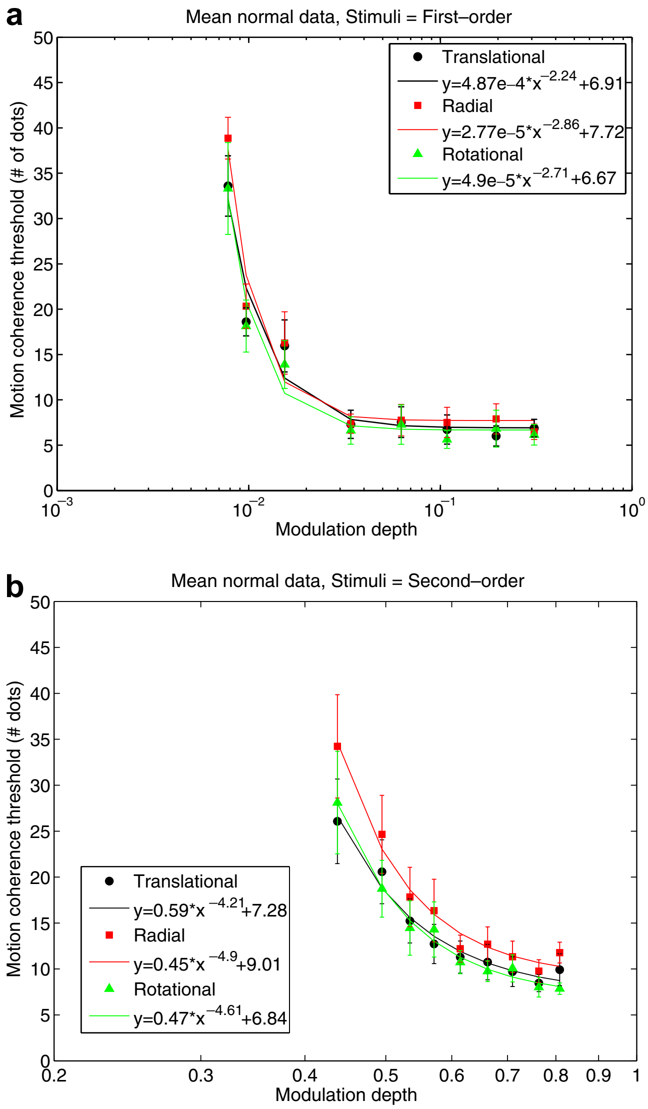

Fig. 1. Coherence thresholds for translational, radial and rotational first-order (a) and second-order (b) motion. Note the change of scale between first- and second-order. Each data point represents the mean threshold (±standard error) of six observers. Each observer's threshold represents the mean of five staircases.

high contrasts and increase sharply as modulation depth decreases. The interesting finding here is that for the thresholds for the three different types of second-order motion are not the same and radial thresholds are consistently higher than either translational or rotational across the entire range of modulation depths.

An ANOVA carried out on the second-order data showed a significant main effect of both modulation depth ($F(8,40)=16.191$, $p<.001$) and motion type ($F(2,10)=10.574$, $p=.003$). Post-hoc *t*-tests showed that radial motion was significantly different from both translational and rotational motion ($p<.001$ in both cases). Translational and rotational motion did not differ significantly from each other, therefore a simple 'loss of efficiency' in motion processing between MT and MST cannot account for this data. This contradicts previous findings (Bertone & Faubert, 2003) showing a clear difference between *optic flow* thresholds (in the sense of both radial *and* rotational motion) and translational motion thresholds.

2.4.1. An asymmetry of radial motion detection?

What could account for the higher observed thresholds for radial motion? There is some suggestion in the literature that expansion and contraction may be processed differently (Dumoulin et al., 2001; Edwards & Badcock, 1993; Takeuchi, 1997). As the task in Experiment 1 is a 2AFC direction-discrimination judgment, the observer's ability to detect motion in both directions contributes to the final observed motion coherence threshold. A higher threshold for detection of one direction of radial motion (expansion or contraction) could be responsible for the observed increase in radial motion thresholds. Using a global motion stimulus similar to the one employed here, Edwards and Badcock (1993) found that sensitivity to centripetal motion is higher than to centrifugal motion. Furthermore it has been reported that expansion is detected easily in a field of moving distractors and the latency to detection does not increase with the number of distractors (Takeuchi, 1997). Contraction, on the other hand, is harder to detect and the latency to detection increases with the number of distractors, implying that a serial visual search strategy must be employed to locate it. However, Takeuchi (1997) briefly reviews the evidence for an asymmetry between expansion and contraction and concludes that "both centrifugal and centripetal biases have been observed," and appear to be dependent upon the type of stimulus.

There is also some evidence to suggest that sensitivity to the motion of second-order stimuli is higher if the stimuli are moving centrifugally, than if they are moving centripetally (Dumoulin et al., 2001). It was necessary, therefore, to establish whether such an asymmetry was responsible for raising radial thresholds.

3. Experiment 2

Motion coherence thresholds were obtained for second-order motion of each type (translational, radial and rotational) at both a high and low contrast. Two modulation depth values were chosen; the highest (0.81) available and a low value that produced higher than chance performance (0.42). The stimulus and procedure for this second experiment were otherwise identical to the first, except that two separate staircases were randomly interleaved, one for each direction of motion. This method produced separate motion coherence thresholds for opposite directions of motion. For example, in the translational condition, two separate staircases simultaneously tracked the threshold for correct identification (79%) of upward motion and the equivalent threshold for downward motion. Four observers with normal vision took part in this experiment (mean age 29.5, SD 1.9).

3.1. Results

The mean thresholds for the four observers are shown in Fig. 2. As can be seen, there was a clear effect of stimulus contrast and a trend for radial thresholds to be higher than thresholds for the other types of motion. However, there does not appear to be any difference between the different directions of motion such as the one shown by Dumoulin et al. (2001). A multifactoral ANOVA was carried out on the results, which showed a significant main effect of motion type ($F(2,8)=5.82$, $p=.0325$) and a significant main effect of contrast ($F(1,4)=161.25$, $p<.01$). Motion direction was not significant ($F(1,4)=4.12$, NS), but this factor referred to very different directions according to the type of motion, therefore post-hoc *t*-tests were carried out which confirmed that the differences between thresholds for the different pairs of motion direction (up vs. down, expansion vs. contraction and ACW vs. CW) were all non-significant.

In Dumoulin et al's study, the stimuli were not whole-field optic flow stimuli, but were discrete regions presented

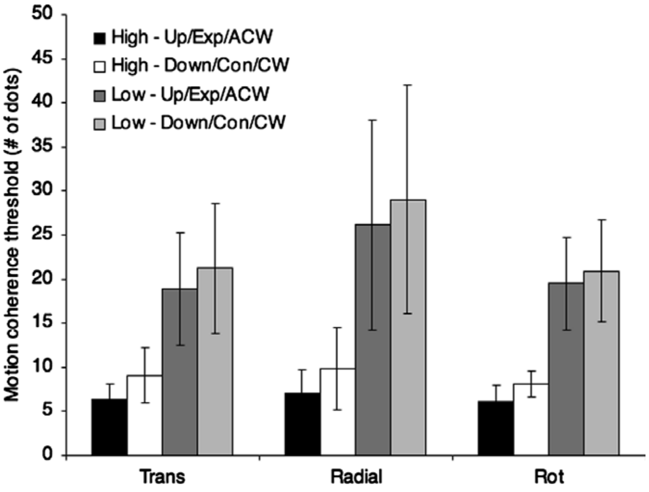

Fig. 2. Coherence thresholds for small-field second-order motion of opposite directions. Thresholds are higher for low contrast stimuli and marginally higher for radial motion, but do not show a clear difference between motion in different directions. Error bars are ±1SD.

in the periphery, which contained multiple Gabor patches. The eccentricity at which they were presented was much greater than the area covered by our stimulus (>14°). We therefore considered it possible that a larger stimulus may selectively disadvantage the processing of second-order radial motion and may also reveal a greater asymmetry of direction-discrimination between opposing directions.

4. Experiment 3

For this experiment, the RDK stimulus was scaled up for viewing on an *Electrohome* (*Retro III*) back-projection CRT monitor (138 cm by 104 cm). The projector was controlled by the same computer as the previous experiments. The projector was gamma corrected psychophysically (Ledgeway & Smith, 1994). The screen resolution was 1024×768 pixels with frame rate of 75 Hz and the screen mean luminance was ~67 cd/m^2. The stimulus on this display, from a viewing distance of 57 cm, was 66° in diameter. The dots were 1.3° in diameter and were displaced 1.7° on each frame giving them a linear velocity of 32°/s. The larger size and the greater speed of the dots were required to ensure that the stimuli were readily visible out to the periphery, but make direct comparisons with the previous experiments difficult. A pilot study in which the signal dots were restricted to the outer region of the RDK showed that observers' peripheral acuity was sufficient to detect the dots and reliably discriminate the direction of motion. Two observers, who had participated in the previous experiments, took part in Experiment 3.

4.1. Results

The first-order large-field data (see Fig. 3, top) showed very little difference from the small-field data (see Section

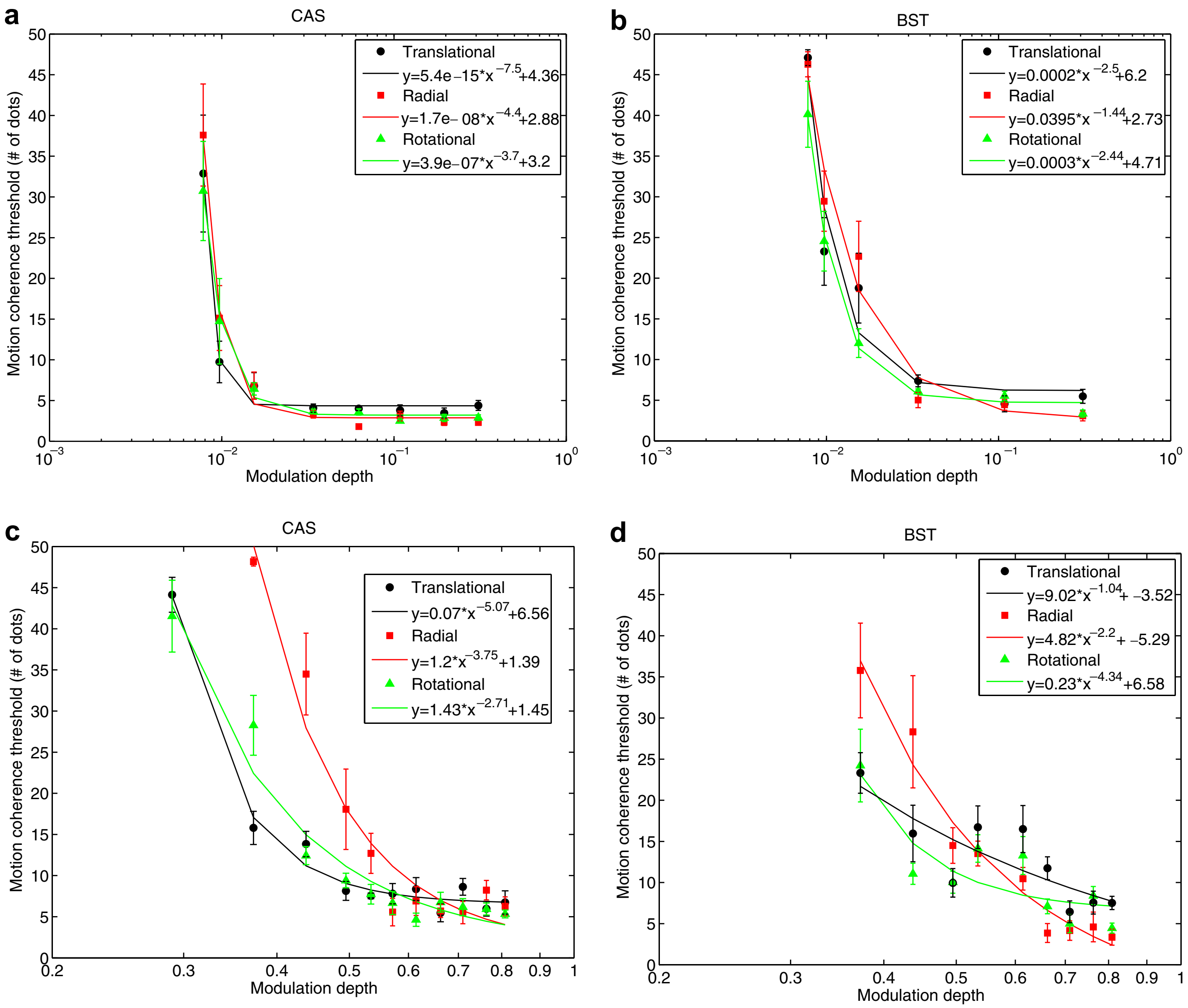

Fig. 3. Coherence thresholds for first-order (a and b) and second-order (c and d) large-field stimuli for two observers. Note the change of scale between first- and second-order. Second-order radial motion shows a deficit at low contrasts.

2). Translational, radial and rotational coherence thresholds were effectively indistinguishable across the range of contrasts tested. The second-order data, however, were quite different (see Fig. 3, bottom). Translational and rotational coherence thresholds were very similar, again suggesting that there is no simple loss of efficiency in motion processing between MT and MST. Second-order radial motion, on the other hand, was selectively impaired at low contrasts for both observers.

In order to ascertain whether an asymmetry in radial motion processing was responsible for this radial deficit or disadvantage, Experiment 4 used interleaved staircases to produce motion coherence thresholds for different directions of second-order global motion and optic flow.

5. Experiment 4

Separate motion coherence thresholds were obtained for opposite directions of second-order motion of each type (translational, radial and rotational) at both a high and low contrast. The 'interleaved staircase' procedure described in Experiment 2 was used for this experiment. The large-field display and stimulus parameters were otherwise identical to Experiment 3. The same four observers who participated in Experiment 2 took part in this experiment.

5.1. Results

The mean thresholds for the four observers are shown in Fig. 4. Once again, thresholds for low contrast stimuli were elevated relative to those for the high contrast stimuli, but the trend for radial thresholds to be uniformly higher is no longer evident. Two observers showed a clear difference between low contrast expansion and contraction thresholds, with elevated performance for contraction. However, the two other observers showed either no difference or an opposite effect. A *t*-test carried out on the means for low-contrast expansion and contraction was non-significant.

The stimuli in Experiments 3 and 4 were large-field second-order optic flow stimuli, which extended far into the periphery. Previous work with small stimuli presented peripherally has shown a centrifugal bias for second-order stimuli (Dumoulin et al., 2001). The results of Experiment 4 suggest that this bias (found with small, eccentrically-presented stimuli) does not extend to full-field radial stimuli. Therefore, they discredit the hypothesis that poorer performance for centripetal (contracting) second-order stimuli may be responsible for the impairment in second-order radial thresholds observed in large-field stimuli at low contrast (Experiment 3).

6. Experiment 5

Burr and Santoro (2001) demonstrated that contrast sensitivity and motion coherence for first-order optic flow have different integration periods. The current experiment used a fixed duration for all stimuli (427 ms). It is possible that radial second-order motion requires a longer integration period than translational or rotational second-order motion and this may explain the higher coherence thresholds. Experiment 5 investigates this possibility.

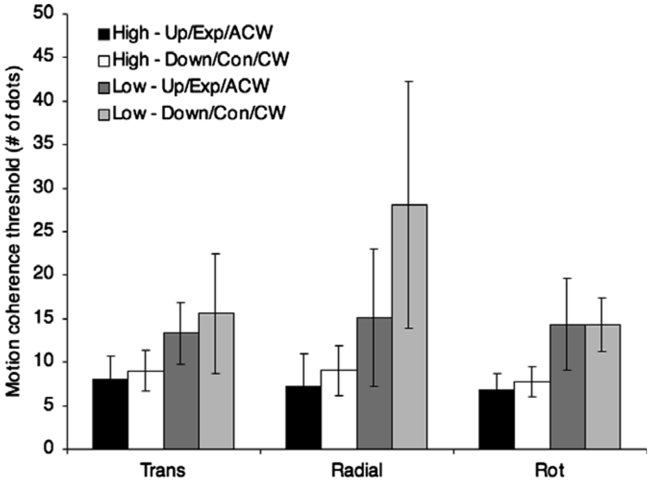

Fig. 4. Coherence thresholds for large-field second-order motion of opposite directions. Thresholds are again higher for low contrast stimuli, but thresholds do not show a clear difference between motion in different directions. Error bars are ±1SD.

6.1. Methods

Motion coherence thresholds were obtained for the three types of second-order motion from one of the authors (CAS) and 4 experienced observers naïve to the purpose of the experiment. The stimuli were shown on the same CRT monitor used for Experiments 1 and 2. The display parameters were identical to Experiments 1 and 2, except that the

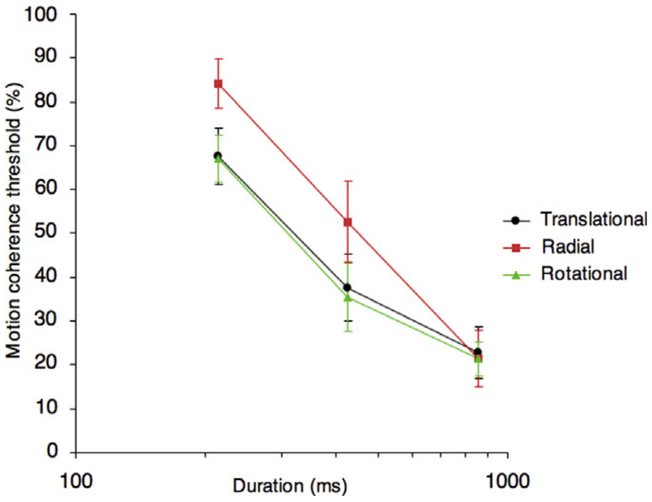

Fig. 5. Temporal integration of second-order optic flow. Data points show the mean motion coherence threshold for five observers (±standard error) for translational, radial and rotational global motion. Integration is slower for radial second-order motion.

duration of the stimulus was varied by either removing or adding frames to the sequence. The standard condition (427 ms) was repeated along with one shorter (213 ms) and one longer (854 ms) duration.

6.2. Results

The mean data for the five observers are shown in Fig. 5. It appears from these data that the temporal integration period for second-order translational and rotational motion is shorter than that for radial motion. Coherence thresholds are lower at the shortest duration, and reach their asymptote sooner.

7. Discussion

For luminance-defined (first-order) random dot stimuli, no difference was found between translational motion and optic flow for either small- or large-field stimuli. Performance at intermediate and high contrasts was constant, reflecting the threshold for global motion integration. At the lowest contrasts tested, thresholds increased sharply. That first-order global translational motion and the more complex radial and rotational optic flow stimuli produce identical response characteristics suggests that if the human homologue of MST utilises input directly from an area like MT, there is no intervening loss of efficiency. These results replicate previous results with first-order stimuli (Bertone & Faubert, 2003; Simmers et al., 2006).

Second-order thresholds, although generally worse than first-order, can reach levels equivalent to first-order motion provided the modulation depth (stimulus visibility) is sufficiently high. This suggests that integration of second-order motion can be as efficient as first-order, and the widely reported difference in sensitivity between the two systems must, according to the two-stage model of global motion processing, occur early in the motion pathway (e.g. V1).

Second-order translational and rotational thresholds were virtually identical in all conditions tested, but radial thresholds were markedly elevated for small-field stimuli and showed a clear contrast deficit for large-field stimuli. The contrast-dependence of this deficit suggests a low-level explanation. However, Experiments 2 and 4 discounted the idea that the elevation in radial second-order thresholds for small- and large-field stimuli is caused by an asymmetry in second-order radial motion detection.

Bertone and Faubert (2003) found that thresholds for second-order optic flow patterns (radial *and* rotational) were elevated over thresholds for second-order translational motion. They explained this result by suggesting that if second-order stimuli are analysed at a coarser spatial scale than first-order signals, as they are in filter-rectify-filter models (e.g. Chubb & Sperling, 1988), the orientation-tuning of second-order motion detectors is correspondingly broader and this produces less efficient pooling of responses in MST. The result of this loss of efficiency is to raise motion detection thresholds for so-called “complex” motion (or optic flow). However, more evidence would be needed to support this hypothesis. The results of the experiments reported here are inconsistent with the idea that pooling of second order responses in MST is necessarily less efficient than the equivalent processing for first-order motion.

The stimuli used in the current study do not contain any spatial (form) information that could be used as a cue to assist direction-discrimination. Bertone and Faubert’s optic flow stimuli, on the other hand, were circular or radial gratings. The periodic spatial structure of these stimuli provides a cue to their likely direction of movement and, in principle, direction-discrimination could proceed by purely local mechanisms. It could be argued that this is not ideal for isolating global motion processing mechanisms. In RDK stimuli, the motion direction is globally distributed and motion analysis cannot proceed via local mechanisms. Consequently RDK stimuli are particularly well-suited for isolating and probing the properties of the mechanisms that mediate optic flow processing per se.

Bertone and Faubert used contrast threshold as their dependent variable, whilst in the present study we used the global coherence threshold. However, the technique that we have employed in this study gives us a measure of both motion coherence thresholds and contrast encoding. The psychophysical functions we have obtained for the three different types of motion did not differ in a way that could be interpreted as a simple difference between global translational motion vs. optic flow processing (MT vs. MST). On the contrary: performance for rotational and translational second-order motion was comparable in all cases, whilst radial second-order motion, specifically, appeared to be processed in a less efficient manner for both small- and large-field stimuli.

The most interesting aspect of our results is the finding that radial second-order motion appears to be impaired relative to translational and rotational motion. It is often assumed that rotational and radial motion are processed in an identical fashion, and that the only difference between the two types of optic flow detector is the spatial arrangement of MT receptive fields that serve as their inputs (e.g. Perrone, 1992) and our first-order results support this contention. However, our results suggest that this cannot be the case for radial and rotational second-order motion. Detection of second-order radial motion is markedly worse than rotational motion, perhaps the first evidence of a clear difference in the two types of motion analysis.

The impairment in detection of second-order radial motion appears to depend on both the modulation depth and size of the stimulus. For small-field stimuli the impairment is constant across the range of modulation depths tested and does not appear to be caused by an asymmetry in encoding opposing directions. For large-field stimuli, the impairment is only evident at relatively low modulation depths and is substantial. It was considered that this could be caused by a centrifugal bias for detection of second-order motion in the periphery (Dumoulin et al., 2001).

The fact that performance for large-field stimuli is impaired at low contrasts, whilst performance at high contrasts is normal, suggests that a bias or asymmetry at the level of *local* second-order detectors (i.e. first-stage mechanisms) could be responsible for the performance loss for large-field stimuli. Experiment 4 showed that no such asymmetry exists for large-field second-order radial motion. Experiment 5 demonstrated that a longer period of temporal integration for global motion may be responsible for the consistently higher thresholds shown for second-order radial motion.

7.1. Second-order optic flow processing

The findings presented here do not support a simple direction-mosaic model of MST processing, in which an optic flow detector is constructed from translational motion detectors that are arranged in different geometries (Perrone, 1992), at least for second-order stimuli. If the only difference between radial and rotational detectors in MST were the spatial layout of MT receptive field subunits, then detection should be equally efficient. The results of Experiments 1 and 3 demonstrate that this is not the case and the findings of Experiment 2 and 4 show that the difference between radial and rotational–translational thresholds is not the result of an asymmetry between expansion and contraction. Therefore, some other factor must be responsible for this consistent impairment in radial processing.

Burr & Santoro (2001) demonstrated that contrast sensitivity and motion coherence for first-order optic flow have different integration periods. The current experiment used a fixed duration for all stimuli (427 ms). It is possible that radial second-order motion had higher coherence thresholds because it requires a longer integration period than translational or rotational second-order motion. Bertone & Faubert (2003) varied the exposure duration of their stimulus and their results show that temporal integration of contrast is similar for all three types of motion, but thresholds for rotational and radial motion (optic flow or “complex motion”) remain consistently higher than translational motion. Our Experiment 5 showed that, for global motion stimuli at least, the temporal integration period for second-order translational and rotational motion is equivalent, but shorter than that for radial motion. One possible reason for this difference in processing time for second-order radial motion could be the fact that, whilst translational and rotational motion depict planar motion which is often caused by movements of the head and eyes, radial motion normally results from locomotion and motion in-depth. It has already been observed that radial motion is perceived to be moving faster than both translational (Bex & Makous, 1997) or rotational (Geesaman & Qian, 1996) motion of similar velocity, which Bex and Makous attribute to the interpretation of a radial motion stimulus as an optic flow field. This suggests that radial motion is analysed as motion in-depth, perhaps by different mechanisms that compute a 3D optic flow field from the 2D input. The separability of rotational and radial motion analyses has been demonstrated by the fact that these two types of motion do not mask each other (Freeman & Harris, 1992). Why, if planar (translational and rotational) motion and motion in-depth (radial) are analysed by different mechanisms, do we find poorer performance only for *second-order* radial motion? It has been demonstrated that the second-order system is deficient at detecting motion in-depth (Landy, Dosher, Sperling, & Perkins, 1991) whilst the first-order system is not. If radial motion was analysed by motion in-depth mechanisms, we should perhaps expect an impairment for second-order radial motion whilst first-order radial motion is processed with equal efficiency to planar motion.

7.2. Cue-invariance in MST

If given sufficient dot modulation depth, coherence thresholds for second-order global motion and optic flow can reach levels similar to those obtained with first-order stimuli. This could be interpreted as evidence for cue-invariance at the level of MT and MST. However, the observed differences between first- and second-order radial motion processing are problematic for a model of the visual system in which these motion streams are simply combined in a mandatory fashion at the level of MT (Wilson et al., 1992). The fact that radial and rotational thresholds are identical for first-order stimuli and different for second-order stimuli has an important bearing upon the degree of cue-invariance within extra-striate cortical areas such as MST (Geesaman & Andersen, 1996). If most MST neurons are cue-invariant (respond to both first-order and second-order motion) we should expect second-order optic flow thresholds to follow a similar pattern to first-order optic flow thresholds (albeit with the poorer sensitivity that characterises second-order motion generally). The findings presented here lend support to previous work that has suggested that first- and second-order motion may be processed to some extent by different populations of cells at the level of MST (Badcock & Khuu, 2001). Whether the mechanisms that process optic flow for first-order stimuli and those that process optic flow for second-order stimuli are truly independent (Badcock & Khuu, 2001) is currently under investigation.

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