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Vision Research 43 (2003) 2591–2601

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How is complex second-order motion processed?

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Received 8 May 2003; received in revised form 4 July 2003

Abstract

Converging psychophysical and electrophysiological evidence suggests that first-order (luminance-defined) complex motion types i.e., radial and rotational motion, are processed by specialized extrastriate motion mechanisms. We ask whether radial and rotational second-order (texture-defined) motion patterns are processed in a similar manner. The motion sensitivity to translating, radiating and rotating motion patterns of both first-order (luminance-modulated noise) and second-order (contrast-modulated noise) were measured for patterns presented at four different exposure durations (106, 240, 500 and 750 ms). No significant difference in motion sensitivity was found across motion type for the first-order motion class across exposure duration (i.e., from 240 to 750 ms) whereas direction-identification thresholds for radiating and rotating second-order motion were significantly greater than that of the second-order translational stimuli. Furthermore, thresholds to all second-order motion stimuli increased at a significantly faster rate with decreasing exposure duration compared to those of first-order motion. Interestingly, simple and complex second-order thresholds increased at similar rates. Taken together, the results suggest that complex second-order motion is not analyzed in a sequential manner. Rather, it seems that the same 'hard-wired' mechanisms responsible for complex first-order motion processing also mediate complex second-order motion, but not before the pre-processing (i.e., rectification) of local second-order motion signals.

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Keywords: Motion perception; First-order; Second-order; Radial motion; Rotational motion

1. Introduction

Psychophysical investigations of human motion perception have attempted to define and distinguish between motion systems differing in functional architecture and complexity. The simplest of these systems, the 'first-order' system, extracts motion signals through standard motion analysis (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985) by operating on local luminance variations in the retinal image. The 'second-order' motion system (Cavanagh & Mather, 1989; Chubb & Sperling, 1988) is believed to extract motion signals from non-luminance defined visual information (i.e., texture, contrast and disparity, etc.). In the latter case, additional nonlinear processing, such as rectification or response squaring, is required before standard motion analysis results in a motion percept. One class of second-order motion models suggest that first- and second-order motion are initially

processed in parallel by separate passive mechanisms using similar motion detection principles (i.e., Chubb & Sperling, 1988; Nishida, Ledgeway, & Edwards, 1997; Wilson, Ferrera, & Yo, 1992). Experimental support for such second-order motion detection has been provided for the most part by psychophysical studies which have demonstrated differences between first- and second-order motion detection over a large range of stimulus parameters and experimental paradigms (see Chubb, Olzak, & Derrington, 2001; Clifford & Vaina, 1999, for review).

The dichotomy between the two motion classes has been based for the most part on findings comparing 'simple' (i.e., translational or unidirectional), first- and second-order motion. Although potential mechanisms underlying the processing of simple second-order motion have been developed and elucidated, relatively little is known about how 'complex' second-order motion, such as radial and rotational motion types, is processed by the visual system. To better understand the ecological function and importance of second-order motion information on behaviors such as heading and navigation,

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we measured the sensitivity to such complex types of motion configurations since they approximate to a greater extent the visual array produced by self-motion.

1.1. Specialized detection for complex first-order motion

Several authors have postulated that complex first-order motion is processed by specialized motion mechanisms operating in extrastriate brain areas (i.e., Burr, Morrone, & Vaina, 1998; Freeman & Harris, 1992). These mechanisms are believed to integrate local motion signals from directionally selective neurons belonging to the standard motion analysis mechanism, operating locally at the primary visual cortex (V1). Specialized motion mechanisms differ functionally from those underlying standard motion analysis because they specifically and efficiently detect complex motion types, such as radial and rotational motion. Psychophysical evidence for such a specialized or ‘multi-staged’ motion detection mechanism is considerable (Bex, Metha, & Makous, 1998; Burr et al., 1998; Freeman & Harris, 1992; Gurney & Wright, 1996; Morrone, Burr, & Vaina, 1995; Regan & Beverley, 1978, 1985; Snowden & Milne, 1996). Physiological evidence has shown that motion information is analyzed at various cortical levels within a hierarchical motion pathway which includes the primary visual cortex (V1), and extrastriate motion areas MT (medial temporal) and MST (medial superior temporal). Dorsal MST (dMST) neurons, which have characteristically large receptive fields and receive input significant from MT, are selectively activated by radial and rotational motion patterns (i.e., Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Tanaka & Saito, 1989). These neurons have been shown to be involved in the processing of wide-field movements caused by ecologically important behaviors of heading and locomotion.

1.2. Complex second-order motion perception and heading

A relatively small but growing body of research has addressed the general question regarding ‘complex’ second-order motion detection and its relation to heading judgements. Although a dynamic visual array produced by self-motion may contain both first- and second-order motion information, the extent to which second-order information contributes to the computation of heading behaviors remains unclear. Gurnsey, Fleet, and Potechin (1998) demonstrated that second-order motion signals alone are sufficient to produce the illusion of self-motion, albeit to a significantly lesser extent than first-order information. Since this illusory percept is believed to be dependent on the analysis of optic flow information, the authors suggest that mechanisms mediating optic flow perception (i.e., dorsal MST) may use both first- and second-order motion signals to resolve heading

direction after being integrated in area MT. Additional support for second-order involvement in optic flow processing was put forth by for Dumoulin, Baker, and Hess (2001) who found a centrifugal bias for second-order motion detection (i.e., selective bias to expanding Gabor micropatterns) in the peripheral visual field. Finally, Hanada and Ejima (2000) demonstrated that heading judgements, as measured by the preciseness of the perceived heading with simulated pursuit, differed significantly for first- and second-order defined optic flow arrays. A possible interpretation put forth by these authors was the less accurate speed estimates (i.e., velocity and directional tuning) for second-order information needed for correct heading recovery. More recently, Badcock and Khuu (2001) used a radial global motion task consisting of first- and second-order signals (Edwards & Badcock, 1995) to show that first- and second-order motion are processed independently after MT (i.e., MST), where the specialized motion mechanisms are believed to operate. Based on these findings, the authors suggested that radial optic flow patterns defined by first- and second-order characteristics are detected by separate mechanisms after MT.

1.3. Main goal of the present study

The results derived from the studies mentioned in the previous section provide important information regarding the involvement of first- and second-order motion signals towards optic flow perception and heading behavior. However, the functional nature of the mechanisms mediating the analysis of complex second-order information has yet not been elaborated. The purpose of the present study is to further explore the characteristics of mechanisms mediating radial and rotational second-order motion perception to better understand *how* such second-order configurations are analyzed by motion mechanisms operating after MT. For example, can specialized or ‘multi-staged’ motion analysis that underlie complex first-order motion be applied to moving patterns defined purely by second-order characteristics? If not, how is complex second-order motion analyzed? We approached this question by comparing the direction-identification thresholds of simple (i.e., translational) and complex (i.e., radial and rotational) motion types in both first- and second-order motion classes. In order to elaborate possible differences underlying complex motion processing between the two motion classes, we manipulated stimulus exposure duration. This was done since it has been demonstrated that reducing the exposure duration decreases the sensitivity to simple second-order stimuli to a greater extent when compared to first-order stimuli, possibly reflecting additional neural operations required for simple second-order motion perception (Derrington, Badcock, & Henning, 1993; Schofield & Georgeson, 2000; see Smith &

Ledgeway, 1998 for alternative view). Using complex optic flow patterns constructed using local first- and second-order motion apertures, Allen and Derrington (2000) demonstrated that observers' ability to discriminate between centered (i.e., coherently expanding or contracting) and distorted (i.e., directionally incoherent local patterns) patterns was affected by their being defined by first- or second-order characteristics. They found that the detection of the complex second-order optic flow patterns took a much greater amount of time (i.e., 2 s compared to 100 ms) when compared to first-order patterns. Based on these results, Allen and Derrington (2000) suggested that complex second-order motion analysis is not mediated by specialized mechanisms (i.e., 'second-order driven' optic flow detectors) but rather, by the sequential analysis of local second-order motion signals.

In the present experiment, direction-identification thresholds for simple and complex motion patterns were measured in both first- and second-order motion classes. The spatial and temporal characteristics of first- and second-order patterns were identical except for the characteristic defining their movement; luminance-modulation for the first-order stimuli and contrast-modulation for the second-order stimuli. If complex second-order motion analysis is mediated by sequential processing, it is expected that the direction-identification thresholds for complex types of second-order motion (i.e., radial and rotational) will increase at a faster rate compared to simple (i.e., translational) second-order motion as stimulus duration is decreased. However, if some type of specialized analysis is involved, no differential effect of exposure duration would be expected between simple and complex second-order direction-identification thresholds. Since it is well accepted that complex first-order motion is efficiently mediated by 'hard-wired' specialized mechanisms, it is expected that reducing stimulus duration should have no differential effect, or at least less of a differential effect, on simple and complex first-order thresholds.

Our results demonstrated that direction-identification thresholds to complex second-order motion stimuli were significantly increased at all exposure durations compared to that of simple second-order motion. This was not the case for the first-order motion class where the thresholds for all motion types (i.e., simple and complex) were similar, at least for those presented longer than 240 ms. Furthermore, we found that the motion sensitivity to *all* second-order motion types decline at a faster rate relative to those of first-order motion with decreasing stimulus exposure duration, suggesting separate initial analysis of first- and second-order motion processing. However, the rate with which simple and complex second-order thresholds increased with decreasing exposure duration was similar. Finally, at very brief exposure durations (106 ms), correct direction-

identification was difficult only for complex second-order motion stimuli. Interpretations of these results as well as a proposed working model for complex second-order motion analysis are presented in the discussion.

2. Methods

2.1. Observers

Seven psychophysically experienced observers ranging between 23 and 43 years of age participated in all conditions of the study. Five of the observers were naive to its purpose and all had normal or corrected-to-normal vision.

2.2. Apparatus and display

Stimulus presentation and data collection were controlled by a Power Macintosh G3 computer and presented on a 16-inch AppleVision 1710 monitor (frame refresh rate of 75 Hz) which was gamma-corrected using a color look-up table. The screen resolution was 832×624 pixels. The motion stimuli were generation and animation by the VPixx[®] graphics program (www.vpixx.com). Color calibration and luminance readings were taken using the Minolta Chromameter. The mean luminance of the display was 32.30 cd/m^2 ($u' = 0.1832$, $v' = 0.4608$ in CIE (Commission Internationale de l'Eclairage) $u'v'$ color space) where L_{\min} and L_{\max} were 0.19 and 64.60 cd/m^2 , respectively.

2.3. Stimuli

Motion stimuli used in this study are shown in Fig. 1. They consisted of first- and second-order translating, radiating and rotating patterns, constructed by either adding or multiplying static greyscale noise to a modulating sinewave of different profiles e.g., a vertical sinusoid for translational motion, a radially symmetrical sinusoid for radial motion and an angled sinusoid for rotational motion (Bertone, Mottron, Jelenic, & Faubert, 2003).

The stimuli were presented within a hard-edged circular region at the center of the display subtending a visual angle of 5° in diameter when viewed from a distance of 114 cm. The noise consisted of dots ($1 \text{ pixel} \times 1 \text{ pixel}$, measuring approximately $2.235'$) whose individual luminances were randomly assigned as a function of $\sin(x)$, where (x) ranged from 0 to 2π . The average contrast of the noise was set at half its maximum. For the translating and radiating patterns, the spatial and temporal frequency of the modulation were identical for points proximal to their horizontal radius. All observers were tested with motion patterns with spatial and drift frequencies were 1 cycle per degree (cpd) and 2 cycles/s

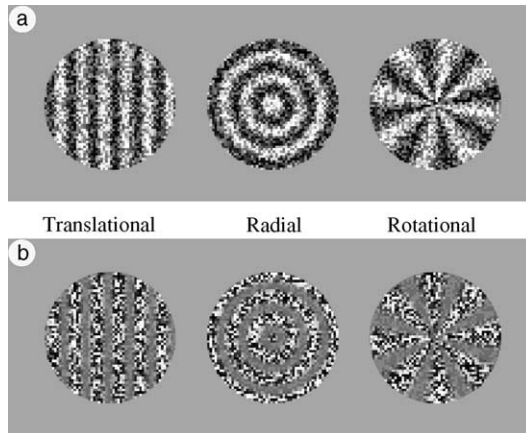


Fig. 1. A schematic representation of the motion stimuli used in the present experiment. The upper panel (a) shows the luminance-defined or first-order translational, radial and rotational motion patterns. The lower panel (b) shows the same types of texture-defined or second-order patterns.

(Hz), respectively. The angled modulation of the rotating pattern went through 8 cycles per its 360° and its angular velocity was $\pi/2$ rad/s. Direction-identification thresholds for all first-order patterns were found by varying the contrast (luminance modulation or luminance modulation depth), defined as the amplitude of the modulating sinewave, which ranged between 0.0 and 0.5:

luminance modulation depth

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

where L_{\max} and L_{\min} refer to the average highest and lowest local luminances in the pattern. Second-order patterns were produced by multiplying the same modulating sinewaves with grayscale noise. Direction-identification thresholds for the second-order patterns were found by varying the contrast modulation (contrast modulation depth) of the motion patterns, defined as the amplitude of the modulating sinewave, which ranged between 0.0 and 1.0:

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

where C_{\max} and C_{\min} are the maximum and minimum local contrasts in the pattern.

2.4. Procedure

Participants were tested individually in a dimly lit laboratory room and viewed the display binocularly from a distance of 114 cm for all conditions. Head movements were minimized using a head and chin rest. Within a given experimental session, each participant was presented with trials consisting of first- and second-order stimuli for a particular motion type moving in either of two possible and opposing directions (i.e., left

vs. right for translational motion session, inward vs. outward for radial motion session, etc.). Each stimuli were presented for either 106, 240, 500 and 750 ms. The method of constant stimuli was used to measure direction-identification thresholds for each experimental motion condition that included six levels of luminance modulation and five levels of contrast modulation for the first- and second-order motion stimuli, respectively. Stimuli were presented 10 times in either direction at each level of modulation (for a total of 20 trials at each level of modulation). Participants were asked to identify the direction of motion by making a two alternative forced choice (2AFC) by pressing one of two buttons on a keypad. Weibull (1951) functions were fitted to the responses for each motion condition in order to derive direction-identification thresholds at a 75% correct level of performance. Each observer completed the three different experimental motion sessions (i.e., translational, radial and rotational).

3. Results

Statistical analysis was performed on averaged group data. Fig. 2 shows the mean thresholds as a function of stimulus exposure duration and motion type for the first-order (right panel) and second-order (left panel) motion classes.

3.1. First-order motion

A two way within subjects ANOVA (motion type by exposure duration) was used to analyze first-order motion sensitivity. As shown in Fig. 2, the sensitivity to first-order motion patterns did not differ as a function of motion type ($F(2, 12) = 2.743$, $p > 0.05$) at all stimulus exposure durations and the difference between them did not significantly vary as stimulus exposure duration decreased ($F(6, 36) = 1.926$, $p > 0.05$). A significant effect of stimulus exposure duration was found for all motion types ($F(3, 18) = 317.346$, $p < 0.05$), due primarily to the drop in sensitivity from 250 to 106 ms. However, an analysis of simple effects showed that decreasing the exposure duration from 750 to 250 ms significantly reduced the sensitivity to the radial motion while that of the translational and rotational stimuli remained constant.

3.2. Second-order motion

Since motion direction discrimination at very brief exposure duration was not possible for some observers (4 of 8 for radial motion and 2 of 8 for rotational motion), data from the 106 ms condition was not included in statistical analysis for the second-order motion class. As represented by the right panel in Fig. 2, the sensi-

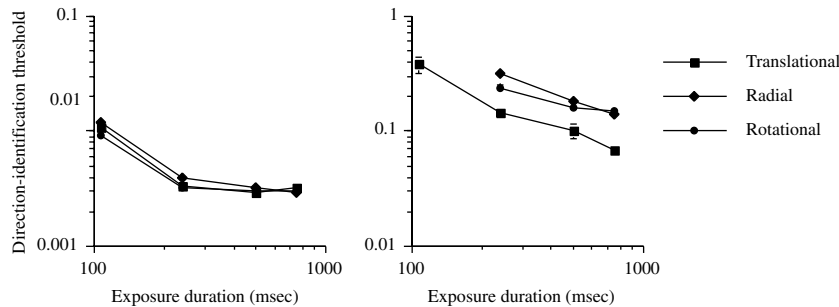


Fig. 2. Mean direction-identification thresholds for translational, radial and rotational motion types as a function of stimulus exposure duration for first-order (left panel) and second-order (right panel) motion classes. Standard error bars are included. If not shown, then the standard error is smaller than the symbols used to represent it for any given motion condition.

tivity to translational second-order motion was significantly greater compared to that of radial and rotational motion ($F(2, 12) = 26.869, p < 0.05$) when presented for 750, 500 and 250 ms. As stimulus exposure duration decreased from 750 to 250 ms, the sensitivity of all three second-order motion types decreased significantly ($F(2, 12) = 25.545, p < 0.05$). The rate at which the sensitivity decreased as stimulus exposure duration decreased was equal for the three motion types and reflected by a non-significant exposure duration by motion type interaction ($F(4, 24) = 0.448, p > 0.05$).

All the participants showed similar patterns or responding across motion condition. As shown in Fig. 3, the individual results from five of the seven participants are representative of the grouped data as direction-identification thresholds for radial and rotational second-order motion were consistently greater when compared to translational second-order motion at longer exposure durations (i.e., 750 ms). Since individual thresholds were calculated using responses from one testing session, the stability of the fitted Weibull functions are represented by 95% confidence intervals obtained using a bootstrap program developed by Foster and Bischof (1991). Qualitatively, at very brief exposure durations (i.e., 106 ms), correct direction-identification of complex second-order motion patterns was not possible for all of the observers. However, all observers were able to discriminate the motion direction of second-order translational patterns, as well as all the types of the first-order patterns.

3.3. Spatial and temporal characteristics

Additional testing by the author (AB) and a second psychophysically inexperienced observer (LAT) naive to the purpose of the study aimed to generalize the pattern of results across different spatial and temporal stimulus parameters. Direction-identification thresholds were measured only for the longest exposure duration since decreasing exposure did not differentially affect the relative sensitivity of translational, radial and rotational

motion types for either the first- or second-order motion classes (see Fig. 2). The additional spatial frequency conditions chosen were 0.5, 0.75 and 2.0 cpd with all patterns drifting a temporal frequency of 2 Hz. The angled modulation of these patterns went through 4, 6 and 16 cycles per 360°, respectively. As shown in Fig. 4, first-order motion thresholds were similar for each motion type at all the spatial frequencies tested for both observers. In contrast, the second-order thresholds for radial and rotational motion were consistently higher than those for the translational motion condition across all spatial frequency conditions. Fig. 5 shows direction-identification thresholds across different temporal frequencies for each observer. The spatial frequency for each motion condition was held constant at 1 cpd (i.e., 8 cycles per their 360° for the rotational condition) and thresholds were measured for patterns moving at 1, 4 and 8 Hz (i.e., an angular velocity of $\pi/4, \pi$ and 2π rad/s). Again, direction-identification thresholds for complex second-order motion were higher than those of translational motion across all the drift frequencies tested.

4. General discussion

4.1. Simple vs. complex second-order motion direction-identification

Specialized motion mechanisms differ functionally from those underlying standard motion analysis because they specifically and efficiently detect complex configurations of motion information (i.e., Freeman & Harris, 1992; Morrone et al., 1995; Regan & Beverly, 1978; Snowden & Milne, 1996). The results from the first-order motion class in our study are in accordance with such 'hard-wired' specialized mechanisms since direction of complex first-order motion patterns was identified as efficiently as simple first-order motion, reflected by the similar direction-identification thresholds for all first-order motion types across stimulus duration. Further

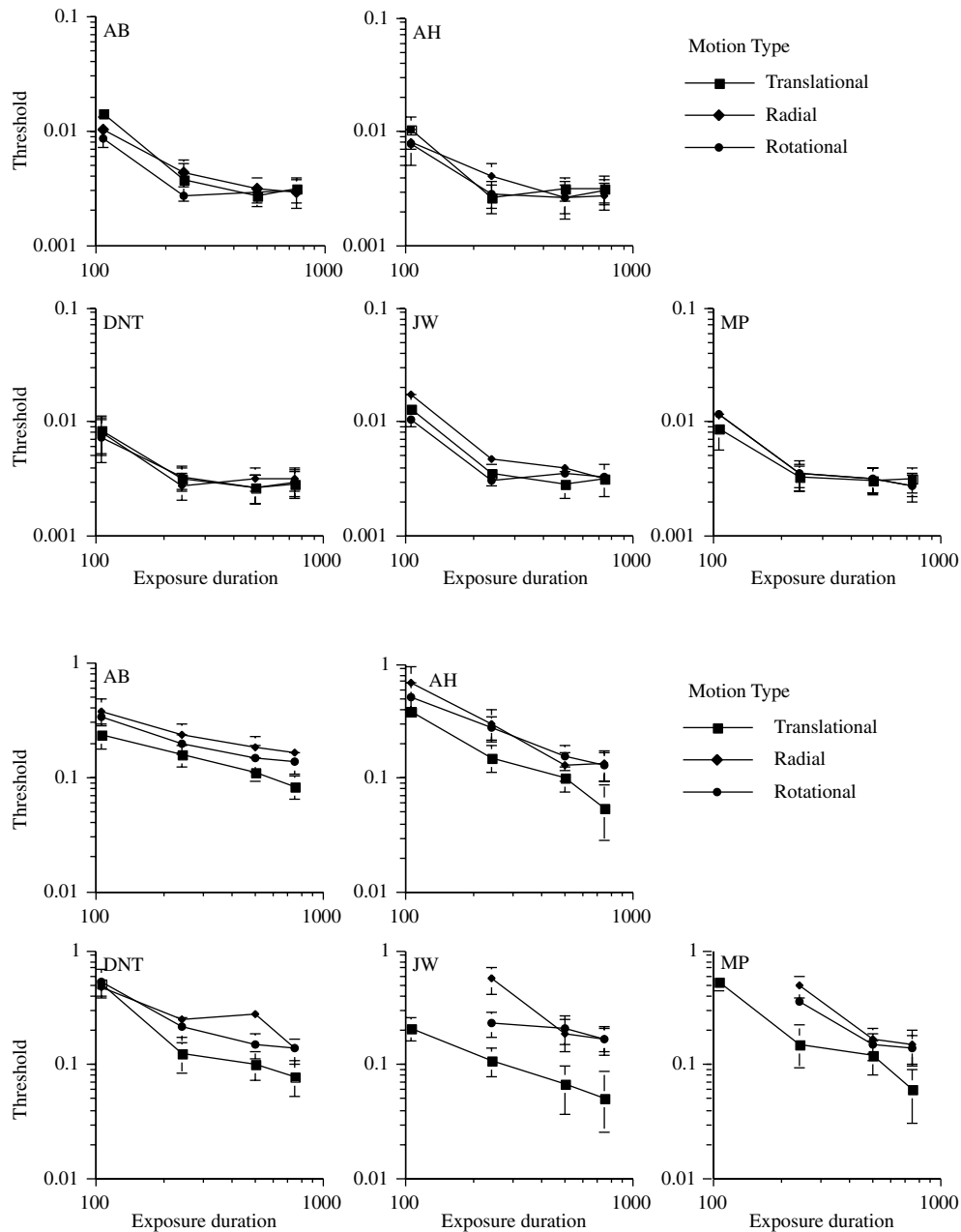


Fig. 3. Individual direction-identification thresholds for five of the seven observers. For all observers tested, thresholds for simple, translational second-order motion (lower panel) were consistently lower compared to radial and rotational motion across stimulus duration.

support for specialized processing is indicated by our finding that decreasing exposure duration (i.e., from 750 to 240 ms) did not differentially increase the thresholds for simple or complex first-order motion; thresholds were similar for simple and complex first-order motion across stimulus duration.

The main purpose of the present study was to explore the mechanisms mediating complex second-order motion processing. Although working models describing specialized or ‘multi-staged’ motion detection mechanisms have been developed for luminance-defined or first-order motion perception, hypotheses regarding the

functional mechanisms involved in complex second-order motion perception have yet to be advanced. The main result from the present experiments demonstrates that direction-identification thresholds to complex motion are significantly reduced compared to simple motion at different stimulus exposure durations for the second-order motion class only. This finding suggests that when compared to simple motion sensitivity, complex second-order motion configurations are not processed as efficiently as their first-order counterparts. This difference in sensitivity was consistently found under various spatial and temporal stimulus parameters at

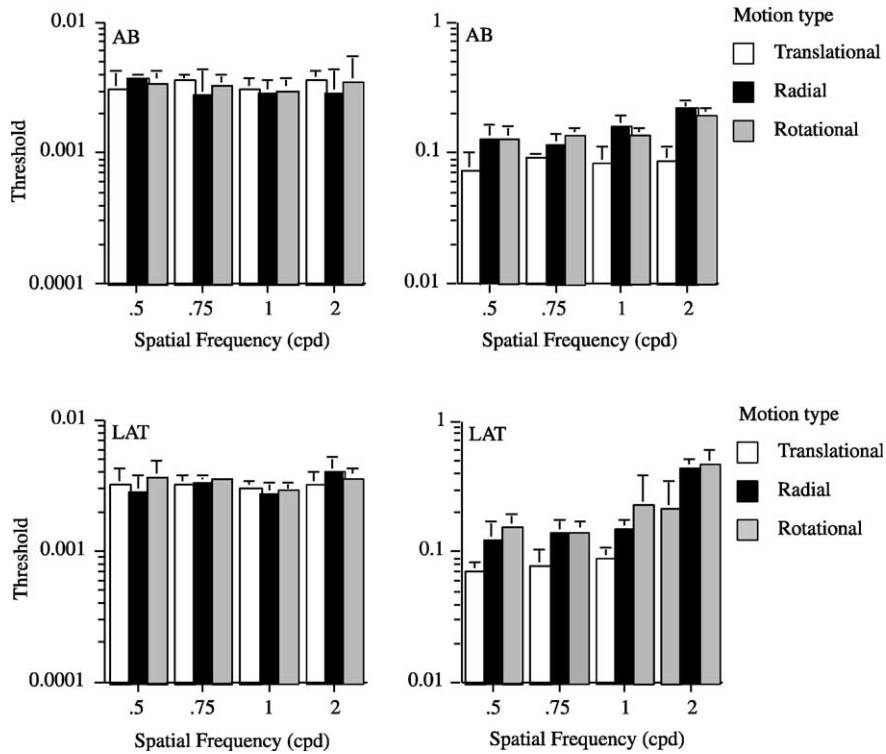


Fig. 4. Direction-identification thresholds for motion types as a function of spatial frequency for first-order (left panel) and second-order (right panel) motion classes for an author (AB) and a naive observer (LAT). All stimuli were presented for 750 ms and their temporal frequency was kept constant at 1 Hz.

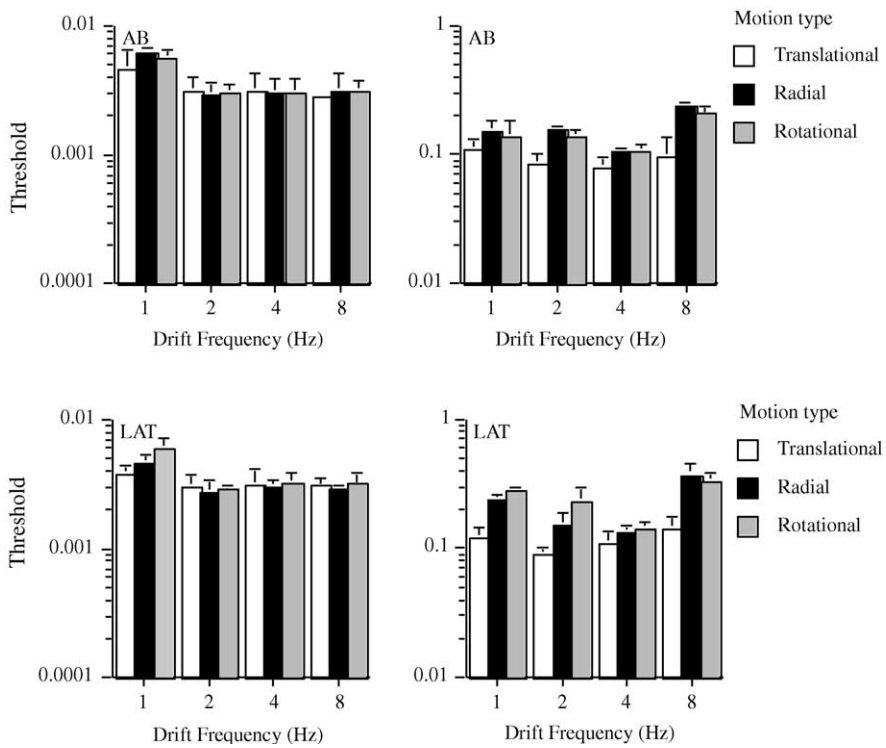


Fig. 5. Direction-identification thresholds for motion types as a function of drift frequency for first-order (left panel) and second-order (right panel) motion classes for an author (AB) and a naive observer (LAT). All stimuli were presented for 750 ms and their spatial frequency was kept constant at 1 cpd.

longer exposure durations (i.e., 750 ms; see Figs. 4 and 5), suggesting that the summation process underlying the elevated thresholds for complex second-order direction identification is not related to the spatial nor temporal characteristics of the motion stimuli. Similarly, Burr and Santoro (2001) demonstrated that the coherence sensitivity of random dot patterns moving in radial and rotational configurations (in the absence of spurious noise) was lower than that of translating motion, decreasing linearly as exposure duration increased, suggesting the differential analysis of simple and complex motion patterns.

4.2. *The effect of stimulus duration*

As shown in Fig. 2, direction-identification thresholds for all second-order stimuli increased at a significantly faster rate as compared to first-order thresholds with decreasing stimulus duration, particularly from 750 to 240 ms. This result may reflect reduced temporal resolution of second-order motion processing, possibly due to additional cortical pre-processing (i.e., rectification) before exact motion direction can be extracted (Derrington et al., 1993; Smith & Ledgeway, 1998; Wilson & Kim, 1994; Wilson et al., 1992). The different rate of threshold increase between the two motion classes also provides further evidence for models suggesting that first- and second-order motion are initially processed in parallel by separate passive mechanisms using similar motion detection principles (Baker, 1999; Chubb & Sperling, 1988; Chubb et al., 2001; Wilson et al., 1992).

Correct identification of direction was possible for simple, translating second-order motion for exposure durations as low as 106 ms for all observers and complex second-order motion direction-identification was possible at 240 ms for most observers (i.e., for patterns drifting at 2 Hz and spatial frequency of 1 cpd). Based on these findings, the second-order motion processing mediating direction identification seems to be less affected by temporal constraints (i.e., the ‘temporal hypothesis’) than previously believed (Schofield & Georgeson, 2000). It therefore seems improbable that direction-identification of complex second-order motion patterns in the present study is the result of a sequential analysis of local motion signals as described by Allen and Derrington (2000). It is important to note that the motion discrimination task used by these authors differed from ours in that higher-order attentional processing, such as visual scanning, may have been implicated during their second-order motion discrimination task and may have possibly contributed to the significant threshold increases (Ashida, Seiffert, & Osaka, 2001).

An alternative explanation for the increased rate of second-order threshold with decreasing stimulus duration is based on the ‘direction-selectivity hypothesis’ (Ledgeway & Hess, 2002). It contends that the mecha-

nisms encoding second-order stimuli are significantly less selective for motion direction than those mediating first-order motion and that the selectivity of these mechanisms may be increasingly compromised with decreased stimulus duration. Based on our results, either one of the ‘temporal’ or ‘direction-selectivity’ hypotheses may explain the overall and differential effect of stimulus duration of first- and second-order thresholds.

4.3. *How is complex second-order motion processed?*

4.3.1. *Sequential local analysis of complex second-order motion*

Present views regarding complex second-order motion processing vary, the most elaborated of which is presented by Allen and Derrington (2000) who suggest that complex second-order motion perception is probably not used by specialized mechanisms mediating optic flow analysis. Instead, they contend that complex second-order motion analysis may implicate the integration of separate and sequential local analyses of second-order information across the visual field, a much more sequential cortical processing with respect to that of translational second-order motion. Additional cortical processing in this case could take the form of the rectification of local second-order information and higher-order integration of the rectified motion signals into radial and rotational configurations. According to the ‘temporal’ hypotheses, increasingly higher thresholds would be expected for complex second-order motion perception with decreased stimulus duration relative to simple motion because of sequential processing. However, our results demonstrate that stimulus duration did not differentially affect simple and complex second-order motion thresholds, suggesting that complex second-order motion analysis is not mediated by sequential processing.

4.3.2. *Specialized processing exclusive to complex second-order motion*

Alternative hypotheses suggesting that complex second-order motion perception is mediated by specialized processing can also be forwarded. The first possibility is the existence of extrastriate motion mechanisms that are *exclusively* selective to complex second-order motion information. Such mechanisms are theoretically plausible since early and late filters belonging to filter–rectify–filter models (i.e., Lu & Sperling, 1995; Wilson et al., 1992) could be arranged so that these filter sets selectively respond to radial and rotational second-order motion configurations (Baker & Mareschal, 2001). However, our results do not support the existence of such filter sets for the following reason. It has recently been demonstrated that mechanisms that encode second-order motion are less selective for direction as compared to those mediating first-order analysis

(Ledgeway, 1999; Ledgeway & Hess, 2002). In addition, Ledgeway and Hess (2002) have convincingly demonstrated that the directional selectivity of simple second-order motion filters decreases with decreasing exposure duration, particularly at durations <200 ms. Based on this finding, the resulting directional ambiguity of a set of individual filters (capable of mediating complex second-order motion direction) should increase at a faster rate compared to an individual filter (capable of resolving simple second-order motion direction) as exposure duration is decreased. Behaviorally, one would predict that complex second-order thresholds should increase at a faster rate with decreasing exposure duration when compared to simple second-order motion thresholds. In contrast, our results demonstrate that simple and complex second-order motion thresholds decrease at a similar rate, suggesting that such higher-order mechanisms exclusively selective for complex second-order motion configurations, defined by such oriented filter sets, is unlikely. Additional experimental support against mechanisms exclusive to complex second-order motion processing is available from neurophysiological studies. These studies have failed to demonstrate the existence of mechanisms that respond exclusively to second-order motion in both lower and higher visual areas of the cat and primate (Churan & Ilg, 2001; Mareschal & Baker, 1999; O'Keefe & Movshon, 1998; Zhou & Baker, 1993).

4.3.3. *Specialized processing common to both first- and second-order complex motion*

A second possibility is that complex second-order motion analysis is mediated by the *same* specialized mechanisms that underlies complex first-order motion processing. This notion is supported in part by findings demonstrating a second-order contribution to vection, suggesting that both first- and second-order motion signals are combined (i.e., by mechanisms operating at MT) before being fed-forward to specialized mechanisms mediating optic flow analysis (Gurnsey et al., 1998). Second-order contribution to optic flow analysis is also supported by the results of Dumoulin et al. (2001), Ptito, Kupers, Faubert, and Gjedde (2001) and Hanada and Ejima (2000) (i.e., under specific experimental conditions). Furthermore, Smith, Greenlee, Singh, Kraemer, and Henning (1998) demonstrated that the human 'MT complex' (thought to be analogous to monkey MST) was activated by both first- and second-order radial patterns, similar to those used in the present experiment (see Fig. 1). Taken together, these findings suggest that meaningful configurations of local second-order motion information are processed by the same specialized 'hard-wired' mechanisms that underlie complex first-order processing. This interpretation is the most congruent with the results of the present study and will be discussed in the next section.

4.4. *A proposed model for complex second-order motion processing*

The present study has demonstrated two important findings regarding complex second-order motion processing. Firstly, direction identification thresholds for complex second-order motion are significantly elevated compared to simple second-order motion at various stimulus durations (from 240 to 750 ms) and over a wide range of spatial and temporal stimulus parameters, a result not observed in the first-order motion class. Secondly, complex second-order thresholds did not increase at a significantly higher rate with decreasing stimulus duration compared to simple second-order motion, an expected result if complex second-order motion was analyzed in sequential manner. These results suggest that second-order complex motion configurations are analyzed less efficiently than complex first-order motion and involve specialized motion analysis. The question then is where and how is complex second-order motion processed?

The difference regarding the efficiency with which such mechanisms are able to identify complex first- and second-order motion direction may depend on the properties of the motion signals originating from lower-level motion areas. A schematic representation of complex first-order motion analysis is presented in Fig. 6(a) where MST cells are shown to respond selectively to contracting radial motion. Although the exact nature of the functional motion hierarchy including the role of MT is debatable (Gurney & Wright, 1996), it is generally accepted that MST receives its primary input via adjacent MT which in turn receives local input from V1 and V2. Furthermore, response properties of MST neurons suggest that they integrate over specific configurations of locally oriented motion signals defined by specific spatio-temporal characteristics. Fig. 6(b) represents a hypothetical model delineating the analysis of complex second-order motion. The main difference between the two analyses is that in the latter case, local motion information must be rectified before it can be used by higher-level mechanisms. According to 'filter-rectify-filter' models, oriented first-order filters are modeled as having higher spatial-frequency selectivity compared to second-order filters (i.e., Wilson et al., 1992). Therefore, local second-order motion signals prior to the MT level operations remain oriented but are characterized by a coarser spatial frequency tuning (Clifford & Vaina, 1999; Sutter, Sperling, & Chubb, 1995). Assuming that the sensitivity of the specialized mechanisms to complex motion depends on the tuning selectivity of each of the local motion inputs, it can be expected that such mechanisms would be less sensitive to configurations of local second-order motion signals since each contributing signal is less selective for orientation. Consequently, direction-identification thresholds for complex

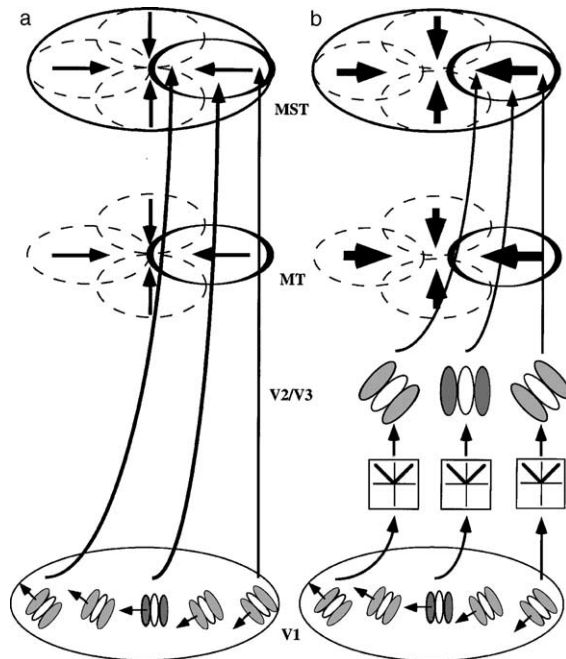


Fig. 6. Schematic diagram depicting a hierarchical model for (a) first- and (b) the proposed analysis of complex second-order motion. The first-order model shows that simple first-order motion signals are available after standard motion analysis at the primary visual cortex (V1). Locally oriented motion signals are then projected via area MT to specialized motion mechanisms operating after MT (i.e., MT complex or MST) that are able to efficiently detect to complex configurations of relatively well finely tuned spatio-temporal local motion signals, as depicted by the thin arrows. The proposed functional pathway for complex second-order is shown in the right panel (b). Unlike first-order motion analysis, simple or unidirectional second-order motion signals can be analyzed by standard motion analysis only after they are pre-processed (i.e., rectification) and extracted by mechanisms operating within areas V2 or V3 at a relatively coarser spatial scale. Therefore, such signals are available for further analysis by higher-order motion mechanisms at a coarser spatial scale (i.e., depicted by the thick arrows), possibly resulting in less efficient ‘pooling’ of overall second-order motion direction at the level where specialized motion mechanisms operate.

second-order patterns thresholds would be elevated with respect to simple motion in the same class, since less ‘pooling’ is involved in simple motion identification. As mentioned previously, the finding that simple and complex motion identification thresholds in the second-order class increased at a similar rate with decreasing stimulus duration suggests that although complex motion is less efficient with regards to simple second-order motion, it is processed by specialized mechanisms.

In conclusion, complex second-order motion analysis might not be as inefficient or qualitatively different from that mediating complex first-order motion as previously believed (Allen & Derrington, 2000; Badcock & Khuu, 2001). Instead, the same ‘hard-wired’ mechanisms may be responsible for the analysis of both first- and second-order complex motion, possibly resulting in the responding of higher-order motion areas to both first- and

second-order motion in human and non-human studies (i.e., Churan & Ilg, 2001; O’Keefe & Movshon, 1998).

Acknowledgements

This research was supported by a Canadian Institutes of Health Research (CIHR) graduate fellowship to AB and a NSERC research grant (OGP0121333) to JF.

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