

Exploring the spatiotemporal properties of fractal rotation perception

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A series of three experiments was conducted with the aim of determining the processing nature of the fractal rotation stimulus introduced by C. P. Benton, J. M. O'Brien, and W. Curran (2007). This stimulus has been proposed to be invisible to first-order sensitive mechanisms considering it is drift-balanced. Rather, motion perception would require the analysis of spatial structure (orientation) changing over time. In [Experiment 1](#), spatiotemporal properties of fractal rotation perception have been explored, in comparison with first-order rotation perception. In [Experiment 2](#), a motion paradigm similar to the one developed by K. Nakayama and C. W. Tyler (1981) and later used by A. E. Seiffert and P. Cavanagh (1998) has been used to characterize the motion processing mechanism responsible for fractal rotation perception. In [Experiment 3](#), we have used a paradigm similar to N. E. Scott-Samuel and A. T. Smith (2000) to evaluate whether fractal rotation perception is analyzed by common or distinct mechanisms to those for first-order rotation perception. Results indicate that fractal rotation perception involves feature-tracking processes with mechanisms responding to global orientation-based changes of the image. Given the absence of cancellation of first-order and fractal rotation motion signals, we can therefore conclude that the first-order and fractal motion sensitive pathways are dissociable at early stages of the visual processing stream.

Keywords: fractal, rotation, feature tracking, linear/nonlinear systems, motion perception, motion processing, spatial structure

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Introduction

Motion perception ensures the execution of safe navigation, as well as efficient interaction with the environment. Accordingly, it is essential for figure ground segregation (Kandil & Fahle, 2004; Regan, 1986; Regan & Beverley, 1984), evaluating the tridimensional structure of our environment (Eby, 1992; Hegdé, Albright, & Stoner, 2004; Ullman, 1979) and determining distance between an object and its observer (Gray & Regan, 1999).

Motion perception can be induced through first- and second-order variations of the spatiotemporal properties of an image (Cavanagh & Mather, 1989; Chubb & Sperling, 1988, 1989). First-order stimuli, often termed Fourier motion, are those defined by local variation of luminosity (Anstis & Mather, 1985; Cavanagh & Mather, 1989; Chubb & Sperling, 1988, 1989; Wilson, Ferrera, & Yo, 1992). Motion energy being found at the modulating frequency in the Fourier spatiotemporal frequency domain, these stimuli are directly accessible to linear filters of the visual system (Campbell & Robson, 1968;

Chubb & Sperling, 1988, 1991; Watson & Ahumada, 1985). Second-order stimuli, also called non-Fourier motion, are those defined by other attributes than luminance or color. These stimuli are defined by properties for which higher level cortical visual processing is required (Chubb & Sperling, 1988, 1989; Wilson et al., 1992). For example, variations of contrast, polarity, orientation, binocular disparity, and spatial length are all considered as stimuli attributes defining second-order motion (Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Hutchinson & Ledgeway, 2006; Seiffert & Cavanagh, 1998). These stimuli are all considered invisible to standard linear motion sensitive mechanisms. Accordingly, nonlinear processing of the signal is required for motion to be perceived by the visual system (Benton & Johnston, 2001; Benton, Johnston, McOwan, & Victor, 2001; Chubb & Sperling, 1988, 1991; Solomon & Sperling, 1994; Taub, Victor, & Conte, 1997; Wilson et al., 1992). As such, several models integrating such nonlinear transformation have been proposed. Full- and half-wave rectification (Chubb & Sperling, 1988, 1991; Solomon & Sperling, 1994), filter–rectify–filter (Wilson et al., 1992), and spatiotemporal gradient (Benton & Johnston, 2001;

Benton, Johnston, & McOwan, 2000; Benton et al., 2001; Johnston, Benton, & McOwan, 1999) all constitute examples of models using nonlinear transformation to extract second-order motion signal.

First- and second-order motion processing

Sensitivity to direction, velocity, and orientation of luminosity are found as early as the primary visual cortex (Hubel & Wiesel, 1959, 1962; Movshon, 1975). As such, first-order motion signal could be extracted based on the responses of the striate cortex, at which level an oriented spatiotemporal filtering is performed (Dumoulin, Baker, Hess, & Evans, 2003). Therefore, luminance-based motion analysis is thought to occur at lower levels of the visual system, through local integrative processes (Dumoulin et al., 2003; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Wilson et al., 1992). In contrast, because in second-order stimuli spatiotemporal frequency content is drift-balanced (Chubb & Sperling, 1988; Solomon & Sperling, 1994), second-order motion perception would arise at higher levels of the visual system, possibly at the level of the extrastriate cortex (Dumoulin et al., 2003; Smith et al., 1998; Wenderoth, Watson, Egan, Tochon-Danguy, & O’Keefe, 1999). Second-order processing mechanisms are believed to operate through a filter–rectify–filter (Chubb & Sperling, 1988; Wilson et al., 1992) or position-based analysis (Del Viva & Morrone, 1998; Derrington & Ukkonen, 1999; Lu & Sperling, 1995; Scott-Samuel & Georgeson, 1999b; Seiffert & Cavanagh, 1998; Smith, 1994). Indeed, Seiffert and Cavanagh (1998) demonstrated that various types of second-order motion stimuli, such as contrast-, orientation- and stereo-defined, are analyzed by position-based mechanisms. Similar results have been obtained by Derrington and Ukkonen (1999) using contrast-modulated stimuli. These authors demonstrated that second-order mechanisms are sensitive to changes in spatial location of features of the image under motion, using a pedestal motion paradigm (Derrington & Ukkonen, 1999). Although position-based mechanisms or feature-tracking mechanisms are generally considered second-order mechanisms (i.e., not first-order mechanisms), some authors have also classified them as third-order mechanisms (Lu & Sperling, 1995, 2001). In the present paper, we will not make the distinction between second- and third-order properties, as this is not the essence of our study. Rather, we attempt to determine whether the perception of fractal rotation has characteristics that abide to higher order properties. As with most previous authors, we will therefore refer to second-order mechanisms in this broader sense throughout the paper.

Uncertainty remains as to the specific cortical regions involved in the analysis of second-order motion percept. One study suggests that V3 and VP correspond to the first cortical regions responsible for second-order motion

processing (Smith et al., 1998), as recorded using functional magnetic resonance imaging (fMRI). Another study recorded a specific increase in activity, again using fMRI, in the lateral occipital lobe and anterior superior parietal lobule, following the presentation of a second-order motion stimulus (Dumoulin et al., 2003). Together, these studies suggest that higher level visual cortical areas are involved in second-order motion processing.

Fractal rotation

Fractal rotation is a novel type of stimulus introduced by Benton, O’Brien, and Curran (2007). It has been created to isolate mechanisms responsible for form-dependent motion analysis. The stimulus is obtained using an orientation filter rotating around the origin in the Fourier domain. Consequently, there is no feature rotating around a given center point even though the stimulus is perceived as such. Any random aperture positioned onto a fractal rotation stimulus contains an equal strength of oppositely drifting motion directional components. As a result, the local motion direction cannot be extracted only by the local information since it also depends on the aperture. For instance, the same local information can either be perceived moving leftward or rightward depending if it is presented above or below the center of the aperture. Therefore, such a stimulus would be invisible to first-order motion processing mechanisms, i.e., on mechanisms based on local luminance translation analysis. Accordingly, a significant reduction in the motion after-effect elicited following presentation of fractal rotation, as compared to first-order rotation, was observed by Benton et al. (2007). These results suggest that different mechanisms than those responsible for processing of first-order stimulus are involved in the analysis of fractal rotation. The only motion cues available being orientation changes and the aperture, mechanisms sensitive to fractal rotation would need to extract such spatial structures prior to motion analysis. Uncertainty remains as to whether such form-dependent motion constitutes feature tracking. As stated by Benton et al. (2007), fractal rotation is characterized by the absence of spatial features that can be tracked. It thus constitutes an excellent means for selectively stimulating mechanisms responsible for perception of form-dependent motion.

Common or distinct mechanisms?

A debate remains as to whether first- and second-order motion sensitive mechanisms constitute common or distinct pathways. From a psychophysical point of view, several studies suggest that distinct mechanisms are required to integrate second-order motion, at least at

lower stages of the visual processing stream (Ledgeway & Hutchinson, 2005; Nishida, Ledgeway, & Edwards, 1997; Schofield & Georgeson, 1999, 2003; Schofield, Ledgeway, & Hutchinson, 2007; Scott-Samuel & Smith, 2000; Solomon & Sperling, 1994). However, this may depend on the stimulus parameters such as motion speed (Allard & Faubert, 2008a). Similarly, several neuroimaging and neurophysiological studies reported such a dichotomy of the visual motion perception system (Dumoulin et al., 2003; Mareschal & Baker, 1998; Smith et al., 1998). Moreover, selective deficit for non-Fourier motion has been reported following lateral occipital lobe lesions (Plant, Laxer, Barbaro, Schiffman, & Nakayama, 1993; Plant & Nakayama, 1993; Vaina & Soloviev, 2004). The above-mentioned studies all support the existence of initially distinct processing streams for first- and second-order motion information. However, these do not exclude the possibility of later interaction in the visual system. As such, Smith et al. (1998) demonstrated a selective activation of V3/VP by second-order, but equal activation of V5 by first- and second-order motion signals. This suggests that areas V3/VP constitute the initial step in the processing of second-order motion, but that V5 would merge first- and second-order motion signals for further processing. Such a common integration of both types of motion signals can be evidenced by the existence of cross-adaptation between first- and second-order motion (Ledgeway & Smith, 1994). Nevertheless, a growing number of evidence suggests that a dissociation of both processing streams exists within the visual system.

Objectives

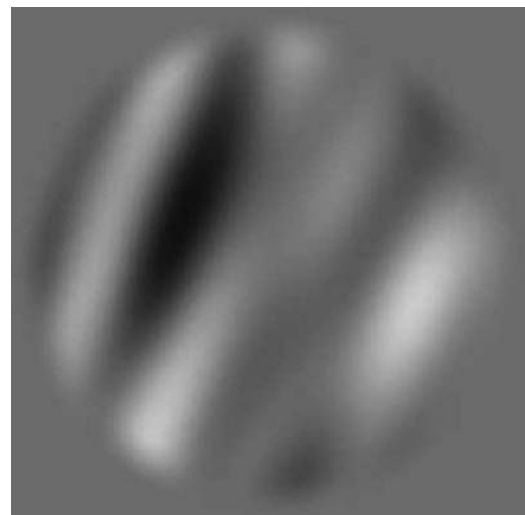
The present study aimed at determining the specific nature of fractal rotation perception. That is, to evaluate whether fractal rotation is analyzed by second-order motion mechanisms or not. Using a motion paradigm that could reveal the nature of the motion mechanisms, Seiffert and Cavanagh (1998) were able to demonstrate that both contrast and orientation-modulated stimuli are processed by mechanisms sensitive to position changes. Because fractal rotation perception requires the analysis of changes in spatial structure, i.e., orientation, over time, this type of stimulus could potentially be analyzed by second-order motion mechanism. A series of three experiments has been conducted. In [Experiment 1](#), the temporal properties of fractal rotation have been explored, in comparison with first-order rotation. In [Experiment 2](#), a motion paradigm similar to the one developed by Nakayama and Tyler (1981) and later used by Seiffert and Cavanagh (1998) has been employed to determine whether mechanisms sensitive to fractal rotation are position or energy based. Finally, in [Experiment 3](#), we adapted a paradigm developed by Scott-Samuel and Smith (2000) to evaluate

whether fractal rotation is analyzed by common or distinct mechanisms than those responsible for first-order rotation processing.

Experiment 1: Temporal frequency function of fractal rotation perception

Distinct spatiotemporal properties have been reported for first- and second-order types of stimuli (Elleberg, Allen, & Hess, 2006; Hutchinson & Ledgeway, 2006; Lu & Sperling, 1995). For example, Hutchinson and Ledgeway (2006) have demonstrated that sensitivity to first-order stimuli is bandpass in nature. Accordingly, sensitivity to direction of motion was optimal for temporal frequencies between 2 and 4 Hz. A relatively good sensitivity could be preserved for temporal frequencies up to 8 Hz. By opposition, second-order sensitive mechanisms presented low-pass properties. As measured by Hutchinson and Ledgeway (2006), sensitivities to contrast-, polarity-, and spatial length-modulated stimuli were optimal for temporal frequencies lower than 2 Hz. Moreover, discrimination of motion direction of second-order stimuli became impossible for stimuli presented at temporal frequencies equal or above 4 Hz. Results reported by the authors were obtained at a relatively low spatial frequency, i.e., 1 cycle per degree (cpd; Hutchinson & Ledgeway, 2006). These results clearly highlight the low-pass responses to spatial and temporal frequencies of second-order sensitive mechanisms.

Similarly to contrast-, polarity-, and spatial length-modulated stimuli, fractal rotation presents no net local



Movie 1. Example of first-order rotation stimulus.

variation of luminosity. Hence, in the following experiment, we attempted to determine if fractal rotation presents spatiotemporal properties similar to those reported for second-order type of stimuli.

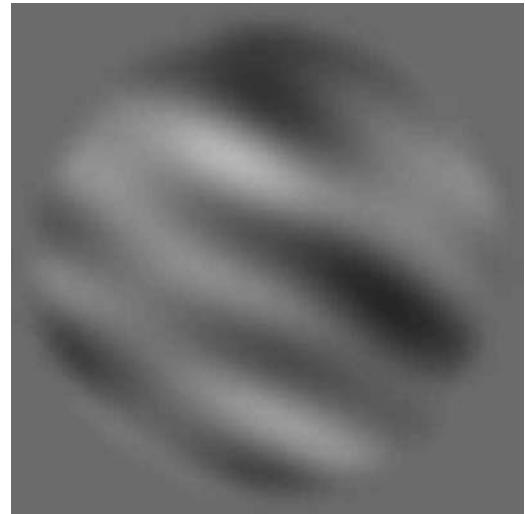
Methods

Subject selection

Participants were aged between 18 and 30 years old (mean age = 21.2 ± 1.53 for [Experiment 1](#), mean age = 26.2 ± 1.46 for [Experiment 2](#), mean age = 23.6 ± 2.06 for [Experiment 3](#)). Four subjects for [Experiment 1](#), while five for [Experiments 2](#) and [3](#) have participated. Subjects needed to have a minimal binocular acuity of 6/6 after optimal optical correction. Moreover, participants presenting strabismus and/or amblyopia were excluded. Informed consent was given by each participant upon evaluation.

Apparatus and stimuli

Stimuli were generated by a Pentium 4 computer. Images were presented on a ViewSonic E90FB.25CRT computer screen using a Matrox Parhelia 512 graphic card. The Noisy-Bit method (Allard & Faubert, 2008b) implemented with the error of the green color gun inversely correlated with the error of the two other color guns made the 8-bit display perceptually equivalent to an analog display having a continuous luminance resolution. Mean luminance of the screen was 47 cd/m^2 and refresh rate was 60 Hz. A new pattern was generated every fourth frame. Each pixel possessed $1/64$ degrees of visual angle for a viewing distance of 114 cm. The monitor was the only source of light in the room. A Minolta CS100 photometer interfaced with a homemade program calibrated the output intensity of each gun. Two types of stimuli were presented: first-order and fractal rotation. Fractal rotation stimulus used in this experiment was similar to the one introduced by Benton et al. (2007). To reproduce such a stimulus, a rotating oriented filtered noise pattern was utilized, for which orientation varied from frame to frame. Moreover, noise was resampled for every presented frame (i.e., 15 Hz). The first-order rotation stimulus was identical to fractal rotation, except a single rotating oriented filtered noise frame was used. Stimuli were built using $1/f$ noise pattern, which has been shown to be scale invariant (Field, 1987). Both stimuli were circular soft, half cosine edge patches displayed on a gray background. At a viewing distance of 114 cm, stimuli subtended 4 degrees of visual angle (dva). A bandpass spatial filter ranging from 0.25 to 1 cpd was applied to each noise frame. Starting orientation of the spatial filter was randomized on every trial. The purpose of such a filter was twofold. First, it ensured optimal recruitment of first- and second-order motion sensitive mechanisms (Elleberg et al., 2006; Hutchinson

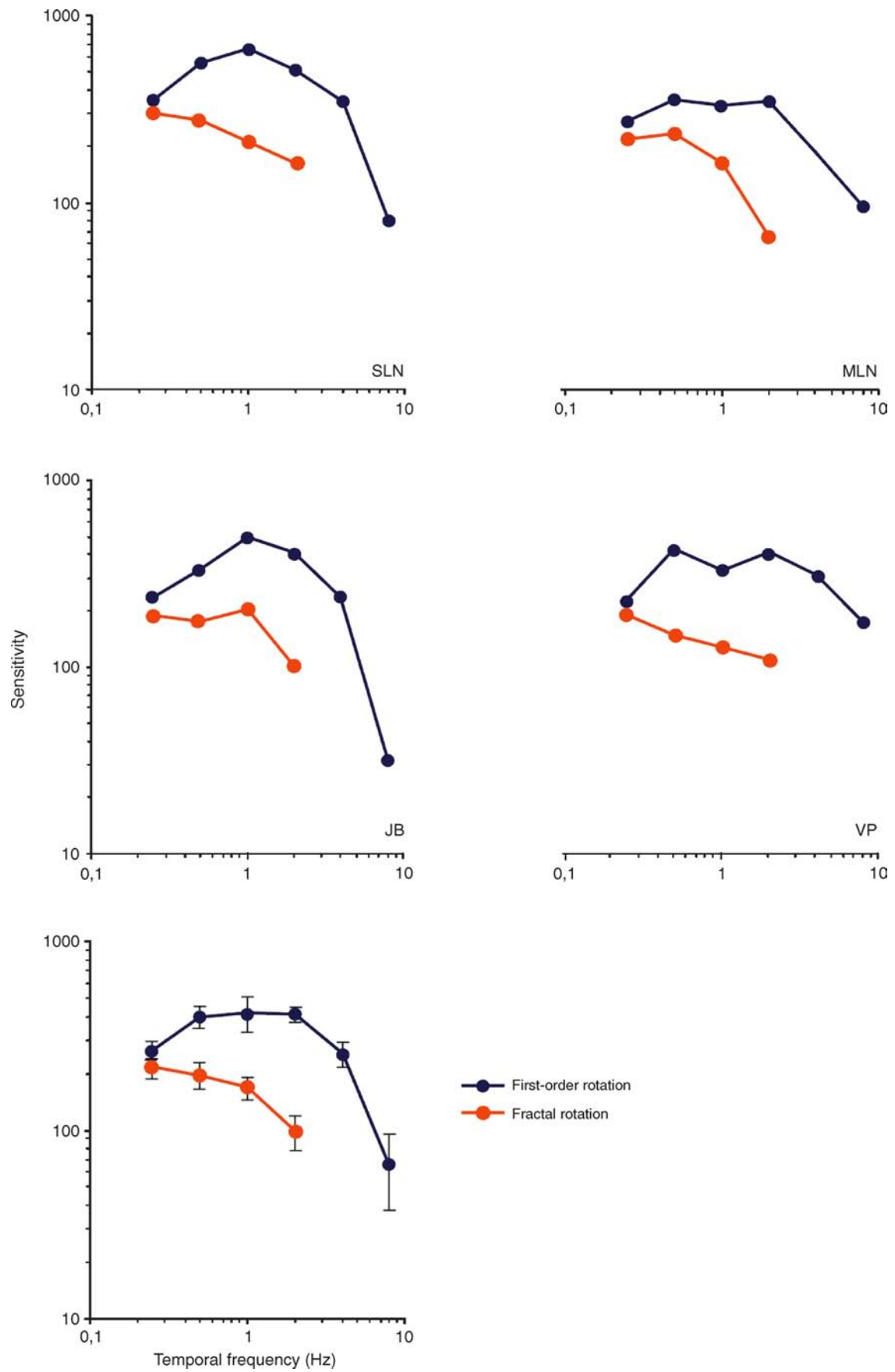


Movie 2. Example of fractal rotation stimulus.

& Ledgeway, 2006; Smith & Ledgeway, 1998). Second, it allowed us to obtain a second-order motion stimulus defined solely by low spatial frequencies. This was of significance, considering we aimed at using fractal rotation in future research to assess higher order perceptual processing of older observers (Faubert, 2002; Habak & Faubert, 2000). Most studies looking at second-order motion sensitive mechanisms have used carrier rich in high spatial frequencies (Allard & Faubert, 2008a; Benton & Johnston, 2001; Derrington & Ukkonen, 1999; Johnston & Benton, 1997; Ledgeway & Smith, 1994; Lu & Sperling, 1995; Nishida et al., 1997; Schofield et al., 2007; Scott-Samuel & Smith, 2000). However, a decrease in contrast sensitivity to static stimuli presented at high spatial frequencies is observed with normal aging (Crassini, Brown, & Bowman, 1988; Kline, Schieber, Abusamra, & Coyne, 1983; Morrison & McGrath, 1985; Owsley, Sekuler, & Siemsen, 1983). This could constitute a confounding factor in studying motion sensitivity with advancing age. Examples of resulting stimuli are given in [Movies 1](#) and [2](#). As stated previously, considering the absence of local motion energy, fractal rotation stimulus should be invisible to first-order motion sensitive mechanisms. Consequently, motion perception would need to be based on the analysis of the spatial structure of the stimulus (orientation) changing over time. For a first-order rotation stimulus, motion energy is readily available to standard motion detectors by way of a pure autocorrelation of spatiotemporal luminance intensity distribution.

Procedure

A single-interval, two-alternative-forced choice procedure was used with a direction discrimination task. A



staircase protocol of 2-down, 1-up type has been utilized to measure contrast thresholds. One staircase comprised 10 reversals, but threshold was obtained on the basis of the last 6 contrast values for reversal. Trials always started with the onset of the fixation bull's-eye. Subjects were asked to always maintain fixation in the course of the experiment. On the onset of the stimulus, subjects were required to identify whether it was turning clockwise or counterclockwise. Responses were given by participants using a keyboard. Moreover, a computer-generated auditory feedback was provided to participants. Stimulus and interstimulus durations were 1 s and 0.5 s, respectively. For each type of stimuli, various temporal frequencies were tested, i.e., 0.25, 0.5, 1, 2, 4, and 8 Hz. Within a single block of trials, only one type of stimulus, presented at one temporal frequency, was used. A total of 12 conditions was tested. Fourteen blocks of trials were executed by each participant. Two of them constituted practice trials to ensure participants understood the task. Presentation order of conditions was randomized. Thresholds were defined as the minimal contrast required to produce a 70.7% correct performance level. Contrast thresholds were calculated for each stimulus at each temporal frequency. Sensitivity was defined as the reciprocal of the contrast threshold.

Results and discussion

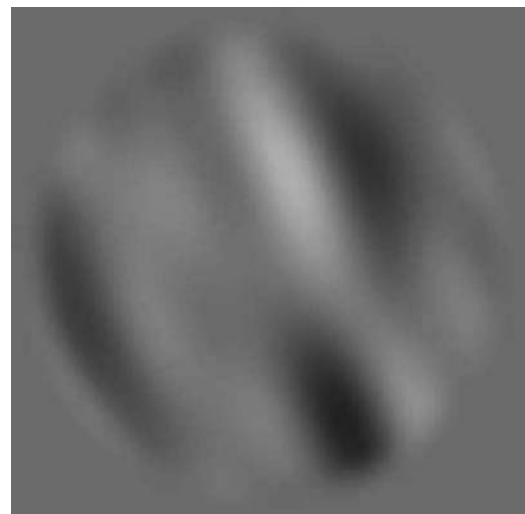
Figure 1 shows contrast sensitivity for direction discrimination as a function of temporal frequencies for both first-order and fractal rotation. Individual and group results are reported. Based on these psychometric functions, it can be seen that the mechanisms sensitive to first-order rotation presents the expected bandpass spatiotemporal properties. Accordingly, optimal sensitivity was observed for stimuli presented at temporal frequencies located between 0.5 and 2 Hz. As well, discrimination of direction was still possible for stimuli presented at temporal frequencies as high as 8 Hz. On the contrary, results clearly indicate mechanisms sensitive to fractal rotation are low pass in nature. Indeed, contrast sensitivity was optimal for temporal frequencies ranging from 0.25 to 0.5 Hz, after which sensitivity started decreasing. Similarly, it was impossible to obtain threshold values for temporal frequencies equal or above 4 Hz. Moreover, sensitivity to direction

was considerably lower for fractal rotation stimulus than that for first-order rotation, for temporal frequencies equal or above 0.5 Hz.

Experiment 2: Orientation-based or energy-based mechanisms?

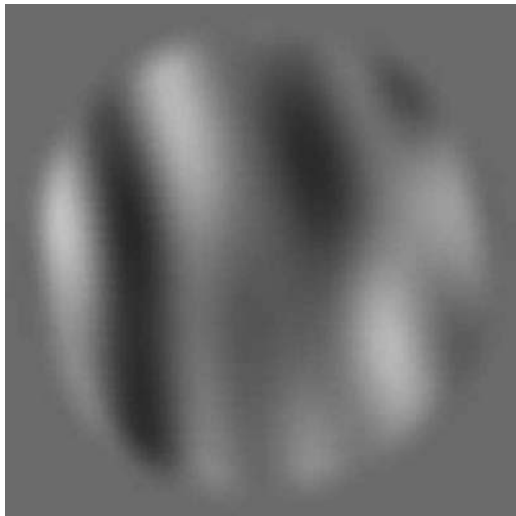
Seiffert and Cavanagh (1998) demonstrated that second-order types of stimuli are processed by position-based mechanisms, whereas first-order types of stimuli are analyzed by energy-based mechanisms. To do so, these authors have used a motion paradigm that was developed initially by Nakayama and Tyler (1981). The motion paradigm, as adapted by Seiffert and Cavanagh (1998), used oscillation as a means to dissociate between velocity and displacement of the stimulus. Accordingly, displacement thresholds have been measured at various temporal frequencies for first- and second-order oscillating stimuli. If the stimulus was to be processed by a velocity-dependent mechanism, then displacement threshold should decrease with an increase in temporal frequency. As demonstrated by Seiffert and Cavanagh (1998) and Nakayama and Tyler (1981), this reduction is expected to follow a slope of approximately -1 for temporal frequencies ranging between 0.1 and 1 Hz. By opposition, stimuli analyzed by position-based mechanisms should be insensitive to variation of temporal frequency. In other words, for any given spatial displacement, position-based mechanisms should remain relatively unaffected by the speed at which such a displacement is executed and thresholds should therefore remain unchanged.

In the case of fractal rotation, every part of the image undergoes an equal amount of rotation on each presented



Movie 3. Example of first-order oscillating stimulus.

Figure 1. The first four graphics show individual results on Experiment 1. The last graph represents group results. All graphs represent sensitivity to discrimination of direction of first-order and fractal rotation stimuli as a function of temporal frequency. Blue and orange lines represent results obtained for first-order and fractal rotation stimuli, respectively. Error bars correspond to the standard error.



Movie 4. Example of fractal oscillating stimulus.

frame. Such a stimulus characterizes itself by the absence of any position changes, with the only cue being orientation changes over time. Hence, any mechanism sensitive to changes in the spatial structure, such as position-based mechanisms as described by Seiffert and Cavanagh (1998) and Lu and Sperling (1995), would need to extract orientation changes to perceive fractal rotation. For this reason, such mechanisms will be called orientation based, rather than position based, in the present study. To determine whether fractal rotation is analyzed by mechanism sensitive to velocity or orientation, we have used the paradigm mentioned above.

Methods

Stimuli

Stimuli were identical to those used in the first experiment except that they oscillated sinusoidally about the vertical axis. Initial phase of stimuli was randomized on each trial.

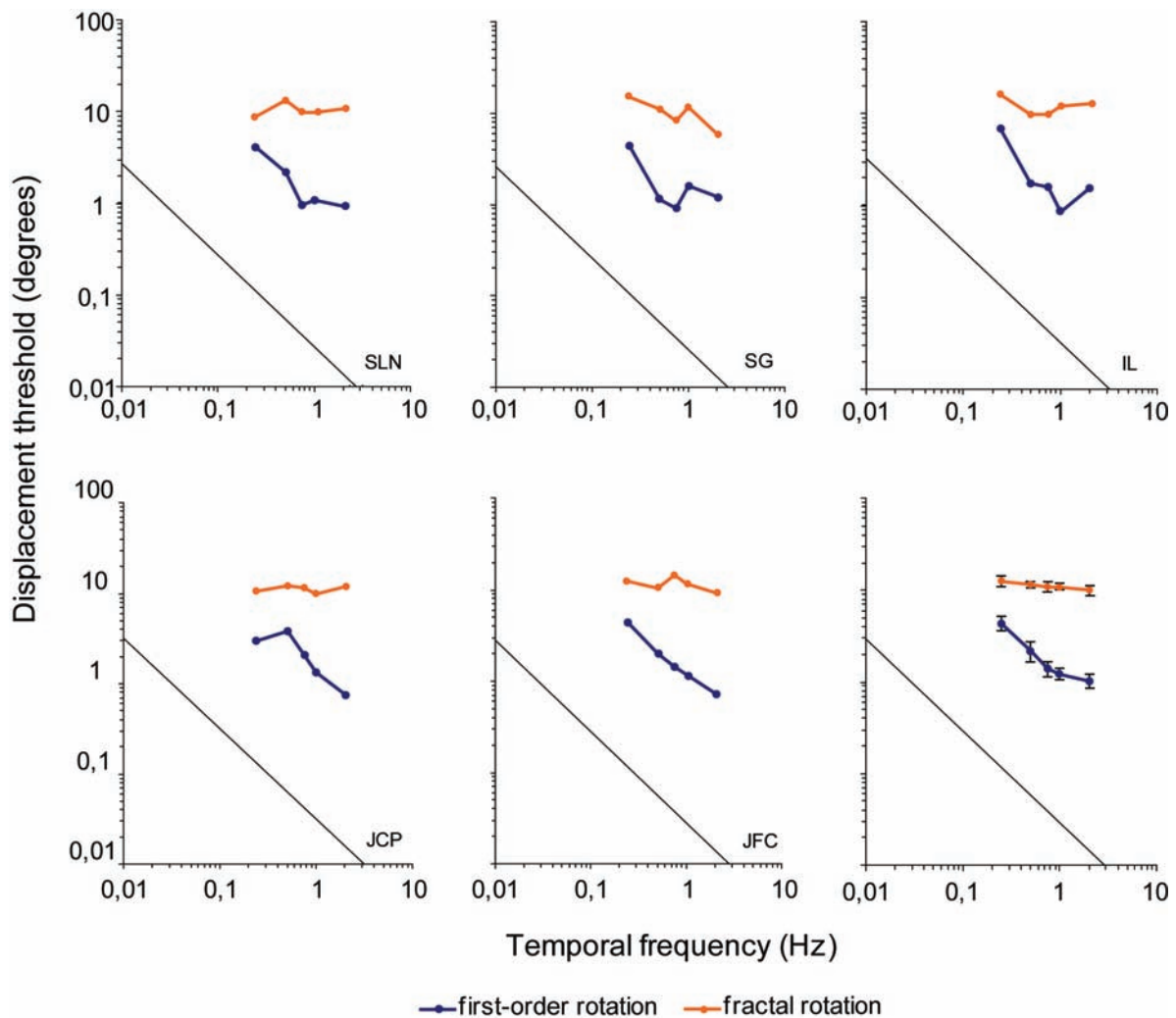


Figure 2. The first five graphs constitute individual results and the last graph represents group results for Experiment 2. All graphics represent displacement thresholds on a motion detection task as a function of temporal frequency. Blue and orange lines indicate first-order and fractal rotation stimuli, respectively. Error bars correspond to the standard error.

Temporal frequencies of oscillating stimuli were 0.25, 0.5, 0.75, 1, and 2 Hz. These parameters were defined based on the sensitivity profile of first-order and fractal rotation sensitive mechanisms obtained in the previous experiment. Stimulus presentation time was 4 s to allow for a complete cycle of oscillation to occur at the lowest temporal frequency, i.e., 0.25 Hz. Interstimulus presentation time was 0.5 s. Examples of oscillating first-order and fractal rotation stimuli are provided in [Movies 3](#) and [4](#), respectively.

Procedure

A two-alternative-temporal-forced choice procedure was used with a motion detection task. A 2-down, 1-up staircase protocol was used to measure thresholds. Subject's task consisted in identifying which of the two intervals comprised the oscillating pattern. The non-stimulus and stimulus intervals consisted, respectively, in a static replica and an oscillating pattern of first-order or fractal rotation stimulus, depending on the tested condition. Each block of trials consisted of a single temporal frequency and rotation type, i.e., first-order or fractal rotation. Two practice trials were executed at the beginning of each session to ensure subjects understood the task correctly. A total of 12 conditions was tested for each participant. Displacement thresholds for detecting oscillation of fractal and first-order stimuli were measured for each stimulus type and temporal frequency. Displacement threshold represented the minimal spatial shift, expressed in degrees, required to perceived oscillation. A linear regression analysis was performed on the results to verify the dependence of fractal and first-order rotation on temporal frequency.

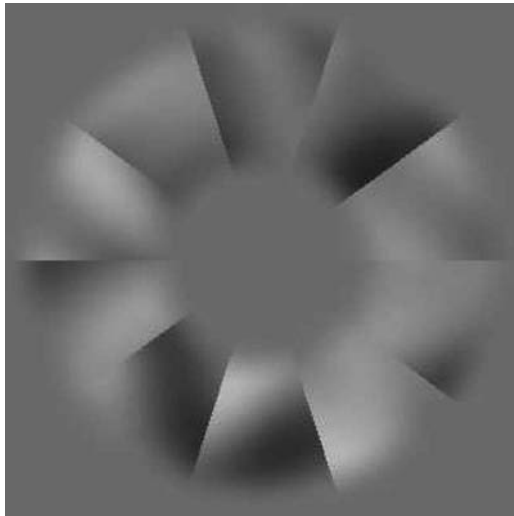
Results and discussion

For each observer, displacement thresholds as a function of temporal frequency, for first-order and fractal rotation, were obtained ([Figure 2](#)). Results shown in blue and orange correspond to first-order and fractal rotation displacement thresholds, respectively. As well, a black curve corresponding to a -1 slope of a linear regression function has been represented on every graph to allow direct comparison between the first-order psychometric function slopes and the -1 slope expected for velocity-based mechanisms. As seen in [Figure 2](#), displacement thresholds for first-order rotation decreased with increasing temporal frequency. The observed reduction is proportional to the increase in temporal frequency. Accordingly, following linear regression analysis, an average slope of -0.95 ± 0.138 has been obtained for thresholds measured at temporal frequencies ranging between 0.25 and 1 Hz, thereby revealing the velocity-dependent nature of first-order rotation sensitive mechanisms. By opposition, displacement thresholds for fractal

rotation remained unchanged at all temporal frequencies for all observers. Hence, it can be established that fractal rotation processing mechanisms are, within the spatio-temporal sensitivity limits established in [Experiment 1](#), unaffected by velocity changes of oscillating stimuli. Therefore, it can be concluded that mechanisms responsible for fractal rotation perception are not operating by means of a pure motion energy analysis. Rather, one can imagine a motion detection mechanism apparent to feature-tracking mechanisms as proposed by several authors (Del Viva & Morrone, 1998; Derrington & Ukkonen, 1999; Lu & Sperling, 1995) able to identify changes of spatial structure of the image over time.

Experiment 3: Common or distinct motion processing pathways?

Results obtained from the first experiment demonstrated the low-pass nature of fractal rotation. The second experiment results indicate that mechanisms responsible for analysis of this type of stimulus do not respond to energy and therefore require orientation-based spatiotemporal integration. These findings all suggest that fractal rotation is analyzed by a second-order mechanism, i.e., a mechanism other than a luminance energy-based motion mechanism. However, to further verify this hypothesis, we wanted to directly contrast whether fractal rotation is processed by common mechanisms than those responsible for analysis of first-order rotation. In this perspective, we adapted a paradigm developed by Scott-Samuel and Smith (2000), which was initially elaborated based on the results of Qian, Andersen, and Adelson (1994). According to Qian et al. (1994), cancellation of motion transparency can be obtained after locally balancing motion signals, so that oppositely drifting motion signals fall within a single receptive field. Scott-Samuel and Smith (2000) integrated this principle into a motion paradigm to investigate whether first- and second-order motion perceptions are using a single or multiple processing mechanisms. In their study, a stimulus composed of spatially alternating segments of oppositely drifting sinusoidal modulation of first- and/or second-order type was used. By using segment height, cancellation of motion signals was induced when stimuli were constructed exclusively of first- or second-order type of modulation. However, when stimuli composed of both first- and second-order were used, there was no motion cancellation. These results suggested that first- and second-order stimuli (contrast-modulated stimuli) were processed by separate pathways (Scott-Samuel & Smith, 2000). Our third experiment aimed at determining whether these findings can be reproduced using first-order and fractal rotation.



Movie 5. Example of first-order stimulus used in [Experiment 3](#).

The last experiment was divided into three parts, following Scott-Samuel and Smith (2000). The first two manipulations were aimed at equating the visibility of first-order and fractal rotation motion signals. The third manipulation allowed us to establish whether first-order and fractal rotation stimuli are processed by common or distinct mechanism.

Methods

Stimuli

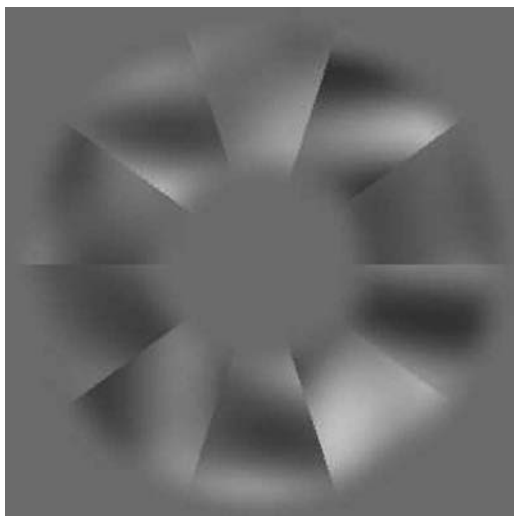
Stimuli consisted in radial gratings displayed in an annulus of 1.5–4 dva of eccentricity to homogenize the

temporal frequency content of the stimuli. The annuli were composed of spatially alternating and oppositely rotating segments of either first-order or fractal rotation stimuli, or both (composite). First-order and fractal stimuli were each composed exclusively of first-order and fractal rotation segments, respectively. Composite stimuli were made of spatially alternating first-order and fractal rotation segments. First-order and fractal rotation segments were constructed following the same procedure as described in the first experiment. An example of each of these stimuli is provided in [Movies 5–7](#).

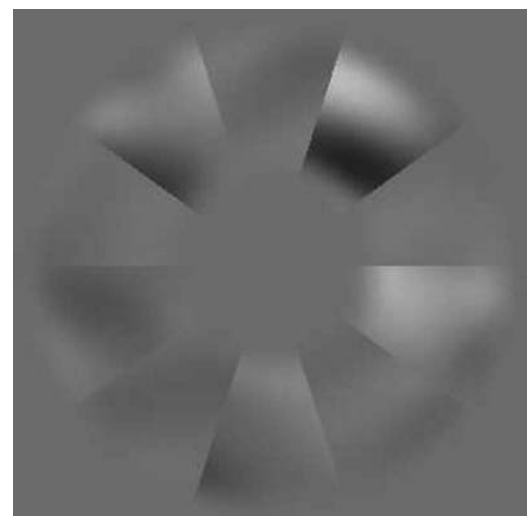
Procedure

A two-alternative-forced choice procedure was used in combination with a direction discrimination task for all three manipulations. A fixation bull's-eye was always visible during the experiment. The subjects were asked to identify direction of rotation of the central segment located directly above the fixation point. A staircase protocol of 2-down, 1-up type was used for the first two manipulations; whereas a constant stimuli protocol was used for the last manipulation.

For the first manipulation, the width of the fractal rotation stimuli segments was reduced until cancellation of motion signals was obtained. Segments all had a Michelson contrast fixed at 1 before spatial filtering of the noise frame. These threshold values were then used to determine the width of the segments for the first-order rotation stimuli used in the next manipulation. The second manipulation served to establish the contrast value at which local cancellation of motion signal of first-order rotation was obtained with the predetermined segment width from the first manipulation. The third manipulation consisted of determining the performance of subjects using the



Movie 6. Example of fractal rotation stimulus used in [Experiment 3](#).



Movie 7. Example of composite stimulus used in [Experiment 3](#).

composite stimuli. Segment width of fractal rotation stimuli was fixed at threshold, as determined from the first manipulation. A Michelson contrast value of 1, before filtering, was applied. The first-order stimuli had the same segment width as was used in manipulation 2. The threshold contrast value, as determined in the second manipulation, was used. For all manipulations, segment width and contrast thresholds corresponded to a 70.7% performance criterion. In the third manipulation, discrimination of direction performance, expressed in percentages, was measured.

Results and discussion

Motion cancellation was obtained for fractal rotation stimuli presented at a Michelson contrast of 1 before filtering, with a mean segment width of 27.56 ± 2.79 degrees. Similarly, motion cancellation could also be observed for first-order stimuli presented at the segment width value determined in the first manipulation, with a mean Michelson contrast value of 0.26 ± 0.027 before filtering. Unlike first-order and fractal rotation stimuli, motion transparency was observed for composite stimuli. Therefore, for images presented at threshold levels for motion direction discrimination of first-order and fractal rotation, performance for each observer in the composite condition was above threshold levels as shown in [Table 1](#). As such, mean performance for discrimination of direction of composite stimuli was $93.83 \pm 1.66\%$. A one-sample *t*-test indicates a statistically significant difference between group performance on third manipulation and threshold value ($t = 26.25$, $df = 19$, $p < 0.01$). Motion transparency for equal strength oppositely rotating motion signals of first-order and fractal stimuli indicates that separate mechanisms are responsible, at least initially, for perception of each stimuli type. As such, if first-order and fractal rotation were analyzed by a single pathway, then performance would have been at threshold value, i.e., 70.7%, for the third manipulation, as suggested by Scott-Samuel and Smith (2000). However, results do not exclude the possibility of a later interaction between first-order and fractal rotation processing mechanisms. However, this interaction remains marginal as suggested

by the 93.83% performance level for the third manipulation. Hence, it is quite improbable that fractal rotation is processed by the same mechanism as first-order rotation.

Discussion

Fractal rotation is analyzed by feature-tracking mechanisms

Results from [Experiments 1](#) and [2](#) suggest that fractal and first-order rotation are analyzed by feature-tracking and first-order sensitive mechanisms, respectively. Accordingly, [Experiment 1](#) has shown that mechanisms sensitive to first-order rotation are bandpass in nature in accordance with the temporal window of visibility of luminance-based motion stimuli (Derrington & Cox, 1998; Hutchinson & Ledgeway, 2006; Kelly, 1979; Lu & Sperling, 1995; Smith & Ledgeway, 1998). More importantly, results from the second experiment demonstrated that first-order rotation perception is ensured by velocity-based mechanisms. These findings are in accordance with those obtained by Seiffert and Cavanagh (1998) for luminance-defined stimuli. Moreover, first-order rotation sensitivity was greater, for temporal frequencies above 0.5 Hz, than that for fractal rotation stimuli. These results are in accordance with the difference in sensitivity to discrimination of direction of first- and second-order motion stimuli (Bertone & Faubert, 2003; Derrington & Cox, 1998; Ledgeway & Hutchinson, 2006). Therefore, our first-order rotation stimulus constitutes an appropriate comparison stimulus. In contrast, fractal rotation can be considered as being processed by second-order motion mechanisms based on the findings of the first and second experiments. Accordingly, in [Experiment 1](#), mechanisms sensitive to fractal rotation presented low-pass temporal sensitivity profile. These findings are compatible with those reported for different stimuli types such as contrast-, polarity-, spatial length-, and stereo-depth-modulated stimuli (Derrington & Cox, 1998; Ledgeway & Hutchinson, 2006; Lu & Sperling, 1995; Smith & Ledgeway, 1998). Consequently, the spatiotemporal properties of fractal rotation correspond with those of other second-order motion stimuli. Similarly, results from [Experiment 2](#) have shown that fractal rotation perception is ensured by orientation-based rather than energy-based mechanisms. These are consistent with the findings reported by Seiffert and Cavanagh (1998). Accordingly, contrast-, orientation-, and stereo-defined stimuli were all found to be analyzed by mechanisms sensitive to changes in spatial structure, i.e., position, rather than to energy (Seiffert & Cavanagh, 1998). These findings suggest that some higher order motion stimuli are processed by a filter–rectify–filter independent mechanism. Hence, computational processing

Observer	Mean performance (%)	SE
SLN	91.65	0.95
JFC	97.5	1.6
MLN	94.17	1.6
DNT	90.83	2.5
VP	95.00	1.7
Average	93.83	1.66

Table 1. Performance for discrimination of direction task on third manipulation.

of fractal rotation is apparent to those of other stimuli in second-order motion class that are analyzed through a feature-tracking mechanism.

Several studies have reported that first-order artifacts can be found within certain second-order motion stimuli, such as contrast modulation of a static carrier (Scott-Samuel & Georgeson, 1999a; Smith & Ledgeway, 1997). However, fractal rotation requires global integration because the perceived local motion direction depends on the stimulus spatial window and not only on local spatiotemporal integration. As such, the perceived local motion direction of fractal rotation requires the extraction of the spatial structure of the entire image and cannot be performed locally.

Because the nature of the carrier can sometimes influence the pattern of response (Benton, Johnston, & McOwan, 1997), we have conducted a pilot experiment with fractal stimuli generated with a static carrier (instead of dynamic) and found similar results as for the previous stimulus. It appears, therefore, that the nature of the fractal motion perception mechanisms remains similar in these conditions.

Separate pathways ensure first-order and fractal rotation perception

Looking more specifically at mechanisms responsible for fractal rotation perception, [Experiment 3](#) demonstrated that motion transparency could be observed for oppositely rotating first-order and fractal motion information segments of equal saliency. Therefore, fractal rotation perception must be ensured by distinct pathways from those responsible for first-order rotation. Findings obtained in the course of the third experiment once again suggest the second-order nature of mechanisms sensitive to fractal rotation. Our results are in accordance with those presented by Scott-Samuel and Smith (2000), showing motion transparency for stimuli composed of superposed rows of spatially alternating luminance- and contrast-modulated strips.

Orientation-based mechanisms?

The second-order properties of fractal rotation perception have been revealed through [Experiments 1–3](#). Results of the present experiments indicate that fractal motion sensitive mechanisms have the capacity to extract spatial structure information on the sole basis of orientation changes. Similarly, another study reported the ability of the visual system to perceive motion from the prior

extraction of spatial structure (Schrater, Knill, & Simoncelli, 2001). As such, using a sequence of spatially bandpass filtered, uncorrelated noise frame, for which filter central frequency decreased in an exponential manner over time, these authors demonstrated that expansion rate could still be inferred from changes in spatial scale in the absence of optic flow. These results combined with those of the present study suggest that the visual system has the ability to analyze the spatial structure of an image and this, even in the absence of features, as suggested by Benton et al. (2007). In other words, the visual system can perceive motion even in the absence of local translation of features or zero-crossing segments, as initially described by Marr and Hildreth (1980) and Ullman (1979), from one position to another.

By definition, second-order motion processing requires some form of nonlinear analysis (Cavanagh & Mather, 1989; Chubb & Sperling, 1988, 1991). However, a debate remains as to the precise nature of second-order processing mechanisms. As mentioned previously, several studies proposed that a specialized non-Fourier energy-based processing pathway, of the form of a filter–rectify–filter mechanism, would account for the perception of second-order motion stimuli (Chubb & Sperling, 1988, 1991; Solomon & Sperling, 1994; Wilson et al., 1992). Such a model requires rectification of the signal followed by analysis by a correlation motion system. Specifically, these motion detectors would be able to extract velocity information but unable to extract orientation information. Hence, fractal rotation would be invisible to a filter–rectify–filter mechanism. Others suggest that a correspondence-based process, feature tracking, would ensure the perception of second-order motion stimuli (Del Viva & Morrone, 1998; Derrington & Ukkonen, 1999; Lu & Sperling, 1995; Scott-Samuel & Georgeson, 1999b; Seiffert & Cavanagh, 1998; Smith, 1994). Interestingly, several studies indicate that second-order motion stimuli are either analyzed by energy- or position-based mechanisms, depending on the viewing conditions (Derrington & Ukkonen, 1999; Seiffert & Cavanagh, 1999). As such, Derrington and Ukkonen (1999) suggest that contrast-modulated stimuli are processed by energy-based processes at high, but by position-based mechanisms at low carrier contrast. Similarly, Seiffert and Cavanagh (1999) demonstrated that texture-defined motion stimuli are analyzed by position-based mechanisms in conditions of low contrast and slow speeds. However, with increasing contrast and speed, these stimuli are perceived by energy-based mechanisms. Allard and Faubert (2008a) also reported that distinct mechanisms were required for the perception of luminance- and contrast-modulated stimuli at low temporal frequencies. However, at high temporal frequencies, common mechanisms analyzed first- and second-order motion stimuli. These results once again suggest that distinct pathways could ensure the perception of second-order motion, depending on the testing parameters

(speed). Results obtained in the present study demonstrate that fractal rotation is processed by orientation-based mechanisms, at the selected viewing parameters.

Conclusion

The present study establishes the second-order nature of fractal rotation processing mechanisms. As such, fractal rotation perception is ensured by orientation-based mechanisms, similar to contrast-, orientation-, and stereo-defined stimuli (Seiffert & Cavanagh, 1998). Moreover, results of Experiments 2 and 3 reinforce the notion that first- and second-order motion stimuli are initially processed by distinct mechanisms.

Of interest would be to determine whether fractal rotation is still analyzed by feature-tracking mechanisms in condition of high carrier contrast as energy-based mechanisms might be more sensitive in conditions of high contrast (Derrington & Ukkonen, 1999; Seiffert & Cavanagh, 1999). The present series of experiments demonstrates that fractal rotation perception is ensured by orientation-based mechanisms, at low carrier contrast. Hence, feature-tracking mechanisms, as initially described by Ullman (1979) could be able to perceive motion in the absence of any position cues. This study demonstrates that the visual system has not only the ability to extract the spatial structure of an image prior to motion analysis but also to track changes in its structure over time.

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References

Allard, R., & Faubert, J. (2008a). First- and second-order motion mechanisms are distinct at low but common at high temporal frequencies. *Journal of Vision*, 8(2):12, 1–17, <http://journalofvision.org/8/2/12/>, doi:10.1167/8.2.12. [PubMed] [Article]

Allard, R., & Faubert, J. (2008b). The noisy-bit method for digital displays: Converting a 256 luminance resolution into a continuous resolution. *Behavior Research Methods*, 40, 735–743. [PubMed]

Anstis, S. M., & Mather, G. (1985). Effects of luminance and contrast on direction of ambiguous apparent motion. *Perception*, 14, 167–179. [PubMed]

Benton, C. P., & Johnston, A. (2001). A new approach to analysing texture-defined motion. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 2435–2443. [PubMed] [Article]

Benton, C. P., Johnston, A., & McOwan, P. W. (1997). Perception of motion direction in luminance- and contrast-defined reversed-phi motion sequences. *Vision Research*, 37, 2381–2399. [PubMed]

Benton, C. P., Johnston, A., & McOwan, P. W. (2000). Computational modelling of interleaved first- and second-order motion sequences and translating 3f+4f beat patterns. *Vision Research*, 40, 1135–1142. [PubMed]

Benton, C. P., Johnston, A., McOwan, P. W., & Victor, J. D. (2001). Computational modeling of non-Fourier motion: Further evidence for a single luminance-based mechanism. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 18, 2204–2208. [PubMed]

Benton, C. P., O'Brien, J. M., & Curran, W. (2007). Fractal rotation isolates mechanisms for form-dependent motion in human vision. *Biology Letters*, 3, 306–308. [PubMed] [Article]

Bertone, A., & Faubert, J. (2003). How is complex second-order motion processed? *Vision Research*, 43, 2591–2601. [PubMed]

Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *The Journal of Physiology*, 197, 551–566. [PubMed] [Article]

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

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

Chubb, C., & Sperling, G. (1989). Two motion perception mechanisms revealed through distance-driven reversal of apparent motion. *Proceedings of the National Academy of Sciences of the United States of America*, 86, 2985–2989. [PubMed] [Article]

Chubb, C., & Sperling, G. (1991). Texture quilts: Basic tools for studying motion-from-texture. *Journal of Mathematical Psychology*, 35, 411–442.

Crassini, B., Brown, B., & Bowman, K. (1988). Age-related changes in contrast sensitivity in central and peripheral retina. *Perception*, 17, 315–332. [PubMed]

Del Viva, M. M., & Morrone, M. C. (1998). Motion analysis by feature tracking. *Vision Research*, 38, 3633–3653. [PubMed]

- Derrington, A., & Cox, M. (1998). Temporal resolution of dichoptic and second-order motion mechanisms. *Vision Research*, *38*, 3531–3539. [PubMed]
- Derrington, A. M., & Ukkonen, O. I. (1999). Second-order motion discrimination by feature-tracking. *Vision Research*, *39*, 1465–1475. [PubMed]
- Dumoulin, S. O., Baker, C. L., Jr., Hess, R. F., & Evans, A. C. (2003). Cortical specialization for processing first- and second-order motion. *Cerebral Cortex*, *13*, 1375–1385. [PubMed]
- Eby, D. W. (1992). The spatial and temporal characteristics of perceiving 3-D structure from motion. *Perception & Psychophysics*, *51*, 163–178. [PubMed]
- Elleberg, D., Allen, H. A., & Hess, R. F. (2006). Second-order spatial frequency and orientation channels in human vision. *Vision Research*, *46*, 2798–2803. [PubMed]
- Faubert, J. (2002). Visual perception and aging. *Canadian Journal of Experimental Psychology*, *56*, 164–176. [PubMed]
- Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America A, Optics and Image Science*, *4*, 2379–2394. [PubMed]
- Gray, R., & Regan, D. (1999). Do monocular time-to-collision estimates necessarily involve perceived distance? *Perception*, *28*, 1257–1264. [PubMed]
- Habak, C., & Faubert, J. (2000). Larger effect of aging on the perception of higher-order stimuli. *Vision Research*, *40*, 943–950. [PubMed]
- Hegd , J., Albright, T. D., & Stoner, G. R. (2004). Second-order motion conveys depth-order information. *Journal of Vision*, *4*(10):1, 838–842, <http://journalofvision.org/4/10/1/>, doi:10.1167/4.10.1. [PubMed] [Article]
- Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *The Journal of Physiology*, *148*, 574–591. [PubMed] [Article]
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of Physiology*, *160*, 106–154. [PubMed] [Article]
- Hutchinson, C. V., & Ledgeway, T. (2006). Sensitivity to spatial and temporal modulations of first-order and second-order motion. *Vision Research*, *46*, 324–335. [PubMed]
- Johnston, A., & Benton, C. P. (1997). Speed discrimination thresholds for first- and second-order bars and edges. *Vision Research*, *37*, 2217–2226. [PubMed]
- Johnston, A., Benton, C. P., & McOwan, P. W. (1999). Induced motion at texture-defined motion boundaries. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*, 2441–2450. [PubMed] [Article]
- Kandil, F. I., & Fahle, M. (2004). Figure-ground segregation can rely on differences in motion direction. *Vision Research*, *44*, 3177–3182. [PubMed]
- Kelly, D. H. (1979). Motion and vision. II. Stabilized spatio-temporal threshold surface. *Journal of the Optical Society of America*, *69*, 1340–1349. [PubMed]
- Kline, D. W., Schieber, F., Abusamra, L. C., & Coyne, A. C. (1983). Age, the eye, and the visual channels: Contrast sensitivity and response speed. *Journal of Gerontology*, *38*, 211–216. [PubMed]
- Ledgeway, T., & Hutchinson, C. V. (2005). The influence of spatial and temporal noise on the detection of first-order and second-order orientation and motion direction. *Vision Research*, *45*, 2081–2094. [PubMed]
- Ledgeway, T., & Hutchinson, C. V. (2006). Is the direction of second-order, contrast-defined motion patterns visible to standard motion-energy detectors: A model answer? *Vision Research*, *46*, 556–567. [PubMed]
- Ledgeway, T., & Smith, A. T. (1994). The duration of the motion aftereffect following adaptation to first-order and second-order motion. *Perception*, *23*, 1211–1219. [PubMed]
- Lu, Z. L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*, 2697–2722. [PubMed]
- Lu, Z. L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *18*, 2331–2369. [PubMed]
- Mareschal, I., & Baker, C. L., Jr. (1998). Temporal and spatial response to second-order stimuli in cat area 18. *Journal of Neurophysiology*, *80*, 2811–2823. [PubMed] [Article]
- Marr, D., & Hildreth, E. (1980). Theory of edge detection. *Proceedings of the Royal Society of London B: Biological Sciences*, *207*, 187–217. [PubMed]
- Morrison, J. D., & McGrath, C. (1985). Assessment of the optical contributions to the age-related deterioration in vision. *Quarterly Journal of Experimental Physiology*, *70*, 249–269. [PubMed] [Article]
- Movshon, J. A. (1975). The velocity tuning of single units in cat striate cortex. *The Journal of Physiology*, *249*, 445–468. [PubMed] [Article]

- Nakayama, K., & Tyler, C. W. (1981). Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision Research*, *21*, 427–433. [PubMed]
- Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system. *Vision Research*, *37*, 2685–2698. [PubMed]
- Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research*, *23*, 689–699. [PubMed]
- Plant, G. T., Laxer, K. D., Barbaro, N. M., Schiffman, J. S., & Nakayama, K. (1993). Impaired visual motion perception in the contralateral hemifield following unilateral posterior cerebral lesions in humans. *Brain*, *116*, 1303–1335. [PubMed]
- Plant, G. T., & Nakayama, K. (1993). The characteristics of residual motion perception in the hemifield contralateral to lateral occipital lesions in humans. *Brain*, *116*, 1337–1353. [PubMed]
- Qian, N., Andersen, R. A., & Adelson, E. H. (1994). Transparent motion perception as detection of unbalanced motion signals. I. Psychophysics. *Journal of Neuroscience*, *14*, 7357–7366. [PubMed] [Article]
- Regan, D. (1986). Form from motion parallax and form from luminance contrast: Vernier discrimination. *Spatial Vision*, *1*, 305–318. [PubMed]
- Regan, D., & Beverley, K. I. (1984). Figure-ground segregation by motion contrast and by luminance contrast. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *1*, 433–442. [PubMed]
- Schofield, A. J., & Georgeson, M. A. (1999). Sensitivity to modulations of luminance and contrast in visual white noise: Separate mechanisms with similar behaviour. *Vision Research*, *39*, 2697–2716. [PubMed]
- Schofield, A. J., & Georgeson, M. A. (2003). Sensitivity to contrast modulation: The spatial frequency dependence of second-order vision. *Vision Research*, *43*, 243–259. [PubMed]
- Schofield, A. J., Ledgeway, T., & Hutchinson, C. V. (2007). Asymmetric transfer of the dynamic motion aftereffect between first- and second-order cues and among different second-order cues. *Journal of Vision*, *7*(8):1, 1–12, <http://journalofvision.org/7/8/1/>, doi:10.1167/7.8.1. [PubMed] [Article]
- Schrater, P. R., Knill, D. C., & Simoncelli, E. P. (2001). Perceiving visual expansion without optic flow. *Nature*, *410*, 816–819. [PubMed]
- Scott-Samuel, N. E., & Georgeson, M. A. (1999a). Does early non-linearity account for second-order motion? *Vision Research*, *39*, 2853–2865. [PubMed]
- Scott-Samuel, N. E., & Georgeson, M. A. (1999b). Feature matching and segmentation in motion perception. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*, 2289–2294. [PubMed] [Article]
- Scott-Samuel, N. E., & Smith, A. T. (2000). No local cancellation between directionally opposed first-order and second-order motion signals. *Vision Research*, *40*, 3495–3500. [PubMed]
- Seiffert, A. E., & Cavanagh, P. (1998). Position displacement, not velocity, is the cue to motion detection of second-order stimuli. *Vision Research*, *38*, 3569–3582. [PubMed]
- Seiffert, A. E., & Cavanagh, P. (1999). Position-based motion perception for color and texture stimuli: Effects of contrast and speed. *Vision Research*, *39*, 4172–4185. [PubMed]
- Smith, A. T. (1994). Correspondence-based and energy-based detection of second-order motion in human vision. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *11*, 1940–1948. [PubMed]
- Smith, A. T., Greenlee, M. W., Singh, K. D., Kraemer, F. M., & Hennig, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *Journal of Neuroscience*, *18*, 3816–3830. [PubMed] [Article]
- Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: Fact or artifact? *Vision Research*, *37*, 45–62. [PubMed]
- Smith, A. T., & Ledgeway, T. (1998). Sensitivity to second-order motion as a function of temporal frequency and eccentricity. *Vision Research*, *38*, 403–410. [PubMed]
- Solomon, J. A., & Sperling, G. (1994). Full-wave and half-wave rectification in second-order motion perception. *Vision Research*, *34*, 2239–2257. [PubMed]
- Taub, E., Victor, J. D., & Conte, M. M. (1997). Nonlinear preprocessing in short-range motion. *Vision Research*, *37*, 1459–1477. [PubMed]
- Ullman, S. (1979). The interpretation of structure from motion. *Proceedings of the Royal Society of London B: Biological Sciences*, *203*, 405–426. [PubMed]
- Vaina, L. M., & Soloviev, S. (2004). First-order and second-order motion: Neurological evidence for neuroanatomically distinct systems. *Progress in Brain Research*, *144*, 197–212. [PubMed]
- Watson, A. B., & Ahumada, A. J., Jr. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *2*, 322–341. [PubMed]

Wenderoth, P., Watson, J. D., Egan, G. F., Tochon-Danguy, H. J., & O’Keefe G. J. (1999). Second order components of moving plaids activate extrastriate cortex: A positron emission tomography study. *Neuroimage*, 9, 227–234. [[PubMed](#)]

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