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Fractal rotation isolates mechanisms for formdependent motion in human vision

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Neurobiology

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Here, we describe a motion stimulus in which the quality of rotation is fractal. This makes its motion unavailable to the translationbased motion analysis known to underlie much of our motion perception. In contrast, normal rotation can be extracted through the aggregation of the outputs of translational mechanisms. Neural adaptation of these translation-based motion mechanisms is thought to drive the motion after-effect, a phenomenon in which prolonged viewing of motion in one direction leads to a percept of motion in the opposite direction. We measured the motion after-effects induced in static and moving stimuli by fractal rotation. The after-effects found were an order of magnitude smaller than those elicited by normal rotation. Our findings suggest that the analysis of fractal rotation involves different neural processes than those for standard translational motion. Given that the percept of motion elicited by fractal rotation is a clear example of motion derived from form analysis, we propose that the extraction of fractal rotation may reflect the operation of a general mechanism for inferring motion from changes in form.

Keywords: motion; visual perception; after-effect; psychophysics; feature tracking

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1. INTRODUCTION

Motion processing in biological systems is achieved mainly through the operation of neural mechanisms that react directly to translations of local luminance (Albright & Stoner 1995; Clifford & Ibbotson 2003). However, it has been proposed that other forms of motion processing coexist with this system. For example, feature tracking (a process widely accepted to occur in human vision) involves mechanisms that react to translations of features extracted prior to motion analysis (Ullman 1979; Anstis 1980; Lu & Sperling 1995; Del Viva & Morrone 1998). In this paper, we introduce a novel fractal rotation stimulus that directly demonstrates the operation of motion processing dependent upon the prior analysis of

Electronic supplementary material is available at http://dx.doi.org/ 10.1098/rsbl.2007.0056 or via http://www.journals.royalsoc.ac.uk. spatial form; in this case, the analysis of pattern orientation.

Our stimulus is constructed by filtering a noise pattern at different orientations. To construct a single frame, we take the Fourier transform of the noise pattern and then weight the amplitudes of the components with a weighting function (which serves as an orientation filter). We then take the inverse transform to arrive at an image rich in oriented structure (figure 1a). The weighting function is a blurred line falling through the frequency domain origin; its orientation determines the orientation structure of the image. To generate a sequence, we rotate the weighting function, generating a fresh windowed frame at each consecutive angle of rotation (figure 1b). Note that the noise stimulus, before filtering, is the same for every frame. If a new noise stimulus is generated for each frame, then a similar (though noisier) percept is obtained.

In the animated stimulus, it is the weighting function that is being rotated. The centre of rotation is the Fourier domain origin, which has no single location within the resultant sequence. Consequently, the rotational characteristics are the same at every point in the image; in other words, the quality of rotation is fractal. A very striking consequence of this is that rotation is perceived within any arbitrary window applied to the stimulus (electronic supplementary material, movies). The spatio-temporal receptive fields of standard translation-based motion detectors can be thought of as small apertures applied to the image. Within any such aperture applied to our fractal stimulus, there is only local rotation, not the coherent local translation to which such mechanisms respond. The fact that observers can readily perceive fractal rotation is a clear demonstration of motion perception dependent upon the analysis of spatial form (i.e. the extraction of orientation) prior to motion processing. In an attempt to learn something of the nature of this process, we investigated the motion after-effects elicited by adaptation to fractal rotation.

The motion after-effect describes how prolonged viewing of motion in a particular direction results in the illusory movement of a test pattern in the opposite direction. However, it is not a unified phenomenon. The nature of the motion after-effect depends upon whether a static test stimulus or flickering/dynamic test stimulus is employed. There is evidence that these different motion after-effects reflect adaptation of different neural mechanisms (Culham *et al.* 1998). We therefore measured the static, flicker and dynamic motion after-effects following adaptation to fractal rotation. We also measured the after-effects elicited by a comparison stimulus; a standard rotation created by rigidly rotating a single frame from a fractal rotation sequence.

There is good evidence to suggest that the motion after-effect is caused by adaptation-dependent changes in contrast gain in neurons responsive to visual motion in striate cortex (Kohn & Movshon 2003). These neurons are precisely those that respond to local translation-based motion. If this view of human motion processing is correct, then the fractal rotation stimulus should not elicit a strong motion after-effect.



Figure 1. (a) Constructing the fractal rotation stimulus. A 1/f noise pattern (top left) is decomposed into its Fourier components. Its amplitude spectrum is weighted by a weighting function (top right). The weighted amplitude spectrum and phase are recombined and the inverse transform is calculated resulting in the image shown in the bottom left. All frames are presented in a circular aperture (shown bottom right). (b) Images on the top show the weighting function at different orientations and bottom images show the resultant frames. (*c*-*e*) Graphs show the strength of the motion after-effect calculated as half the difference between adaptation to clockwise and anticlockwise adaptors. Positive values indicate the direction of motion required to null the motion after-effect. (*c*) Static motion after-effect: the speed of rotation of a sine wave grating necessary to null the motion after-effect induced by fractal rotation (left panel) and the comparison stimulus (right panel). (*d*) Flicker motion after-effect: the speed of rotation of a counterphasing grating necessary to null the motion after-effect of fractal rotation (left panel). (*e*) Dynamic motion after-effect: the motion coherence necessary to null the motion after-effect of fractal rotation (left panel) and the comparison stimulus (right panel). Error bars indicate limits.

2. MATERIAL AND METHODS

(a) Stimulus generation

Each fractal rotation stimulus is generated from a single 384×384 pixel 1/*f* noise image (Field 1987). To generate a frame, we take the Fourier transform of the noise image and weight the amplitudes of the components. The weighting function is a blurred line through the frequency domain origin that takes a peak value of 1 and falls to 0. The blur function is Gaussian with standard deviation 2°. We combine phase and weighted amplitude and take the inverse Fourier transform.

We rotate the weighting function through 360° in 3° steps, generating a frame at each step. Our stimuli are displayed at 60 Hz, giving a speed of 0.5 r.p.s. Each frame is presented within a circular aperture (372 pixels diameter) with a Gaussian blurred edge (standard deviation 2 pixels). The comparison stimulus is generated by rigidly rotating the first frame of a fractal rotation stimulus through 360° in 3° steps. Pixel values are estimated using bicubic interpolation. All sequences are initially generated as floating point arrays. Each is divided by its standard deviation. All sequences are then scaled by the same factor so that their values fall within 256 discreet grey levels.

(b) Procedure

Linearized stimuli were displayed on an Iiyama Vision Master Pro 410 monitor at 60 Hz with resolution 1024×768 pixels. Mean luminance was 41 cd m⁻², viewing distance was 1 m. Stimuli subtended 6.75° of visual angle. All the stimuli were also presented centrally with a central fixation spot visible at all times. The remainder of the screen was set to mean luminance.

An initial adaptation stimulus was presented for 30 s after which a 500 ms test stimulus was presented. Thereafter, test stimuli were preceded by an adaptation top-up stimulus lasting 6 s. The start frames of the adaptation and top-up stimuli and the initial angle of the test stimulus were randomized. There was a blank interstimulus interval of 250 ms between adaptor and test.

The dynamic motion after-effect test stimulus was a random dot kinematogram (RDK) with dot density 22 dots per deg² presented in a circular window of diameter 6.75°. Dot size was 4.2 arc min. Half the dots were white and half were black. They were presented on a grey mean luminance background. Dot speed was $4^{\circ}s^{-1}$. For each dot, its direction was determined on each frame. If, for example, coherence was 30%, then 70% of the dots translated in a random direction, while the remainder moved coherently in a clockwise trajectory. For negative coherence, the direction of motion was reversed. For measuring the flicker motion after-effect, the test stimulus was a sine wave grating (spatial frequency four cycles per deg, counterphasing at 4 Hz, Michelson contrast of 1) presented in the same blurred circular aperture as the adaptation stimuli. For the static motion after-effect, the test stimulus did not counterphase but was otherwise identical.

Participants indicated the direction of motion of the test stimulus (clockwise or antclockwise). We used an adaptive method of constants procedure (Watt & Andrews 1981) to control the coherence (in the case of the RDK test) or speed of rotation of the test stimulus. We gathered the responses to 64 test stimuli for each psychometric function and fitted probit functions (Wichmann & Hill 2001) to estimate the speed of real rotation or coherence necessary to null the motion after-effect.

When measuring the dynamic and static motion after-effects induced by the fractal rotation stimulus, we gathered four psychometric functions per condition. Otherwise, we gathered only one function per condition. For each function, we generated 10 000 parametric bootstrap estimates of nulling speed/coherence. When averaging across functions, and taking the halved difference, we propagated the bootstrap populations through the relevant calculations (Benton *et al.* 2006). The percentile method was used to calculate 95% confidence limits (Efron & Tibshirani 1993).

3. RESULTS AND DISCUSSION

Results are shown in figure 1. In response to fractal rotation, we obtain robust after-effects for all observers. However, the motion after-effects elicited with the fractal stimulus were approximately an order of magnitude less than those obtained with the comparison stimulus. This difference in magnitude is clearly consonant with a view in which the motion aftereffect is driven mainly by translation-based mechanisms in striate cortex (Kohn & Movshon 2003); mechanisms that fractal rotation fails to adapt.

The small after-effect measured in response to fractal rotation is probably based upon a nontraditional cause of the motion after-effect. One source may be the suppression of eye movements following adaptation (Chaudhuri 1990). This would suppose that involuntary torsional optokinetic nystagmus during adaptation is followed, in the absence of a subsequent test stimulus, by a residual torsional afternystagmus. However, this is suppressed by a motor signal during the test stimulus; the motion after-effect being caused by the perceptual registration of the motor signal. The difference in magnitude between flicker and static motion aftereffect might be accounted for by proposing that the static test stimuli have the stronger suppressive effect on afternystagmus.

Fractal rotation provides a clear example of a stimulus in which motion extraction is dependent upon the prior analysis of some spatial property (in this case, orientation). A similar observation can be made with respect to fractal expansion stimuli (Schrater et al. 2001) although in that case it is spatial scale that is changing. In feature tracking, spatial analysis also precedes motion analysis. However, critically, in fractal rotation, there is no feature that has translated from one position to another upon which the motion percept is based. Indeed, what direction of motion is seen at a particular position is dependent upon the aperture placed over the stimulus. Therefore, either fractal rotation lies outside the bounds of feature tracking or our notion of the characteristics of feature tracking needs to be extended to incorporate fractal rotation and, by extension, fractal expansion.

In standard motion processing, the motion signal is extracted by motion-sensitive neurons in primary visual cortex. In contrast, with fractal rotation, the signal is present as a change of neural activity across neurons selective for orientation in primary visual cortex. A similar argument can be made with respect to fractal expansion (neurons responsive to spatial scale) and feature tracking (neurons responsive to different spatial positions). The point of commonality is the fact that they may all involve the interpretation of changes in neural activity *across* neurons in primary visual cortex. It is tempting to suppose that a single high-level interpretive mechanism underlies the perception of these motion types. This might simply be a reflection of a general mechanism to infer motion based upon general changes in spatial structure. The notion of a single motion-form mechanism is particularly attractive as it obviates the need to provide separate specialized motion-processing mechanisms targeted at stimuli that appear rarely (if at all) in the natural world.

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