Neuromagnetic evoked responses to complex motions are greatest for expansion

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Abstract
We analysed evoked magnetic responses to moving random dot stimuli, initially using a 19-channel magnetoencephalography (MEG) system, and subsequently using a 151-channel MEG system. Random dot displays were used to construct complex motion sequences, which we refer to as expansion, contraction, deformation, and rotation. We also investigated lateral translation and a condition in which the directions of the dots were randomised. In all stimulus conditions, the dots were first stationary, then traveled for a brief period (317 s or 542 ms), and were then stationary again. In all conditions, evoked magnetic responses were observed with a widespread bilateral distribution over the observers’ heads. Initial recordings revealed a substantially larger evoked magnetic response to the expansion condition than the other conditions. In a revised study, we used a 151-channel MEG system and two stimulus diameters (9.3 and 48 deg), the smaller comparable with the first experiment. The responses were analysed using a nonparametric approach and confirmed our initial observations. In a third study, speed gradients were removed and a new design permitted direct comparisons between motion conditions. The results from all three experiments are consistent with the greater ecological validity of the expansion stimulus.

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1. Introduction
To a first approximation, small patches of the optic flow field can be decomposed into a set of six cardinal vector fields. These are four complex motions: expansion, rotation and two orthogonal components of deformation, plus two orthogonal components of translation (Koenderink and van Doorn, 1975, 1976; Koenderink, 1986; see Harris, 1994 and Howard and Rogers, 2002 for reviews). This has prompted a suggestion that the visual system might be specialised for detecting these independent quantities (Longuet-Higgins and Prazdny, 1980; Koenderink, 1986). Although evidence from single-unit physiology (Orban et al., 1992; Graziano et al., 1994; see Orban,
and psychophysics (Meese and Harris, 2001b; Meese and Anderson, 2002) suggests that the visual system does not represent the optic flow field purely in terms of the cardinal components, specialised cells and mechanisms for complex motion have been identified. For example, neurons broadly tuned for particular instances of complex motion have been found with large receptive fields in visual area MSTd (V5 complex) in monkey (Tanaka and Saito, 1989; Tanaka et al., 1989; Dufly and Wurtz, 1991a,b; Graziano et al., 1994; Geesman and Andersen, 1996; Geesman et al., 1997; Li et al., 2000) and a human homologue of this area is implicated in the analysis of complex motion by fMRI (Ahlfors et al., 1999; Morrone et al., 2000) and magnetoencephalography (Ahlfors et al., 1999; Schoenfeld et al., 2003), though other extrastriate areas are probably also involved (de Jong et al., 1994; McKeefry et al., 1997; Ahlfors et al., 1999; Braddick et al., 2001; Holliday and Meese, 2001). Psychophysical work in human also suggests multiple mechanisms (Meese and Harris, 2001a) that are broadly tuned (Snowden and Milne, 1996; Meese and Harris, 2001b, Meese and Anderson, 2002) and perform (linear) summation of complex motion by fMRI (Ahlfors et al., 1999; Morrone et al., 2000) and magnetencephalography (Ahlfors et al., 1999; Schoenfeld et al., 2003), though other extrastriate areas are probably also involved (de Jong et al., 1994; McKeefry et al., 1997; Ahlfors et al., 1999; Braddick et al., 2001; Paradis et al., 2000; Braddick et al., 2001; Holliday and Meese, 2001).

In computer simulations of ego-motion through simulated environments, Ivins et al. (1999) found that the first principal component of their analysis of retinal flow fields was similar to an (asymmetric) expansion component. The expansion stimulus is particularly important for human vision because it warns of imminent danger of collision between an observer and a looming object or surface (e.g., Lee, 1976; Regan and Beverly, 1978; Regan and Hamstra, 1993) and is valuable in computing direction of heading (e.g., Gibson, 1950; Warren and Hammon, 1988; Crowell and Banks, 1993; Freeman et al., 1994). These reasons (prominence and importance) might explain why more neurons have been found with preferences for expansion than for contraction in area MSTd in monkey (Tanaka and Saito, 1989; Tanaka et al., 1989; Graziano et al., 1994; Geesman and Andersen, 1996). Similarly, in monkey visual area MT (V5), Albright (1989) found more neurons with preferences for unidirectional motion away from the fovea than towards it. A related finding has also been reported for cat (Rauschecker et al., 1987; though also see Sherk et al., 1995). Curiously, however, some psychophysical work has revealed an opposing view. In experiments that measured coherence thresholds for random dot kinematograms, Edwards and Badcock (1993) found that for their four observers, sensitivity was greater for contraction than it was for expansion. As the authors pointed out, this concurs with the findings of Steinmetz et al. (1987) who recorded from cells in the parietal cortex (area 7a), though it contrasts with what might be expected from what is found in MSTd (see above). Perception of speed also reveals a directional asymmetry: contracting stimuli are perceived to move faster than expanding stimuli (Geesman and Qian, 1998) and expanding stimuli are perceived to move faster than rotating stimuli (Bex et al., 1999; Geesman and Qian, 1998). Asymmetries have also been found in motion aftereffects (MAE). Adaptation to contracting spirals produces longer-lasting MAEs than adaptation to expanding spirals (e.g., Reinhardt-Rutland, 1994). However, other experiments have failed to reveal some of these asymmetries. In experiments similar to those of Edwards and Badcock (1993), Snowden and Milne (1996) and Morrone et al. (1999) found little or no sensitivity biases, and in two out of three observers, Meese and Harris (2001b) and Meese and Anderson (2002) found small sensitivity biases in the opposite direction (sensitivity to expansion was greater than to contraction). Finally, Bex et al. (1999) found no evidence for directional biases in comparing motion aftereffects (MAE) for expanding and contracting adapters.

We hypothesised that if different complex motions are processed by independent groups of neurones, then the relative numbers (or sensitivities) of the different groups would be given by the relative magnitude of their evoked magnetic responses to complex motion stimuli. Elsewhere, evoked magnetic responses have been recorded for expansion and contraction stimuli (Ahlfors et al., 1999), but the data were not analysed independently leaving the issue unresolved. The present paper provides an overview of our work on this hypothesis conducted over a
period of 6 years in which we have used a variety of experimental designs and stimuli, recording equipment and data analyses. While our data permit source localisation using, for example, dipole fitting, this will not be addressed here. Instead, the current paper emphasises the relative potency of different motion stimuli in terms of the relative magnitudes of their evoked responses. In our preliminary examination, we used a 19-channel MEG system and found greater evoked magnetic responses for expansion than any of the other motion stimuli tested, including contraction. In our second and third experiments, we used a 151-channel MEG system and confirmed this result for small and large stimulus diameters (9.3 and 42 deg), with and without the presence of speed gradients in the stimuli. Our results indicate that looming visual stimuli produce greater evoked magnetic responses in the human brain than other comparable motions and that the important aspect of the stimulus is the radiating component of motion.

Some of these results have been presented previously in abstract form (Holliday et al., 1998; Holliday and Meese, 2001).

2. Experiment 1

2.1. General methods

2.1.1. Stimuli and display equipment

Stimuli were patterns of 241 randomly positioned white dots with a maximum contrast of 90% moving over a dark background within an annulus with external and internal diameters of 9.3 and 0.17 deg, respectively. Dot luminance was linearly ramped over a distance of 13% of the stimulus diameter at both the inner and outer boundaries and was set to zero outside of these boundaries. Stimulus dots were produced by an anti-aliasing algorithm, which uses a square group of four pixels to represent each dot (Georgeson et al., 1996). Throughout the experiment, a small fixation point was presented at the centre of the display where we define the origin. In three conditions of complex motion (expansion, clockwise rotation and positive deformation), dot speed was linearly related to the modulus of its nominal polar coordinate, defined as the midpoint of its trajectory. All dots moved through linear trajectories and the speed gradient was 20%, meaning that each dot traveled through one fifth of its nominal distance from the origin during its 317-ms movie sequence. For the expansion condition, each dot moved radially away from the origin. For the clockwise rotation condition, each dot moved in a straight line in the direction given by the angle of its nominal polar coordinate minus $\pi/2$ (i.e., they did not have curved trajectories). For the ‘positive’ deformation stimulus, dots moved in a direction given by $\pi/2$ minus its nominal polar coordinate. Three further complex motion stimuli (contraction, anticlockwise rotation and ‘negative’ deformation) were exactly the inverse transforms of the first three conditions. In a random condition, the direction of each dot was randomised and in translation conditions dots moved laterally from right to left at a speed matched to either the outermost region of the display (2.93 deg/s) or half of that speed (1.46 deg/s) and for convenience are referred to as fast and slow translation, respectively. Inverse traversals were also generated for the random and translation conditions. Note that the nominal statistical distribution of dot velocities was the same for all six complex motions and the two noise stimuli.

Although our stimulus arrangement does not include the curved and accelerating dot trajectories that are a property of textured surfaces that truly loom, rotate and deform, we found the stimuli to appear smooth and compelling.

The stimuli were generated by a PC and stored on a VSG graphics board (Cambridge Research Systems Ltd, Rochester, Kent, England) and presented on a video display monitor. The frame rate of the monitor was 120 Hz and the movie was updated every five frames giving an image refresh rate of 24 Hz.

2.1.2. Recording equipment

A 19-channel MEG system (Cryoton, Moscow), with second-order gradiometers arranged in a hexagonal array (5-cm baseline, 1.5-cm coil diameter and 3-cm sensor separation) was used to record the data for this experiment (Matlashov et al., 1995). The MEG system was situated within a single layer shielded room (Vacuumschmeltze GmbH). The tail of the dewar (17.5-cm diameter) was placed over the posterior left hemisphere approximately above the temporo-occipito-parietal junction, where the human
homologue of MT has been observed (de Jong et al., 1994; Anderson et al., 1996; Morrone et al., 2000).

2.1.3. Analysis

The acquired evoked response data was DC-corrected and band-pass filtered in the range 2–40 Hz. A noise suppression algorithm was also used that took the simultaneously acquired signal from a vector magnetometer recording the local environmental variation within the MEG dewar to reject 50 Hz powerline interference. The epochs of data were then averaged and an overall evoked response magnitude calculated as the ‘global field power’ (GFP). GFP is simply the squared magnetic field value summed over recording channels at each time point, with units (fT^2/Hz). In some cases, signal-to-noise ratios (SNR) were also calculated by normalizing the square root of the GFP by the mean plus–minus error of the signal. [The plus–minus error is sometime called an anti-average. It is calculated by averaging epochs with successive epochs multiplied alternately by plus or minus 1.0, giving an estimate of the signal variability.] SNR gauges the fidelity of the neural response but the usefulness of this measure would be compromised by signal correlated (e.g., multiplicative) noise. Therefore, we concentrate our quantitative analysis and data presentation around the GFP approach, but also use the more conservative SNR in reporting the qualitative comparisons made in Experiment 1. In practice, we have found that similar results are obtained with both approaches. Comparisons between paired conditions consisting of opposite motion transformations (e.g., expansion/contraction) are possible on a within-subject basis because the dewar position was maintained constant throughout the recording of all stimulus conditions.

2.1.4. Procedure and observers

The only instruction given to the observers was to fixate the central fixation point throughout the experi-

![Graphs](image-url)
ment. In this experiment, data for the pair of deformation stimuli were not recorded, leaving five pairs of motions: two complex motions, one noise and two translations. In all conditions, each consisting of a pair of opposed motions transformations (e.g., clockwise/anti-clockwise), stimulus presentations were in alternating sequence: 317 ms undergoing one sign of motion transformation; 883 ms stationary; 317 ms in the reverse direction; 883 ms stationary. Each opposed motion pair was shown 75 times, giving a total duration of 3 min, and 75 epochs of data for each motion direction. The observer was given a short rest before the measurement sequence for the next pair of stimulus motions commenced.

Data were gathered from two observers (IEH and TSM; the two authors), both male, right handed and with vision within the normal range. Both observers performed the experiment twice, with the five stimulus conditions performed in different random orders. The entire experimental recording took approximately 20 min for each observer.

2.2. Results and discussion (Experiment 1)

SNR are shown for the two observers in Figs. 1 and 2. Each panel shows the results for a single motion pair (i.e., opposite directions of motion). The bottom right panels are for the fast translation condition. The results for the slow translation condition were similar but were of slightly smaller amplitude. For IEH, the direction of motion had little or no effect on the results for the rotation, translation and noise conditions, though the signal to noise ratio was considerably greater for expansion than contraction (compare solid and dashed curves). In fact, the response to expansion was greater than for any of the other patterns of motion. For TSM, the distinction was less clear, though the trends were in similar directions to those for IEH. (See Section 2.1.3 for a discussion of the relationship of GFP and SNR measures.). A replication of this experiment by both observers produced very similar patterns of results, demonstrating the robust nature of these observations.

Fig. 2. Results from Experiment 1 for TSM. Details as for Fig. 1.
3. Experiment 2

3.1. Methods

3.1.1. Stimuli and display equipment

Stimuli were similar to those used in Experiment 1, but contained up to 400 dots. The experiment was repeated for two different display sizes. In a small display condition, the display region was the same as in Experiment 1 (9.3 deg). In a large display condition, the entire display was magnified by a factor of 5.2 giving an outer diameter of 48 deg. This transformation of the display size also transformed the distance of the dot trajectories, maintaining a speed gradient of 20% in the complex motion and noise conditions (see above). Stimulus durations were as before (317 ms of motion, followed by 883 ms of stationary dots). In two translation conditions, the dot speeds were matched to those in the outer region of the display, giving speeds of 9.3 and 15.14 deg/s for the small and large display conditions, respectively.

The stimuli were back projected using a LCD projector onto a screen placed 32 cm in front of the observers. The frame rate of the projector was 60 Hz and the positions of the dots were updated every two frames.

3.1.2. Recording equipment

Whole head MEG recordings were made using a 151-channel neuromagnetometer (CTF Port Coquitlam, BC, Canada). Triggering of the MEG system in synchrony with the recordings is problematic when using LCD projection as the time of stimulus onset is uncertain, due to buffering of the incoming video stream by the projector. This was overcome by incorporating a small white patch, invisible to the observers, on the first frame of the stimulus motion; this patch illuminated a PIN photodiode and the signal produced by the photodiode was recorded and used to

Fig. 3. Results from the large field size condition (48 deg) of Experiment 2. Evoked magnetic responses plotted as global field power (GFP) for each of two observers (left and right panels). Top panels are for expansion (solid curves) and contraction (dashed curves) and bottom panels are for clockwise rotation (solid curves) and anti-clockwise rotation (dashed curves).
accurately time the onset of the motion sequences in the MEG recording.

3.1.3. Analysis

Data was filtered into the range 4–40 Hz within a Hanning window. GFP was calculated as for Experiment 1. The measure used in the statistical analysis was the peak GFP. This measure is not used in our analysis to distinguish the underlying generators of the measured response unlike, for example, identifying the latency and amplitude of individual evoked response components (e.g., P100 m).

Inferential statistical analysis was based on within-subjects normalised GFP values. Sensors were restricted to the parietal, occipital, central and temporal regions. Frontal sensors were excluded to reduce the impact of eye artifacts.

3.1.4. Procedure and observers

The experimental procedure was the same as in Experiment 1. Data for the large display size were gathered before those for the small display size, and in a single recording session the following order of stimulus conditions (indicating paired motions e.g., clockwise/anticlockwise rotation) was always used: deformation, rotation, expansion, translation and noise. Analysis is restricted to paired opposed motion types because (a) participants were permitted to relax between runs of each type of motion, potentially leading to gross head movements between different conditions and (b) to avoid order effects.

Six observers were recruited to the study. All had vision within the normal range and were right handed. We were unable to gather data from one of the observers in the small field size condition, as the participant withdrew from the study.

3.2. Results and discussion (Experiment 2)

Figs. 3 and 4 show the GFP for two observers and two pairs of conditions selected to illustrate the range of amplitudes recorded for the large and small field sizes, respectively. The top panels show clearly that the evoked response for expansion (solid curves) is greater than for contraction (dashed curves) for both field sizes (different figures). For purposes of

![Fig. 4. Results from the small field size condition (9.3 deg) of Experiment 2. Details as for Fig. 3.](image-url)
comparison, a second motion pair (in this case rotation) is shown in the bottom panels. In this case, the responses are smaller, though similar for the two directions of rotation. Of note is the very large difference in response across the two observers (also see Experiment 3).

In general, there was little if any effect of field size on the amplitude of the GFP. For the large condition, there was a sufficient number of observers to perform Wilcoxon signed rank tests on the normalised GFP amplitudes for each of the five stimulus conditions. Only the expansion/contraction comparison was significant ($p<0.05, T=1, n=6$, two-tailed). The finding that expansion produced a significantly greater magnetic response than contraction confirms the trend observed in the two participants from Experiment 1.

On ecological grounds, we might expect the presence of speed gradients to be an important aspect of our stimulus because they are present in the optic array when a rigid object is moved through a rigid transformation (e.g., a looming surface). Certainly, the inclusion of speed gradients impacts greatly upon the appearance of the type of stimuli used in our study (Freeman et al., 1994; De Bruyn and Orban, 1990a; Barraza and Grzywacz, 2002), although psychophysics (Freeman and Harris, 1992; Morrone et al., 1995; Meese and Harris, 2001a) and single-cell physiology (Tanaka et al., 1989; Orban et al., 1995) suggest that their presence is not important for stimulating complex motion mechanisms. In the next experiment, we asked whether the bias of the magnetic response of the human brain towards expansion over contraction requires the inclusion of speed gradients.

4. Experiment 3

4.1. Methods

4.1.1. Stimuli and display equipment

The stimulus conditions were similar to those used in Experiment 2, though the viewing distance was reduced slightly (30 cm) and the display size was 42 deg. However, in this experiment, the speed gradient was removed and all dots moved at a constant speed of 7 deg/s. The display equipment was the same as that used in Experiment 2.

4.1.2. Recording equipment

The recording equipment and triggering procedure was the same as that used in Experiment 2.

4.1.3. Analysis

Analysis of raw data and the application of non-parametric statistics was the same as in Experiment 2.

4.1.4. Procedure and observers

The only instruction given to the observers was to fixate the central fixation point throughout the experiment. Each experiment consisted of a series of blocks comprising fixed sequences of stimuli, namely expansion; rotation; translation; random motion and contraction. One stimulus presentation consisted of (i) a period of 1000 ms in which the dots were stationary; (ii) motion lasting 542 ms; (iii) a period of 1000 ms in which the dots were stationary again; and (iv) resetting of the dots to their initial positions. A block consisted of 10 trials of each stimulus type separated by a period of 10 s during which the dots remained motionless. The block of five motion sequences was repeated 10 times providing 50 epochs of each stimulus type. The initial positions for the dots were recomputed at the beginning of each stimulus type. The entire experimental recording took approximately 20 min.

Seven observers were recruited to the study (ages: 22–45, 4 male and 3 female). All had vision within the normal range and were right handed. For one observer (PF), the data for the contraction condition were lost due to technical malfunction during data recording.

4.2. Results and discussion (Experiment 3)

The overall pattern of responses was similar to those seen in Experiment 2, indicating that the earlier inclusion of speed gradients was not critical to our results. In contrast to Experiment 2, the design of this experiment permits statistical comparisons across all of the motion conditions. (In Experiment 2, it was valid only to compare opposite signs of each motion type). The only significant findings were that expansion was significantly greater than contraction ($p<0.05, T=0, n=6$, two-tailed) and translation ($p<0.05, T=1, n=7$, two-tailed).
A pictorial summary of the data is provided by the bubble plot of Fig. 5. Symbol size indicates the amplitude of the normalised GFP, and the figures at the top of the panel indicate the amplitude of the largest GFP for each observer. (As in Experiment 2, there is a large variation of amplitude across observers). Different colours are for different conditions and for each observer the symbols are plotted in rank order. The expansion condition (red) tends towards the top of the figure and above contraction (blue), while translation (black) tends towards the bottom. Other tendencies can also be observed. For example, translation (black) tends to fall below noise (white), an effect that approached but did not reach 5% significance ($T=2$, $n=7$, two-tailed).

More generally, we wanted to test the hypothesis that the evoked magnetic response to the expansion stimulus was greater than the other motion conditions. To do this, we performed Fisher’s exact test to determine the probability that four or more observers out of seven were most responsive to the expansion stimulus (see Fig. 5). The computed probability was 0.0374, which is significant at the 5% level. Therefore, we conclude that observers can be expected to have a greater evoked magnetic response to expansion than to the other motion patterns tested in this experiment.

5. General discussion

Using both a 19-channel magnetometer and a 151-channel magnetometer, we have found that expansion stimuli produce a greater magnetic response than contraction stimuli (Experiments 1, 2 and 3). In Experiment 3, we found that the inclusion of a speed gradient was not important for observing this response asymmetry. In fact, in this experiment, where all dots moved at the same speed, the expansion stimulus was also shown to produce a greater magnetic response than translation. More generally, the hypothesis that the expansion stimulus was the most provocative complex motion was supported. A particularly striking aspect of our recordings was their repeatability. For example, observer IEH (one of the authors) took part in five recording sessions in which his evoked magnetic response to expansion was compared with that to contraction (two replications of Experiment 1,
two field sizes in Experiments 2 and 3). In all five cases, the evoked response to expansion was greater than that to contraction.

In line with our findings, numerical biases in motion preference have been found in single cell studies in areas MT (Albright, 1989) and MSTd (Tanaka and Saito, 1989; Graziano et al., 1994; Geesman and Andersen, 1996). For example, Tanaka and Saito found a total of 50 cells that responded to rotation (25 to each direction), but 76 cells that responded to expansion and only 11 cells that responded to contraction. Geesman and Andersen (1996) and Graziano et al. (1994) found similar numerical biases towards expansion over other complex motions, though Geesman and Andersen (1996) also found more cells with a preference for contraction than for a particular direction of rotation. One possibility then is that the evoked magnetic responses are larger for motion stimuli that activate a larger pool of neurones. As outlined in the Introduction, there are ecological reasons for supposing a special status for the expansion stimulus, and our results shed further light on this. For example, we found asymmetries for both large (Experiments 2 and 3) and small (Experiments 1 and 2) display sizes. Thus, although the entire visual field is subject to expansion when an organism moves forward through the environment, appropriate mechanisms also appear to be tapped when the region of the display is much smaller than this. This is consistent with psychophysical evidence (Burr et al., 1998) and the properties of individual neurons in MSTd. For example, decreasing the size of a stimulus can reduce the magnitude of response (under some circumstances; see Geesman and Andersen, 1996), but does not change its selectivity (Tanaka and Saito, 1989; Duffy and Wurtz, 1991b). Furthermore, if the potency of the expansion stimulus is due to its importance in processing both optic flow and looming objects (see Introduction), then strong responses for both large and small field sizes would be expected (Geesman and Andersen, 1996). However, we draw caution in associating the evoked magnetic response to our stimuli too closely with the results of these cellular level studies. The parallel between these results and our findings does not implicate specific areas in the generation of the evoked responses we have observed. For example, it is possible that there are other areas contributing to the responses having biases similar to those observed in the MT/MST cell studies. Our preliminary source analysis (the subject of a forthcoming paper) indicates that our stimuli produce activity in several extra-striate regions of the brain (Holliday and Meese, 2001; Holliday et al., 2003) as has also been found with fMRI (Braddick et al., 2000; Braddick et al., 2001). Whether these additional areas also contribute to the differential responses we have recorded remains to be seen. But one possibility is that a substantial part of the evoked response that we have recorded is due to the onset of motion, regardless of the type of motion. The examples of large evoked responses measured in the noise condition (e.g., see Figs. 1, 2 and 5) point to this interpretation. Nevertheless, the differential responses that we have measured require that further processes be involved. It is possible that these differences reflect visual processing at a higher order of response than sensory encoding of basic image features. Our experiments do not suggest what this level of encoding might be, but plausible candidates include surface representation and preparation for action.

Another explanation for our results is that the differential responses we observe might arise from differences in the anatomical distribution of cellular populations underlying the evoked responses for each stimulus class. For example, this would happen if the population of cells selective for expansion were located sufficiently closer to the MEG sensors than those for contraction to register as differences in the GFP magnitude. While this hypothesis is in accord with our findings, we know of no evidence to support it.

The asymmetries in our data run counter to some psychophysical evidence at coherence threshold (Edwards and Badcock, 1993). The reason for this discrepancy is not clear, but it might reflect differences in threshold and suprathreshold response characteristics. For example, our translation and complex motion stimuli were always uncontaminated by noise, but at psychophysical coherence threshold a complex motion stimulus is embedded in a stimulus that contains in the order of 90% noise. Single cell recordings in area MT have shown that these noisy stimuli are provocative for individual neurons (e.g., Britten and Newsome, 1998), but informal observations show that embedding our stimuli in noise results in considerable degradation of their perceptual quality.
For example, an expansion stimulus does not produce a compelling impression of looming when presented at coherence threshold. Although single-cell physiology points to greater representation for expansion than rotation (see above), a direct test of this prediction did not reveal a significant trend in our study. In this case, the variability amongst our observers (see Fig. 5) does have a clear parallel with visual psychophysics. For example, although some individuals have different coherence thresholds for rotation and expansion, there is no clear effect across studies (De Bruyn and Orban, 1990b; Snowden and Milne, 1996; Morrone et al., 1999; Burr and Santoro, 2001; Meese and Harris, 2001a; Meese and Anderson, 2002). Furthermore, at the lowest threshold for motion, rotation and expansion stimuli are similarly detectable (Freeman and Harris, 1992) and above threshold their speeds are similarly discriminable (Sekuler, 1992).

In sum, we conclude that the most provocative of the motion patterns tested in our study is that which approximates a looming stimulus. This is consistent with the greater urgency for action that would normally be associated with this type of stimulus.

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