



Peripheral sensitivity to biological motion conveyed by first and second-order signals

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ABSTRACT

There is evidence that human observers are more sensitive to the direction-of-heading of point-light walkers defined by first-order than second-order motions. We addressed this question by measuring the minimum direction difference (azimuth) that observers could discriminate when the dots composing the walkers were conveyed by first or second-order motions. Sensitivity to azimuth differences for four stimulus types (two first-order and two second-order) was tested at a range of stimulus sizes and at eccentricities of 0–16° in the right visual field. We find that for most stimulus types and eccentricities any azimuth threshold can be obtained by an appropriate adjustment of stimulus size. To achieve a given azimuth threshold second-order stimuli must be larger than the corresponding first-order stimuli. Therefore, stimulus magnification equates sensitivity to walker direction and we may say that sensitivity to walker direction is generally cue-independent. Similarly, in most cases stimulus magnification is sufficient to eliminate eccentricity dependent variability from the azimuth thresholds. Interestingly, the magnification required match peripheral to foveal thresholds increases faster with eccentricity for first-order stimuli than for second-order stimuli, while at the same time thresholds for first-order stimuli are lower than those for second-order stimuli at corresponding sizes and eccentricities.

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1. Introduction

For years vision scientists have been impressed by the vividness and subtly of the percepts that Johansson's (1973) point-light displays elicit. Many studies have addressed the kind of information that can be extracted from point-light displays (Barclay, Cutting, & Kozlowski, 1978; Blakemore & Decety, 2001; Dittrich, Troscianko, Lea, & Morgan, 1996; Mather & Murdoch, 1994; Pollick, Paterson, Bruderlin, & Sanford, 2001; Runeson, 1994; Troje, 2002a, 2002b). Other studies have addressed the stimulus conditions necessary for the recovery of these properties (Aen-Stockdale, Thompson, Hess, & Troje, 2008; Ahlstrom, Blake, & Ahlstrom, 1997; Bellefeuille & Faubert, 1998; Garcia & Grossman, 2008; Mather, Radford, & West, 1992). Studies in this latter group have frequently employed the walker direction discrimination task in which point-light walkers are heading $\pm 90^\circ$ to the left or right (Aen-Stockdale et al., 2008; Mather et al., 1992).

Standard point-light walkers are made of 11–15 white dots on a black background, or vice versa. In this case luminance contrast distinguishes the walker dots from the background. If the dots and background are replaced with two, equiluminant chromatici-

ties one can determine if colour contrast is sufficient to support the detection of biological motion (Garcia & Grossman, 2008). If the dots and background are two, equiluminant dynamic textures one can determine if second-order motion is sufficient to support direction discrimination in biological motions (Aen-Stockdale et al., 2008). If sensitivity to walker properties were independent of the type of contrast that distinguishes walker dots from the background then we would say sensitivity is *cue-independent*. In this paper we ask whether sensitivity to properties of point-light walkers depends on whether their constituent dots are first- or second-order (Cavanagh & Mather, 1989; Chubb & Sperling, 1988) motion signals.

Mather et al. (1992) were the first to address this question. Their walkers were composed of black and white dots that either remained fixed in luminance throughout a trial or changed polarity randomly from frame to frame. The polarity flipping manipulation is a standard method of neutralizing mechanisms sensitive to first-order information (Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Landy, Doshier, Sperling, & Perkins, 1991). Mather et al. employed the walker direction discrimination task. On each trial a single walker was presented heading either straight left or straight right. To increase the difficulty of the task 60 noise dots that changed position randomly from frame to frame were added to the displays. They found that direction discrimination accuracy was much

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higher for the first-order stimulus than the second-order stimulus. In contrast, Ahlstrom et al. (1997) showed that discriminating intact from phase-scrambled point-light human actions (walking, climbing, running, kicking and throwing) was unaffected by random polarity alternations. However, d' values for first- and second-order stimuli were extremely high (>3) meaning that performance was essentially on the ceiling. It is very likely that the main reason for the difference between the results of Mather et al. and Ahlstrom et al. was that Mather et al. used noise dots to limit performance whereas Ahlstrom et al. did not (Aaen-Stockdale et al., 2008).

Noise dots are frequently used to limit performance in biological motion tasks and, in fact, are often used to define thresholds and thus sensitivity to biological motion (Aaen-Stockdale et al., 2008; Ikeda, Blake, & Watanabe, 2005). Aaen-Stockdale et al. (2008) recently employed this technique to determine whether sensitivity to biological motion is cue-independent. They used a walker direction discrimination task in which walkers headed straight left or straight right. Thresholds were defined as the ratio of the number of walker dots to scrambled-walker noise dots (SNR) that brought direction discrimination to 75% correct. In one experiment the dots defining the walkers either maintained a constant polarity throughout a trial (fixed polarity; first-order stimuli) or changed polarity randomly (random polarity; second-order stimuli); this is essentially the same comparison made by Mather et al. (1992), who used scintillating noise dots, and Ahlstrom et al. (1997), who used scrambled-actor noise dots. Thresholds were found to be lower for the first-order stimuli than the second-order stimuli, thus replicating the original result of Mather et al. (1992). In a second condition the dots defining the walkers and noise differed from the background either in mean luminance (luminance modulation; first-order stimuli) or contrast (contrast modulation; second-order stimuli) and again the second-order stimuli produced higher thresholds than the first-order stimuli.

From these studies one might conclude that first and second-order stimuli are unequal in their ability to engage a system responsive to biological motions. However, another interpretation is that second-order stimuli are more susceptible to masking noise. When a point-light walker is presented in noise one could judge any of its properties, including direction of heading, sex, weight or mood, but to do this the walker must first be segregated from the noise. It might be that in the absence of noise first and second-order motions elicit similar sensitivities to walker properties (e.g., direction, sex, attitude) but second-order motions are more susceptible to noise.¹

The main reason noise is used in studies of biological motion is that performance would be on the ceiling without it (e.g., Ahlstrom et al., 1997); walkers heading $\pm 90^\circ$ from the line of sight present no challenge to the visual system. To obviate the use of noise (Roddy, Troje, & Gurnsey, 2009) inferred sensitivity to point-light walkers by measuring *azimuth thresholds* ($\Delta\theta$). Subjects had to discriminate between walkers heading to the left and walkers heading to the right, but the difference between the two orientations was varied and was generally much smaller than $\pm 90^\circ$. The azimuth thresholds ($\Delta\theta$) represent the smallest direction difference that can be detected at some fixed level of accuracy (in this case 81% correct in a 2AFC task). Measuring sensitivity to azimuth differences in the absence of noise eliminates segmentation as an essential component of the task.

¹ It is worth noting, however, that subjects show roughly equal sensitivity to first- and second-order radial, rotational and translational patterns when the depth of modulation of first- and second-order dots reach asymptotically high levels (Aaen-Stockdale, Ledgeway, & Hess, 2007).

It is obviously of interest to determine whether sensitivity to properties of point-light walkers depends on the motion cues (e.g., first- or second-order motions) that define the walker. As mentioned, Aaen-Stockdale et al. (2008) reported that first-order stimuli elicit lower SNR thresholds than second-order stimuli, however, they also showed that if the contrast in first-order walker dots is reduced sufficiently they can be masked by second-order dots. This suggests that first- and second-order signals provide input to a common biological motion system but does not answer why, when first- and second-order signals are at maximal contrast, the first-order signals produce lower noise thresholds. The answer may have to do with the sizes of the first- and second-order dots used. Luminance can be determined, in principle, at a single point whereas contrast is a measure requiring luminance measurements at a minimum of two points. Therefore, one would expect that any comparison between point-light walkers conveyed by first and second-order dots of identical size (as in the case of Aaen-Stockdale et al. (2008)) should favour the first-order stimuli. In other words, sufficient magnification of the second-order walkers might have elicited comparable sensitivities. This may offer a second reason why Aaen-Stockdale et al. found that sensitivity to walkers conveyed by first-order motion was greater than to walkers conveyed by second-order motion.

Our approach to comparing sensitivity to walker direction, when walkers are conveyed by first- and second-order motion signals, is to measure azimuth thresholds as a function of stimulus size. We would predict that for any fixed stimulus size azimuth thresholds would be lower for first-order stimuli than second-order stimuli. A corollary would be that the threshold achieved for any first-order stimulus could also be achieved for some second-order stimulus that is sufficiently magnified.

Measuring thresholds at a range of sizes also makes it possible to assess size dependent changes in threshold across the visual field. The vast majority of studies concerned with first- and second-order motion have involved stimulus presentations at or near fixation. Of course the foveal representation on the cortex far exceeds the proportion of the visual field it represents. Therefore a full understanding of sensitivities to first- and second-order motions, biological motions and their interactions requires measuring sensitivity at a range of eccentricities.

In the present paper we measure azimuth thresholds for first- and second-order point-light walkers at a range of sizes and eccentricities. Our walkers are defined by luminance and contrast modulated dots that are similar, but not identical, to those used by Aaen-Stockdale et al. (2008). We create two versions of both first- and second-order stimuli. In one case the contrast is higher in the walker dots than the background and in the other case the contrast is lower in the walker dots than the background.

2. Experiment 1

2.1. Method

2.1.1. Participants

The participants were two experienced psychophysical observers (GR and P1). Both were female and had normal or corrected-to-normal vision, as assessed by the Freiburg acuity test (Bach, 1996).

2.1.2. Apparatus

The experiments were conducted using a MacPro Computer equipped with a 21-in. multi-scan monitor with the refresh rate set to 85 Hz. All aspects of stimulus generation, presentation and data collection were under the control of MATLAB (Mathworks, Ltd.) with the Psychophysics Toolbox 3 extensions (Kleiner, Brainard, & Pelli, 2007). An adjustable chin rest was used to steady

the participants' gaze. Participants responded on a wireless keyboard.

2.1.3. Stimuli

Point-light walkers were generated from the system first described in 2002 (Troje, 2002a) and further elaborated in 2008 (Troje, 2008). Starting with a Fourier-based representation of human walking, the model encodes the first 20 principal components of a data set representing 100 motion-captured walkers (50 male, 50 female). To synthesize a unique walker we used a vector of 20 numbers (α), representing the weights on the first 20 principle components. The three-dimensional (x, y, z) coordinates for each of 15 points can be generated and projected (orthographically) to the 2D monitor. If all elements of α are set to zero then a neutral, average walker is generated representing the origin of "walker space." Any other vector can be viewed as a direction through walker space and the length of the vector determines how different the walker is from the average walker. Drawing a sample of 20 random numbers generates a random direction in walker-space. If α is such a vector then its length, and thus the distinctiveness of the walker, can be varied by multiplying it by a constant ω .

At each eccentricity seven logarithmically spaced stimulus sizes were chosen such that $\Delta\theta$ thresholds ranged from asymptotically low to roughly 30–70°; these sizes were determined in pilot experiments. The stimuli were presented in the right visual field at eccentricities of 0°, 1°, 2°, 4°, 8° and 16°. Eccentricity of stimulus presentation, defined relative to the center of the stimulus, was manipulated by varying the position of the fixation dot; the stimuli were always presented in the centre of the screen and viewed binocularly.

On each trial a novel walker was created by drawing each coefficient of α from a standard normal distribution. The resulting walker was made to move to the left or right by rotating it about the y -axis. The angle $\Delta\theta$ expresses the orientation of the walker with respect to the frontal view. The objective of the experiment was to find $\Delta\theta$ thresholds for a range of stimulus sizes at eccentricities from 0° to 16° in the right visual field.

There were four conditions in the experiment representing the factorial combination of two variables, each with two levels; viz. (a) first-order vs. second-order motions and (b) dot vs. background contrast. These combinations are shown in Fig. 1. Two of the four stimuli involved second-order motions (panels A and B) and two represented first-order motions (panels C and D). For the second-order stimuli the walker dots had the same mean luminance as the background and for first-order stimuli, which also contained second-order information², the walker dots differed in mean luminance from the background. For two of the four conditions the walker dots had zero contrast and the background noise had high contrast (panels A and C) and for two conditions the walker dots comprised high-contrast noise and the background had zero contrast (panels B and D).

There were two first-order and two second-order stimuli in the experiment. All stimuli were created through α -blending a field of binary checks (C) with a *luminance map* (L) that defines the mean luminance of the dots (L_{dots}) and background (L_{BG}). The α -values scale the luminance range of the checks ($\alpha C_{\text{max}} - \alpha C_{\text{min}}$) at a point. Therefore, the α -map specifies the luminance range in the walker dots (α_{dots}) and background (α_{BG}). C , L and α all take values in the range 0–1. The normalized luminance profile of the stimulus (S) on one frame is defined as:

$$S = \alpha C + (1 - \alpha)L \quad (1)$$

It is important to keep in mind that L and α are not constant across space but specify the mean luminance and luminance range of the noise field C at each point in the image; some regions of α have values of α_{dots} and others have values of α_{BG} ; some regions of L have values of L_{dots} and others have values L_{BG} ; once again, these are respectively the α -map and *luminance-map*.

For second-order stimuli $L_{\text{dots}} = L_{\text{BG}} = .5$. In one condition the walker dots had luminance range $\alpha_{\text{dots}} = 0$ and background checks had luminance range $\alpha_{\text{BG}} = .9$. A single frame of this kind of stimulus is shown in Fig. 1A. In a second condition the walker dots had luminance range $\alpha_{\text{dots}} = .9$ and background checks had luminance range $\alpha_{\text{BG}} = 0$. A single frame of this kind of stimulus is shown in Fig. 1B.

The first-order stimuli were modifications of the second-order stimuli such that the low contrast region had a luminance of .9 rather than .5. When the walker dots had luminance range $\alpha_{\text{dots}} = 0$ and background checks a luminance range $\alpha_{\text{BG}} = .9$, the walker dots had a mean luminance of $L_{\text{dots}} = .9$ and the background checks have mean luminance of $L_{\text{BG}} = .5$. A single frame of this kind of stimulus is shown in Fig. 1C. When the walker dots had luminance range $\alpha_{\text{dots}} = .9$ and background checks a luminance range $\alpha_{\text{BG}} = .0$, the walker dots had a mean luminance of $L_{\text{dots}} = .5$ and the background have mean luminance of $L_{\text{BG}} = .9$. A single frame of this kind of stimulus is shown in Fig. 1D. Note that panels A and C show that when the noise formed the background it was contained within a circular region whose radius was always proportional to stimulus size.

For all stimuli, the walker dot diameters were always 1/24 of the stimulus height and the height and width noise checks were always 1/4 of dot diameter. Stimuli varied in size over an 83-fold range for subject P1 and over a 56-fold range for subject GR. Stimulus size was manipulated by varying viewing distance and/or stimulus size on the monitor. The binary checks alternated randomly between black and white on each frame.

2.1.4. Procedure

On each trial a single walker was presented going through one full gait cycle (approximately 1.2 s) starting at a randomly chosen point (phase) of the cycle. Throughout the trial the participant maintained fixation on a small green dot on the monitor. At the end of each trial the dot turned red and remained red until the participant entered a valid response; 1 to indicate left and 2 to indicate right. When an error was made a 300 Hz tone sounded for 200 ms. An adaptive procedure (QUEST) was used to determine threshold at each stimulus size and eccentricity; threshold is the $\Delta\theta$ eliciting 81% correct in a 2AFC task.

Both subjects had had extensive experience with point-light walker stimuli but prior to data collection both received sufficient practice to become familiar with the task. As part of this practice we determined the approximate size limits on performance. That is, at each eccentricity for each subject we determined the smallest stimulus sizes for which meaningful thresholds could be measured (i.e., $-90^\circ < \theta < 90^\circ$). We also attempted to determine stimulus size at which thresholds become asymptotically small with respect to size. Within these limits seven logarithmically spaced stimulus sizes were chosen.

2.2. Results

The results of Experiment 1 are summarized in Fig. 2. The four rows of panels depict the results from the four conditions of the Experiment. Rows A–D correspond to panels A–D from Fig. 1, respectively. The insets in the bottom left of each of the leftmost panels convey the properties of the stimuli. The left two columns

² We refer to the two stimulus types as first- and second-order to distinguish between stimuli that contain first-order energy (first-order) or not (second-order). A more cumbersome, but also more accurate terminology would be "signals with and without first-order information."

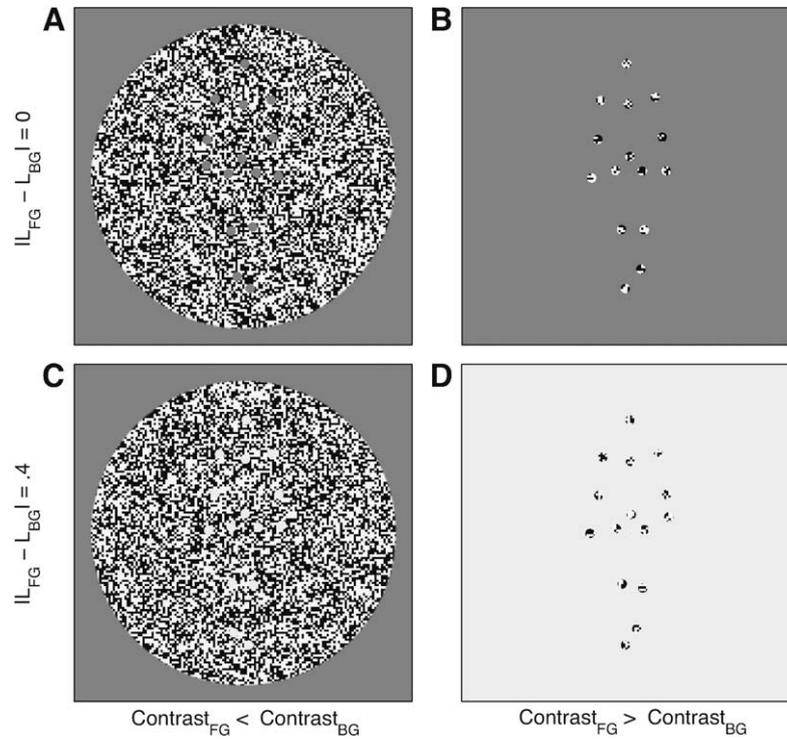


Fig. 1. Examples of the four stimulus types used in the experiment. (A) A second-order walker with high contrast dots in the background. (B) A second-order walker with zero contrast in the background. (C) A first-order walker with high contrast dots in the background. (D) A first-order walker with zero contrast in the background.

show data for GR and the right two panels show results for P1. For each subject we show the raw data for each condition (columns 1 and 3) and the best fit of the data to a parametric curve (columns 2 and 4).

Fig. 2 shows that as stimulus size (σ) increases $\Delta\theta$ thresholds decrease until they reach minima of about 2.5° in most cases. Therefore, at each eccentricity $\Delta\theta$ thresholds can be described by the following negatively accelerated curve

$$\Delta\theta' = \Delta\theta_{\min}(1 + a/\sigma)^b \quad (2)$$

where $\Delta\theta_{\min}$, a and b are free parameters. Because the curves in columns 1 and 3 are shifted versions of each other this suggests that determining $F_E = 1 + E/E_2$ would allow us to collapse all data onto a single curve:

$$\Delta\theta' = \Delta\theta_{\min}[1 + a/(\sigma/F_E)]^b \quad (3)$$

In this case σ/F_E represents *scaled* stimulus size.

For each subject, values were found for $\Delta\theta_{\min}$, a , b and E_2 that minimized the deviation of the data from the parametric curve. The quality of the fit is reported as r^2 to express the proportion of variability in the data explained by the fit; the correlation was formed between $\log(\Delta\theta)$ and $\log(\Delta\theta')$. The data were fit using the error minimization routine (fminsearch) provided in MATLAB (Mathworks Ltd.).

2.2.1. Second-order stimuli

Row A of Fig. 2 summarizes the results for the second-order stimuli for which the walker dots had zero contrast and were embedded within a larger surround of noise checks that had high contrast (see Fig. 1A). The first and third columns of Fig. 2 show the raw data for GR and P1, respectively and the second and fourth columns show the best fits to the data. A notable feature of the data is that subjects could not do the task at 8° and 16° . This is very unusual in this type of study and is most likely a consequence of peripheral sensitivity to noise. Furthermore, stimuli had to be very

large before thresholds could be measured. For GR at 0° (i.e. at fixation) stimulus sizes range from 4.25° to 12° and for P1 stimulus sizes range from 2.25° to 7° . A quick glance at the remaining panels of the figure shows that in other conditions thresholds can be obtained with much smaller stimuli.

The E_2 values were relatively large (3.11 and 2.56 for GR and P1 respectively $\bar{E}_2 = 2.84$). This means that stimuli could be moved about 3° into the periphery before stimulus size had to double to equal foveal performance. This can be appreciated by noting that the four curves (0° , 1° , 2° and 4°) in panels A and C are not widely separated. In other words, there are rather modest changes in performance from 0° to 4° .

Row B of Fig. 2 shows the results for the second-order stimuli for which the walker dots had high contrast and were embedded within a larger surround that had zero contrast (see Fig. 1B). Thresholds could be measured at all eccentricities for both subjects. The E_2 values were again relatively large (2.56 and 1.52 for GR and P1 respectively, $\bar{E}_2 = 2.04$). This means that stimuli could be moved about 2° into the periphery before stimulus size had to double to equal foveal performance. For both subjects thresholds were obtained at a range of sizes much lower than in the obverse condition. For GR at 0° stimulus sizes ranged from 1.2° to 5° and for P1 stimulus sizes range from $.75^\circ$ to 3° .

The second-order conditions reveal an asymmetry. For a given stimulus size, dynamic walker dots embedded in a homogenous (zero contrast) background (Fig. 1B) produce much lower thresholds than zero contrast walker dots embedded in a dynamic background (Fig. 1A). This asymmetry is undoubtedly a consequence of the statistical properties of the displays; a region of activity (dynamic noise) in a region of inactivity (zero contrast) is more salient than the obverse case.

2.2.2. First-order stimuli

Row C of Fig. 2 summarizes the results for the first-order stimuli for which the walker dots had lower contrast and higher lumi-

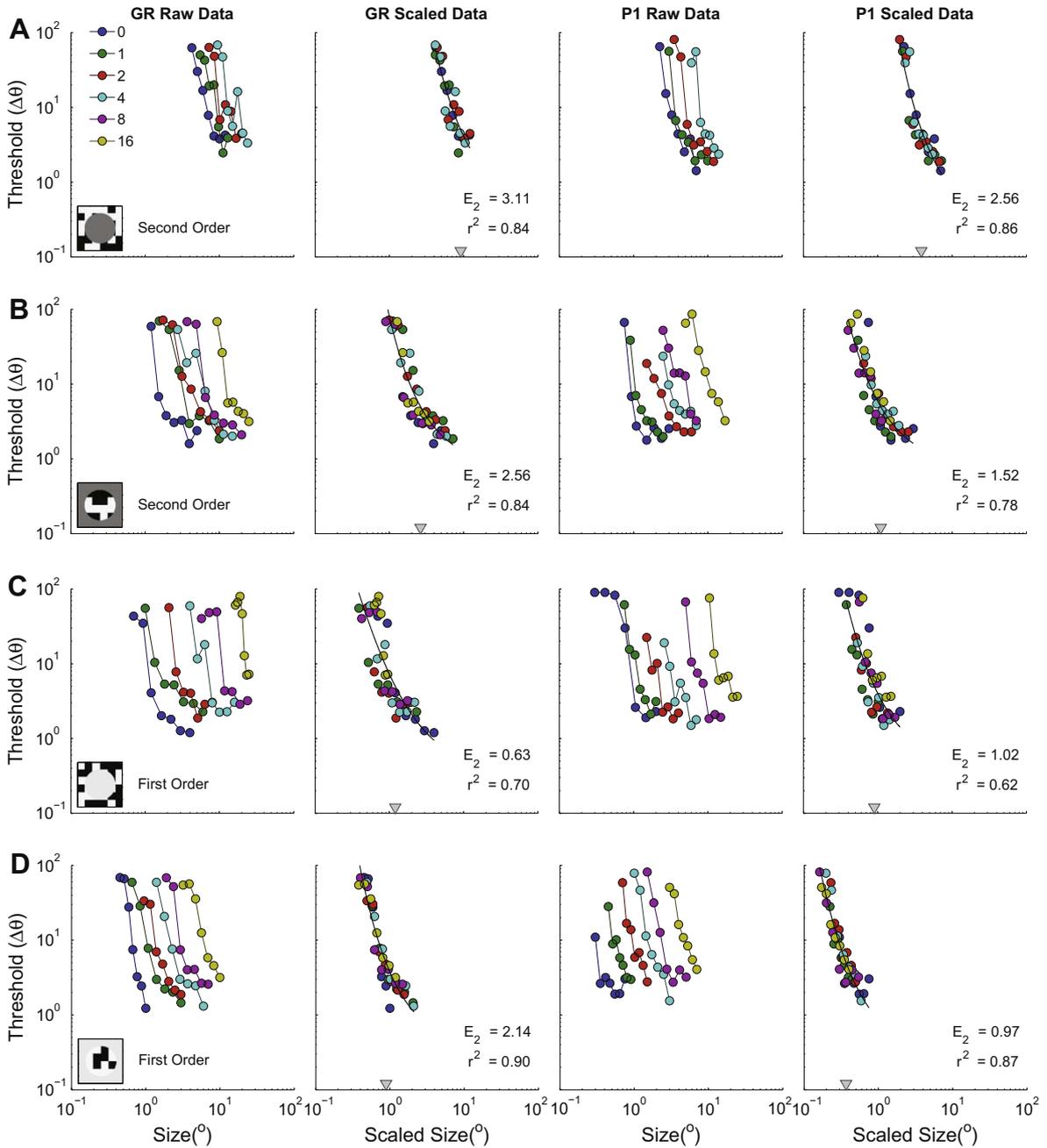


Fig. 2. Results of the experiment. The first and third columns present raw data for GR and P1 respectively. The second and fourth columns present scaled data for GR and P1 respectively. The conditions depicted in rows A–D correspond to panels A–D of Fig. 1 respectively.

nance than the background (see Fig. 1C). Thresholds could be measured at all eccentricities for both subjects. The E_2 values were very small (.63 and 1.02 for GR and P1 respectively, $\bar{E}_2 = .825$). For both subjects thresholds were obtained at a range of sizes much lower than in the two second-order conditions; the foveal functions, onto which the peripheral data have been collapsed (second and fourth columns), are shifted much further to the left than the foveal functions for the second-order data in the two rows above. There is an indication in the raw data for GR that size scaling is *not* sufficient to equate thresholds across the visual field. For subject GR the minimum threshold at 16° is six times greater than that at 0°. It is possible that the large threshold at 16° ($\Delta\theta = 7.25$) would be reduced if larger sizes were used. This threshold was obtained with a stimulus that was 24° in height, which would correspond to a 6 ft person

viewed at 14 feet. Therefore, biologically plausible increases in size are possible.

Row D of Fig. 2 summarizes the results for the first-order stimuli for which the walker dots had higher contrast and lower luminance than the background (see Fig. 1D). Thresholds could be measured at all eccentricities for both subjects. The E_2 values were mixed (2.14 and .97 for GR and P1 respectively, $\bar{E}_2 = 1.555$). Thresholds in this condition were obtained at smaller sizes than in any other condition. Also note that the curves in the second and fourth columns are shifted further to the left than in any other condition.

2.2.3. Size at matched thresholds

Each panel in the second and fourth columns of Fig. 2 shows an inverted triangle on the x-axis. This indicates the stimulus size

corresponding to $\Delta\theta' = 5^\circ$, determined by solving for size ($\sigma_{\Delta\theta'}$) in the function fit to the data:

$$\sigma_{\Delta\theta'} = \frac{a}{(\Delta\theta'/\Delta\theta_{\min})^{1/b} - 1} \quad (4)$$

In each row $\sigma_{\Delta\theta'}$ shifts closer to the y-axis, indicating that the stimuli in Fig. 1 panels A–D, respectively, permit thresholds to be obtained at progressively smaller sizes. Fig. 3 summarizes these data in two ways. The left panel of Fig. 3 plots the mean $\sigma_{\Delta\theta'}$ ($\Delta\theta' = 5^\circ$) for each of the four conditions and the error bars represent the estimated standard error of the mean. The error bars suggest some degree of variability in the data but this is attributable almost entirely to subject differences, not interactions between subjects and conditions. Subject P1 showed greater sensitivity to walkers in the sense that her $\sigma_{\Delta\theta'}$ values were typically half those of GR. To factor out subject effects we divided each $\sigma_{\Delta\theta'}$ by the subject's mean $\sigma_{\Delta\theta'}$ value. The means of these normalized values are shown in the right panel of Fig. 3. There is clearly little variability in the mean scores thus showing that there are systematic differences in the $\sigma_{\Delta\theta'}$ values. The data show that performance between different first and second-order stimuli can be matched (at say $\Delta\theta' = 5^\circ$) but the size required to achieve this differs; second-order stimuli must be larger than the first-order stimuli to achieve the same threshold. Furthermore, the asymmetry for both first- and second-order stimuli is clearly evident; to achieve equivalent performance stimuli must be larger when the background comprises high-contrast noise than in the obverse case.

3. General discussion

The objective of the present study was to assess sensitivity to walker direction, without using noise tolerance to define sensitivity, in order to separate the issue of segmentation from sensitivity to walker direction. Our general conclusion is that sensitivity to walker direction in cue-independent. In all conditions tested we found that azimuth ($\Delta\theta$) thresholds were size dependent. The conclusion would have been different if we had considered only stimuli of a single fixed size. Consider the scaled data of P1 (fourth column) in row D of Fig. 2. The inverted triangle on the x-axis shows the stimulus size ($\sigma_{\Delta\theta'} = 0.37$) at fixation eliciting $\Delta\theta' = 5^\circ$ for a first-order stimulus with zero-contrast background. For the corresponding second-order stimulus (Fig. 2, fourth column of row B) this stimulus size (0.37°) would not have produced a measurable threshold. Similarly the inverted triangle on the x-axis of the scaled data of P1 (fourth column) in row C shows the stimulus size ($\sigma_{\Delta\theta'} = 1.10$) at fixation eliciting $\Delta\theta' = 5^\circ$ for a first-order stim-

ulus with high-contrast background. For the corresponding second-order stimulus (Fig. 2, fourth column of row A) this size (1.10°) would not have produced a measurable threshold. However, as indicated in Fig. 2, almost any $\Delta\theta'$ can be achieved for all first and second-order stimuli at fixation with appropriate stimulus magnification. This is generally true of all eccentricities, except for the second-order stimulus with low contrast walker dots (Fig. 2, row A). It seems therefore, that the mechanism that encodes/discriminates the direction of heading of a point-light walker is generally indifferent to the nature of the image motion that defines the points. However, the inputs to these mechanisms require stimuli of different sizes.

The relationship between contrast in the dots and contrast in the background partly determines the stimulus size required to achieve a particular azimuth threshold (Fig. 3). When $\Delta\theta' = 5^\circ$ (on the best fitting function) for second-order stimuli with the high-contrast noise in the background (Fig. 1A) stimuli must be 3.51 times larger on average than in the obverse case (Fig. 1B) ($\sigma_{\Delta\theta' \text{ HighC}}/\sigma_{\Delta\theta' \text{ Zero}} = 3.48$ and 3.53 for GR and P1 respectively). For first-order stimuli with the high-contrast noise in the background (Fig. 1C) stimuli must be 1.90 times larger on average in the obverse case (Fig. 1D) ($\sigma_{\Delta\theta' \text{ HighC}}/\sigma_{\Delta\theta' \text{ Zero}} = 1.35$ and 2.44 for GR and P1 respectively).

These results are consistent with well-known asymmetries in the texture discrimination (Enns, 1986; Gurnsey & Browse, 1987, 1989; Potechin & Gurnsey, 2006; Rubenstein & Sagi, 1990, 1996) and visual search (Rosenholtz, 2001; Rosenholtz, Nagy, & Bell, 2004; Treisman & Gormican, 1988; Treisman & Souther, 1985) literatures. Such asymmetries can arise when two signals have unequal variances and sizes. The strength of the motion signal arising from the walker dots can be characterize as d' :

$$d' = \frac{|\bar{x}_{\text{dots}} - \bar{x}_{\text{BG}}|}{\sqrt{p_{\text{dots}}s_{\text{dots}}^2 + p_{\text{BG}}s_{\text{BG}}^2}} \quad (5)$$

where \bar{x}_{dots} and \bar{x}_{BG} are the mean responses in the dot and background regions respectively, s_{dots}^2 and s_{BG}^2 are the corresponding variances, and p_{dots} and p_{BG} are proportions (thus summing to 1) representing the relative sizes of the two regions. The measures in question could be luminance (first-order) or energy (second-order). Assuming that $(\bar{x}_{\text{dots}} - \bar{x}_{\text{BG}})$ does not depend on whether the dots or background have the higher contrast then the magnitude of d' depends on the variances and relative sizes of the two regions. Further assuming that $p_{\text{dots}} \ll p_{\text{BG}}$ it is clear that d' will be larger when $s_{\text{dots}}^2 > s_{\text{BG}}^2$ than when $s_{\text{dots}}^2 < s_{\text{BG}}^2$; assuming that both s_{dots}^2 and s_{BG}^2

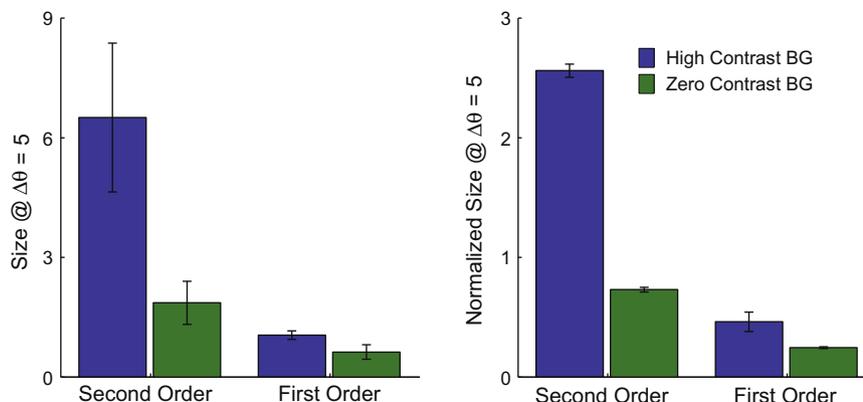


Fig. 3. Stimulus sizes required to elicit $\Delta\theta' = 5^\circ$ in each of the four conditions of the experiment. (A) Average data from two subjects for each of the four conditions. (B) Average normalized data from two subjects for each of the four conditions; $\Delta\theta'$ values were for each subject were divided by the average of the four $\Delta\theta'$ for each subject. Error bars represent \pm estimated SEM.

take on one of two values. This explains the size asymmetry within both first- and second-order stimuli.

The need for larger second-order than first-order stimuli to achieve equivalent thresholds can be cast in similar terms. When $\Delta\theta = 5^\circ$ for high-contrast backgrounds (Fig. 1, panels A and C) the second-order stimulus must be 5.96 times larger on average than the corresponding first-order stimulus ($\sigma_{\Delta\theta'}(\text{SO})/\sigma_{\Delta\theta'}(\text{FO}) = 7.62$ and 4.30 for GR and P1 respectively). For low contrast backgrounds (Fig. 1, panels B and D) the second-order stimulus must be 2.97 times larger on average than the corresponding first-order stimulus ($\sigma_{\Delta\theta'}(\text{SO})/\sigma_{\Delta\theta'}(\text{FO}) = 2.96$ and 2.98 for GR and P1 respectively). As noted in Section 1 first principles indicate that a reliable d' (from Eq. (4)) requires integrating over a larger region of space for second-order vs. first-order signals; this is borne out by the results.

At this point it is worth revisiting the fact that walkers were uniformly magnified so that walker and dot sizes were not independent. Therefore, in the two contrasts between first and second-order stimuli just considered, not only were the dot sizes 5.96 and 2.96 larger in the second-order than first-order cases, so too were the walkers themselves. Thus, one might argue that walker size might have made a contribution independently of dot size. Assuming that size increases lead to lower $\Delta\theta$ thresholds then one might argue that we have underestimated the magnification needed to equate sensitivity to first- and second-order dots. One could verify this by reducing the walker sizes (in the cases discussed in the preceding paragraph) by factors of 5.96 and 2.96 respectively, without changing dot size, then re-measuring $\Delta\theta$ thresholds.

Such a comparison seems questionable, however, because as dot size increases relative to walker size the dots would begin to occlude each other, the realism of the walker would be diminished and consequently, thresholds are more likely to increase than decrease. Specifically, in the case of low contrast dots in a high-contrast background (Fig. 1A) a sixfold increase in dot size (relative to walker size) would make each dot 1/4 walker size rather than 1/24 walker size as in the experiment. Similarly, in the case of high contrast dots in a low contrast background (Fig. 1C) a threefold increase in dot size (relative to walker size) would make each dot 1/8 walker size rather than 1/24 walker size as in the experiment. Once again, we may have underestimated the magnification required to equate sensitivity to first and second-order dots, and subsequent studies could test this directly outside the context of biological motion. Within the context of biological motion, that point remains that across a wide variety of stimulus conditions and eccentricities, almost any $\Delta\theta$ threshold can be obtained with sufficient uniform magnification.

Size scaling eliminated most eccentricity dependent variability from the data, although some fits were clearly better than others. E_2 -values tended to be larger for second-order stimuli than first-order stimuli; $E_2 = 2.44$ and 1.19 respectively, meaning that on average sensitivity dropped more quickly with eccentricity for first-order stimuli ($E_2 = 1.19$) than for second-order stimuli ($E_2 = 2.44$). This might seem counter-intuitive but it must be borne in mind that E_2 is a *relative* measure of how much threshold functions change with eccentricity. First-order foveal functions are shifted further left than second-order foveal functions and the remaining curves are more widely separated across eccentricities. Therefore, the rapid decline with eccentricity for first-order stimuli is not a reflection of poor absolute sensitivity in the periphery, relative to second-order stimuli. In fact, at all eccentricities, the size eliciting a particular azimuth threshold ($\Delta\theta$) is smaller for a first-order stimulus than its second-order counterpart.

The larger E_2 values for second-order stimuli simply mean that the rate at which the sizes of second-order mechanisms increase with eccentricity is relatively slow compared with the rate at

which first-order mechanisms change size with eccentricity. But then, one might ask, why was it impossible to measure thresholds at 8° and 16° for second-order stimuli with high-contrast noise backgrounds (Fig. 1, panel A; Fig. 2, row A)? This is a reasonable question. For subjects GR and P1 the stimulus size ($\sigma_{\Delta\theta'}$) eliciting $\Delta\theta' = 45^\circ$ at fixation were 4.482° and 2.149° , respectively. The E_2 values determined from the first four eccentricities were 3.11 and 2.56, for GR and P1 respectively. Together these data suggest that for GR a stimulus of $4.482 \times (1 + 8/3.11) = 16.01^\circ$ should elicit a threshold of 45° at 8° eccentricity. For P1 a stimulus of $2.149 \times (1 + 8/2.56) = 8.865^\circ$ should elicit a threshold of 45° at 8° eccentricity. The largest stimulus available given the experimental set up was 24° so both of these values (16.01 and 8.865) were within the range of sizes tested, yet we were unable to obtain thresholds from either subject.

The linear extrapolation – just given – from the data at 0° to 4° suggests that we should have been able to achieve thresholds of 45° (and perhaps less) within the range of sizes tested. The fact that we could not suggests that size scaling fails to compensate for eccentricity dependent sensitivity loss for eccentricities beyond 4 – 8° . Anecdotal reports from the subjects (and one from another participant for whom a complete data set was not obtained) indicate that in this condition (Fig. 1A) the dynamic noise simply overwhelms the walker dots at large eccentricities. Thus, even though our paradigm was devised to avoid confounding sensitivity to biological motion and noise sensitivity, the nature of the second-order stimulus (Fig. 1A) reproduced a situation similar to that of Ikeda et al. (2005) who found that size scaling was insufficient to compensate for noise sensitivity in the periphery. Our results may reveal that noise sensitivity increases non-linearly with eccentricity, otherwise we should have been able to measure thresholds at 8° , at least. We note, however, that the failure of size scaling does not apply in the corresponding first-order stimuli (Fig. 1C; Fig. 2, row C), except possibly for GR at 16° . In this case thresholds were obtained at all eccentricities. Therefore, increased sensitivity to noise with eccentricity may interact with the nature of the motion signal (contrast vs. luminance modulation) that conveys walker motion.

Very few studies have examined sensitivity to second-order information across the visual field from a magnification perspective, and those that have involved static stimuli (Poirier & Gurnsey, 2002, 2005; Vakrou, Whitaker, & McGraw, 2007). Poirier and Gurnsey (2002) showed that two magnification factors were required to equate the discrimination of subjective contours across the visual field. One magnification factor ($E_2 = 1.82$) compensated for a loss of sensitivity to the carrier grating and the second compensated for loss of sensitivity to the contour itself ($E_2 = .67$). In the present study we did not vary dot size independently of check size (i.e., carrier size) so we are unable to determine whether separate magnifications were required to equate sensitivity. As noted by Poirier and Gurnsey a single magnification factor may often explain a substantial proportion of eccentricity dependent variation in the data, even when two different limitations are in fact present. This may explain why Vakrou et al. (2007), who examined essentially the same question as Poirier and Gurnsey, using Gabor patches oriented $\pm 45^\circ$ to modulate the contrast in sine wave gratings or random noise, found that a single scaling factor (E_2 of about 2, on average) compensated for eccentricity dependent sensitivity loss. This average E_2 is comparable to the average of 2.44 found here for second-order signals. Therefore, it remains to be seen if there are actually two limitations at play in the current second-order stimuli.

The present results are consistent with the notion that identification of walker direction is cue independent over a very large range of $\Delta\theta$ values. For most conditions and eccentricities, an arbitrary $\Delta\theta$ threshold can be obtained with an appropriate adjustment of stimulus size. These results support our suggestion that Aaen-Stockdale et al. (2008) found lower thresholds for first-order

stimuli in part because their stimuli were equal in size. Had they been different, thresholds may have been more similar. Aaen-Stockdale et al. equated strength (what they call visibility) of first and second-order motions by reducing the luminance contrast in the first-order stimuli. When the luminance was reduced sufficiently then noise thresholds were similar and first and second-order dots interacted to mask each other. These two manipulations (stimulus magnification and contrast attenuation) illustrate the univariate nature of the biological motion system. It seems that the direction discrimination threshold achieved depends on the strength of the input it receives from lower level mechanisms, irrespective of the cue that provides the signal. However, our results do not address the question (discussed in Section 1) whether the conduit for second-order motion is more sensitive to noise than that for first-order motion (but again, cf. Aaen-Stockdale et al., 2007).

The conclusion that walker direction discrimination is cue-independent may seem, *prima facie*, inconsistent with a recent report showing that detection of biological motion fails at isoluminance when walker dots contrast with the background in colour (yellow dots on a gray background). Garcia and Grossman (2008) asked subjects to discriminate displays consisting of point-light actions (e.g., walking, running, jumping) from those consisting of scrambled versions of these actions. Their concern was different from ours; they wanted to determine whether motion signals were required to extract representations of biological motion, as opposed to the information in static frames – hence they used $S/(L + M)$ colour contrast, which is reported to be particularly insensitive to motion. Our question is whether discriminating biological motions is cue-independent. Garcia and Grossman found that sensitivity – defined as the number of noise dots eliciting 79% correct detection accuracy – declined precipitously as the luminance contrast approached 0, which might indicate extreme cue dependence. However, this interpretation may be unjustified because we are simply more sensitive to luminance ($L + M$) contrast than blue–yellow contrast ($S/(L + M)$). The dots used by Garcia and Grossman were very small ($.17^\circ$) and presented 2.2° from fixation. If a $.17^\circ$ dot can be equated to half a cycle of a grating then we could relate it (very roughly) to a three cycle per degree grating. Recent data (Vakrou, Whitaker, McGraw, & McKeefry, 2005) show that sensitivity to a 3 cpd $S/(L + M)$ at the fovea is very low (about 2) and about 13 times lower than sensitivity to luminance contrast. To achieve a 10-fold increase in sensitivity at fixation the $S/(L + M)$ grating would have to be lowered to .2 cpd, which is a 15-fold magnification of the stimulus. Details aside it is clear that sensitivity to colour contrast increases with stimulus size and hence the loss of sensitivity to walker direction at isoluminance might be offset by an increase in stimulus size. Therefore, the results of Garcia and Grossman are not decisive concerning the cue-independence of biological motion.

Several recent reports have shown that identification of point-light walkers and discrimination of their direction of heading can be equated across the visual field if stimuli are sufficiently magnified (Gibson, Sadr, Troje, & Nakayama, 2005; Gurnsey, Roddy, Ouhanna, & Troje, 2008; Roddy et al., 2009). These and the present results are consistent with data showing that stimulus magnification equates identification of structure defined by relative motion and texture across the visual field (Gurnsey, Poirier, Bluett, & Leibov, 2006). Therefore, the evidence does not support the notion that there are qualitative changes in sensitivity to biological motion across the visual field (cf. Ikeda et al., 2005).

First-order stimuli produce a mean E_2 value of 1.19°. This compares reasonably well with previous estimates of E_2 reported for point-light walkers. Roddy et al. (2009) found an average E_2 value of .95 ($N = 4$, estimated SEM = .051, 95% confidence interval = .79 to 1.11) in a task identical in all respects to the present task, except that the walker dots were white on a black background. Similarly,

Gurnsey et al. (2008) found an average E_2 value of 0.87 ($N = 6$, estimated SEM = .136, 95% confidence interval = 0.53–1.22) for point-light walkers, defined by white dots on a black background, heading $\pm 4^\circ$ from straight-ahead. We note that the mean E_2 value of 1.19° is somewhat inflated by the uncharacteristically high E_2 value of 2.14 found for GR for the first-order condition with a low contrast background. With this data point removed, the average E_2 value for first-order stimuli was .87, which fits very well with the mean values reported by Gurnsey et al. (2008) and Roddy et al. (2009).

A distinction has been made (Wilson, Levi, Maffei, Rovamo, & DeValois, 1990) between tasks requiring analysis of spatial detail (spatial tasks) and those involving detection of simple targets such as gratings (resolution tasks). Resolution tasks show more gradual eccentricity dependent sensitivity loss (E_2 values of 2.5 and greater) than spatial tasks (E_2 values of 1 and less) (See Wilson et al., 1990 for a review). The E_2 values for first-order stimuli in the present experiments and related experiments (Gurnsey et al., 2008; Roddy et al., 2009) are clearly in the range typically associated with spatial tasks. This suggests that the limits on walker direction discrimination, for first-order stimuli, are not simple limits on detecting the stimulus itself, as might be imposed by retinal sampling, but limits on extracting information from the display that reveals walker direction.

Associating E_2 values with specific cortical loci can be a challenge because the variability within and between psychophysical tasks (Whitaker, Mäkelä, Rovamo, & Latham, 1992) can be great and the estimated E_2 associated with specific brain regions can also be highly variable. Although brain mapping studies (Serenio et al., 1995; Tyler et al., 2005; Wandell, Dumoulin, & Brewer, 2007) have been among the most important contributions of fMRI research, they have been more successful at identifying borders between brain regions than providing converging evidence for cortical magnification factors characterized by E_2 . Thus, the once hoped for linking propositions (Teller, 1984) between psychophysically determined E_2 values and those determined from physiological and imaging experiments appear beyond reach at the moment.

5. Limitations

In general we can say that stimulus magnification is sufficient to equate walker direction discrimination across the visual field for both first- and second-order stimuli. It must be borne in mind, that for second-order stimuli with high-contrast backgrounds thresholds cannot be achieved at 8° and 16° . Furthermore, we noted that in one condition GR's data at 16° did not reach the same asymptotically low value found at 0° (Fig. 2, row C, column 1). For eccentricities $1\text{--}8^\circ$ in this condition thresholds fall to the same low level. We noted that the discrepancy between 0° and 16° might reflect the limitations of our set up and that further stimulus magnification might have yielded lower thresholds. On the other hand it may also be that for this subject the noise in the background impaired performance as it did for both subjects in the corresponding second-order condition (Fig. 2, row A).

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