Vision Research 48 (2008) 2827–2834

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Stimulus magnification equates identification and discrimination of biological motion across the visual field ☆,☆☆

Rick Gurnsey [a,*], Gabrielle Roddy [a], Marouane Ouhnana [a], Nikolaus F. Troje [b]

[a] Department of Psychology, Concordia University, 7141 Sherbrooke Street West, Montreal, Que., Canada H4B 1R6
[b] Department of Psychology, Queen's University, Kingston, ON, Canada K7M 3N6

ARTICLE INFO

Article history:
Received 9 July 2008
Received in revised form 9 September 2008

Keywords:
Biological motion
Point-light walkers
Size scaling
Cortical magnification
Peripheral vision

ABSTRACT

There is conflicting evidence about whether stimulus magnification is sufficient to equate the discriminability of point-light walkers across the visual field. We measured the accuracy with which observers could report the directions of point-light walkers moving ±4° from the line of sight, and the accuracy with which they could identify five different point-light walkers. In both cases accuracy was measured over a sevenfold range of sizes at eccentricities from 0° to 16° in the right visual field. In most cases observers ($N = 6$) achieved 100% accuracy at the largest stimulus sizes (20° height) at all eccentricities. In both tasks the psychometric functions at each eccentricity were shifted versions of each other on a log-size axis. Therefore, by dividing stimulus size at each eccentricity (E) by an appropriate $F = 1 + E/E_2$ (where E_2 represents the eccentricity at which stimulus size must double to achieve equivalent-to-foveal performance) all data could be fit with a single function. The average E_2 value was .91 ($SEM = .19$, $N = 6$) in the walker-direction discrimination task and 1.34 ($SEM = .21$, $N = 6$) in the walker identification task. We conclude that size scaling is sufficient to equate discrimination and identification of point-light walkers across the visual field.

1. Introduction

The decreased sensitivity to fine details in the visual periphery is a prominent feature of visual experience. Such eccentricity-dependent sensitivity losses may arise from many sources; changes in cone and ganglion cell density, changes in cone size and changes in the cortical magnification factor. However, it has been amply demonstrated that appropriate stimulus magnification can frequently compensate for eccentricity-dependent sensitivity loss. Therefore, performance at some eccentricity (E) can be made equal to that observed at fixation, for a stimulus of size S_0, by setting the size of the peripherally presented stimulus to a multiple (F_E) of the size of the foveal stimulus:

$$S_E = S_0{}^*F_E \quad (1)$$

Furthermore, it has long been observed that many spatial thresholds increase linearly with eccentricity (Weymouth, 1958) and hence

$$F_E = (1 + E/E_2) \quad (2)$$

defines a linear function that specifies that magnification (F_E) at each eccentricity required to elicit performance equivalent to a foveal standard (Levi, Klein, & Aitsebaomo, 1985). The free parameter E_2 indicates the eccentricity at which stimulus size must double to elicit equivalent-to-foveal performance.[1] Therefore, not only does magnification compensate for eccentricity-dependent sensitivity loss, but also the magnification is a linear function of eccentricity.

Over the years there have been claims that the fovea is qualitatively different from the periphery with respect to certain computations. For example, it has been argued that sensitivities to phase relationships (Rentschler & Treutwein, 1985) and color contrast (Mullen, Sakurai, & Chu, 2005) change qualitatively as stimuli are moved into the periphery. Such claims are frequently countered by evidence that with sufficient stimulus magnification (Barrett, Morrill, & Whitaker, 2000; Vakrou, Whitaker, McGraw, & McKeefry, 2005) performance in these tasks can be equated across the visual field. That is, the difference between fovea and periphery is quantitative rather than qualitative. So common are the successes of stimulus magnification (Sally & Gurnsey, 2003, 2004, 2007; Vakrou et al., 2005; Whitaker, Mäkelä, Rovamo, & Latham, 1992) that apparent violations of this rule are noteworthy.

Ikeda, Blake, and Watanabe (2005) recently reported that stimulus magnification was insufficient to equate the detection of

☆ This research was supported by NSERC Research Grants to Rick Gurnsey.
☆☆ Portions of this paper were presented at the Annual meeting of the Vision Sciences Society, 2008, Naples, Florida.
* Corresponding author. Fax: +1 514 848 4545.
E-mail address: Rick.Gurnsey@concordia.ca (R. Gurnsey).

[1] It's worth pointing out that E_2 is inversely related to the magnification needed at any eccentricity.

0042-6989/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2008.09.016

biological motion across the visual field, suggesting that the fovea is specialized to encode biological motion. In their task participants were presented with point-light actors (jumping, running, walking, kicking, or throwing a ball) or scrambled versions of the same stimuli that did not elicit a percept of coherent biological motion. In a two-interval forced-choice task subjects were to determine the interval containing the unscrambled biological motion. Discrimination thresholds were obtained at a range of sizes (.5–16° visual angle) and eccentricities (0°, 4°, and 12°). Thresholds were defined in terms of the number of added noise dots needed to elicit 84% correct detections. Ikeda et al. found that the maximum sensitivity achieved at fixation was never reached in peripheral locations. From this they concluded that perception of biological motion is "unscalably" poor in the periphery.

This conclusion contrasts with three other results in the literature (Gibson, Sadr, Troje, & Nakayama, 2005; Gurnsey, Poirier, Bluett, & Leibov, 2006; Thompson, Hansen, Hess, & Troje, 2007). First, Gibson et al. (2005) had subjects discriminate point-light walker direction (±90° from the line of sight) at a range of sizes and eccentricities (0–40°). Gibson et al. found that ceiling-level performance was obtained at all eccentricities and that, on average, an E_2 of 3.5 was sufficient to compensate for eccentricity-dependent sensitivity loss ($N = 4$, estimated $SEM = .147$, 95% confidence interval = 3.03–3.97). Second, Gurnsey et al. (2006) measured identification accuracy in a structure-from-motion task at a range of sizes and eccentricities. They too found that ceiling-level performance was reached at all eccentricities. In this case an average E_2 value of .61° ($N = 6$, estimated $SEM = .17$, 95% confidence interval = .42–.81) was sufficient to compensate for peripheral sensitivity loss. Gurnsey et al. argued that structure-from-motion and biological motion likely engage many of the same motion selective mechanisms and hence should scale similarly with eccentricity. They suggested that the use of noise to limit performance might explain the discrepancies between the results of Ikeda et al. and those of Gibson et al. and Gurnsey et al. Consistent with this suggestion Thompson et al. (2007) showed that ceiling-level discrimination accuracy was obtained at 0 and 10° eccentricity in a walker-direction discrimination task for stimuli that were 7° in height (essentially replicating Gibson et al.). Furthermore, when scrambled-walker noise was added to the stimuli the peripherally presented stimulus showed impaired performance at noise levels that did not affect foveally presented stimuli.

The results of Gibson et al. (2005) and Thompson et al. (2007) make it clear that under appropriate conditions foveal and peripheral performance can be matched, thus undermining the claim of Ikeda et al. (2005) that size scaling cannot compensate for eccentricity-dependent sensitivity loss in a biological motion task. Nevertheless, there are a number of points that require further examination. Gibson et al. (2005) and Thompson et al. (2007) used a walker-direction discrimination task in which subjects were to discriminate walker directions that were ±90° from the line of sight. Although this is an extremely common task in the biological motion literature, it fails to exploit the richness of the point-light walker display. It is widely reported that subjects can extract a great deal of information from point-light walker displays. For example, several studies have shown that subjects can recognize point-light walkers that portray a familiar person (Cutting & Koslowski, 1977; Troje, Westhoff, & Lavrov, 2005; Westhoff & Troje, 2007). In addition, subjects can extract attributes such the sex, age, mental states, actions, and intentions of unfamiliar individuals from point-light walkers (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). (See Blake & Shiffrar, 2007 and Troje, 2008 for reviews.) In contrast the right–left walker-direction discrimination task is a rather blunt instrument with which to test sensitivity to biological motion.

It may be that a paradigm based on the discrimination of the direction into which a profile view walker is facing does not tap into the unique features of biological motion. For example, contrast sensitivity (i.e., grating detection) can be measured by asking subjects to discriminate gratings oriented ±45° from vertical; in this case if one can detect the grating its orientation is also apparent. Such a task clearly does not challenge orientation acuity and in a similar way the right–left walker discrimination task performed at the limits of detection may have little to do with sensitivity to behaviorally relevant aspects of biological motion. In this context, then, we note that Gibson et al. (2005) found an E_2 of about 3.5 compensated for eccentricity-dependent sensitivity loss in the right–left walker discrimination task; an E_2 in this range is frequently associated with detection tasks (Levi et al., 1985).

It should be noted also that in addition to using noise dots to limit performance Ikeda et al. (2005) presented subjects with a richer set of biological motions than did Gibson et al. (2005) and Thompson et al. (2007). Therefore, it might be argued that the main difference between their experiment and those of Gibson et al. and Thompson et al. is the complexity of the biological motions in question and the difficulty of the task. It might be that more complex judgments about biological motion displays do not scale with eccentricity (as argued by Ikeda et al., 2005) or require substantially more scaling than suggested by the results of Gibson et al. (2005).

In the present study we addressed these questions. In two experiments we presented biological motion stimuli at a range of sizes and eccentricities in the right visual field. The first task was a walker-direction discrimination task in which walker direction was ±4° from the line of sight. This task is more challenging than one in which walker directions are ±90° from the line of sight. The second task required subjects to identify which of five different walkers was presented on a given trial. We found that in both tasks size scaling was sufficient to compensate for eccentricity-dependent limitations and both produced E_2 values well outside the range of those typically associated with retinal limitations (Levi et al., 1985).

2. Methods

2.1. Participants

The participants included three of the authors (RG, MO, GR), two research assistants (P1 and P2) and an undergraduate volunteer (P3). The participants' ages ranged from 20 to 54; there were two women and four men. All participants had normal or corrected-to-normal vision, as assessed by the Freiburg acuity test (Bach, 1996) and all six took part in both experiments.

2.2. Apparatus

The experiments were conducted using an Intel 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.) and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). An adjustable chin rest was used to steady the participant's gaze. Participants responded on a wireless keyboard.

2.3. Stimuli

Point-light walkers were generated from the system first described by Troje (2002a, 2002b) and further elaborated by 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). Here, we use a vector of 20 numbers (α), representing the weights on the first 20 principle components, to synthesize a unique walker. 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. A random direction in walker space can be generated by drawing a sample of 20 random numbers. 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.

Fig. 1 shows a single frame from a point-light walker sequence. The fifteen dots representing each walker were rendered as Gaussian blobs on a black background at 100% contrast. When the stimulus size was 20° the standard deviation of each Gaussian blob was .087° and at all other stimulus sizes the size of the blobs scaled with the size of the stimulus. At the largest stimulus size, 20° of visual angle, the monitor was set to 800 horizontal pixels. For sizes, 10°, 5°, 2.5°, 1.25°, .625°, and .312°, the monitor was set to 1600 horizontal pixels by 1200 vertical. For sizes 20°, 10°, 5°, and 2.5° the viewing distance was 57 cm from the screen. For sizes 1.25°, .625°, and .312°, stimulus size on the screen was held constant and retinal size was manipulated by increasing viewing distance to 114, 228, and 456 cm, respectively. 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 center of the screen. Stimuli were viewed binocularly.

2.3.1. Walker direction stimuli

On each trial a novel walker was created by drawing each coefficient of α from a uniform distribution between 0 and 1 and multiplying it by $\omega = 3$. Prior to the experiment proper a pilot study was run to determine a walker-direction difference that would cover the range of performance from chance (50% correct) to 100% correct over the range of stimulus sizes to be used in the experiment. Stimuli were always presented at fixation and accuracy was measured for walker-direction difference of ±8° to ±.5° from the line of sight. From these data ($N = 8$) it was determined that a direction difference of ±4° covered this range of performance *at fixation*.

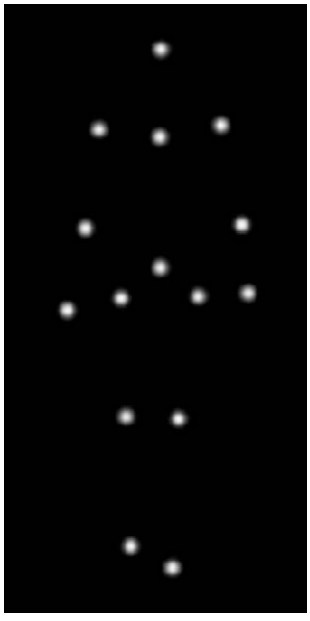

Fig. 1. One frame from a point-light walker display used in the Experiments.

2.3.2. Walker identification stimuli

For the walker identification task five walkers ($\alpha_1, \ldots, \alpha_5$) were chosen arbitrarily. On each trial subjects were asked to identify which of the five walkers had been presented; they entered their responses on the numerical keypad of the computer. Prior to the experiment proper a pilot study was run to determine a value of ω that would produce identification accuracies that cover the range from chance (20% correct) to 100% correct over the range of stimulus sizes to be used in the experiment. Stimuli were always presented at fixation and accuracy was measured for ωs ranging from 1 to 10. From these data ($N = 2$) it was determined that $\omega = 7$ covered this range of performance at fixation.

2.4. Procedure

On each trial a single walker was presented going through one full gait cycle (approximately 1.2 s). The brightness of each dot increased linearly over the first 30 frames (.35 s) from minimum to maximum brightness, remained constant, and then decreased linearly over the last 30 frames to the minimum brightness. On each trial the walker began at a randomly chosen point (phase) of the gait 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 (the digits 1–5 in the identification task, or 1 or 2 in the direction discrimination task). When an error was made a 300 Hz tone sounded for 200 ms. In the identification task the correct walker number appeared at fixation to indicate the correct response.

A block of trials consisted of 25 trials for each combination of size and eccentricity. Eccentricities were always tested from 0° to 16° in that order for a particular stimulus size, and different sizes were tested from largest (20°) to smallest (.312°). All subjects participated in two blocks of trials for a total of 50 trials per condition in both experiments. The testing time for each experiment took approximately 3 h distributed over sessions lasting approximately 45 min. In both tasks subjects received sufficient practice to achieve perfect (or close to perfect) performance at 0° and 16° for the largest stimuli.

3. Results

3.1. Direction discrimination task

The proportion of correct responses was calculated for each eccentricity and stimulus size for each participant. The results of the direction discrimination task are summarized in Fig. 2. Discrimination accuracy improved as the size of the stimulus increased at each eccentricity. In most cases participants reached maximum accuracy at all eccentricities. Therefore, stimulus magnification compensates for eccentricity-dependent sensitivity loss.

To quantify the rate at which stimuli must be scaled with eccentricity, we calculated the E_2 value required to collapse data from all eccentricities onto a single psychometric function. The accuracy data at each eccentricity were assumed to be well described by a Gaussian integral normalized to the range of 1/2 (chance) to 1 when plotted against the logarithm of stimulus size. A mean (μ_E)

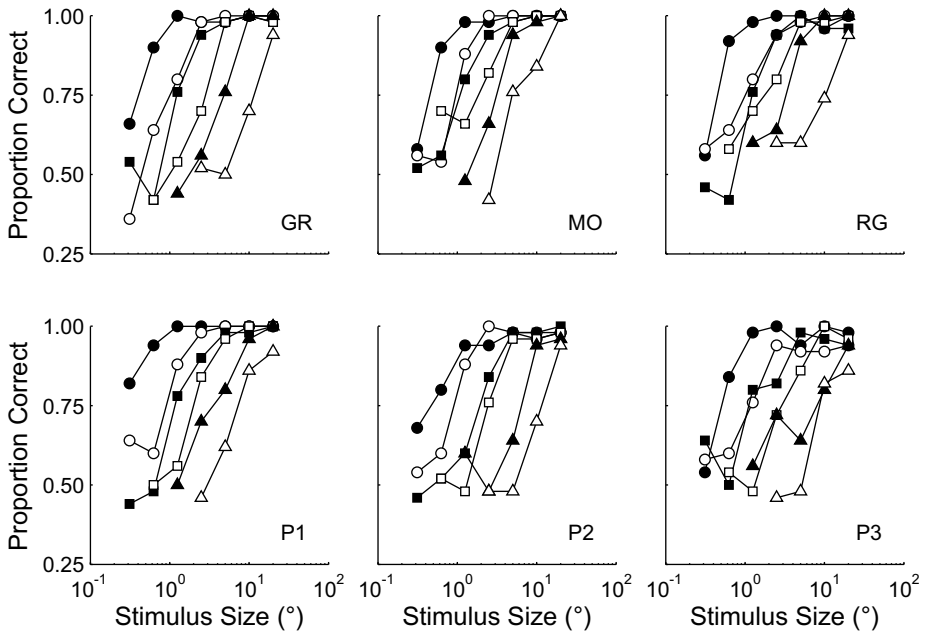

Fig. 2. Raw data from the direction discrimination experiment; 0° (filled circles), 1° (unfilled circles), 2° (filled squares), 4° (unfilled squares), 8° (filled triangles), 16° (unfilled triangles).

and standard deviation (σ_E) characterize the function at each eccentricity (E). Assuming that all σ_E are the same, the changes in μ_E with eccentricity should correspond to a shift along the log-size axis such that $\mu_E = \log(F_E) + \mu_0$, where $F_E = 1 + E/E_2$. Therefore, if the appropriate E_2 is available, all data should collapse to a single function by subtracting $\log(F_E)$ from the logarithm of stimulus size at each eccentricity. In other words, three parameters (μ_0, σ, and E_2) should be sufficient to explain most of the variability in the data. We used an error minimization procedure (fminsearch) available in MATLAB to find the best fitting values of μ_0, σ, and E_2 for each participant. The results are summarized in Fig. 3. On average, the fits explained 94% of the variability in the raw data. The average E_2 value was 0.87 with an estimated *SEM* of .136. Therefore, the 95% confidence interval for E_2 ranges from 0.53 to 1.22.

3.2. Identification task

The results of the walker identification task are summarized in Fig. 4. Identification accuracy improved as the size of the stimulus increased at each eccentricity. In most cases participants reached maximum accuracy at all eccentricities. Therefore, stimulus mag-

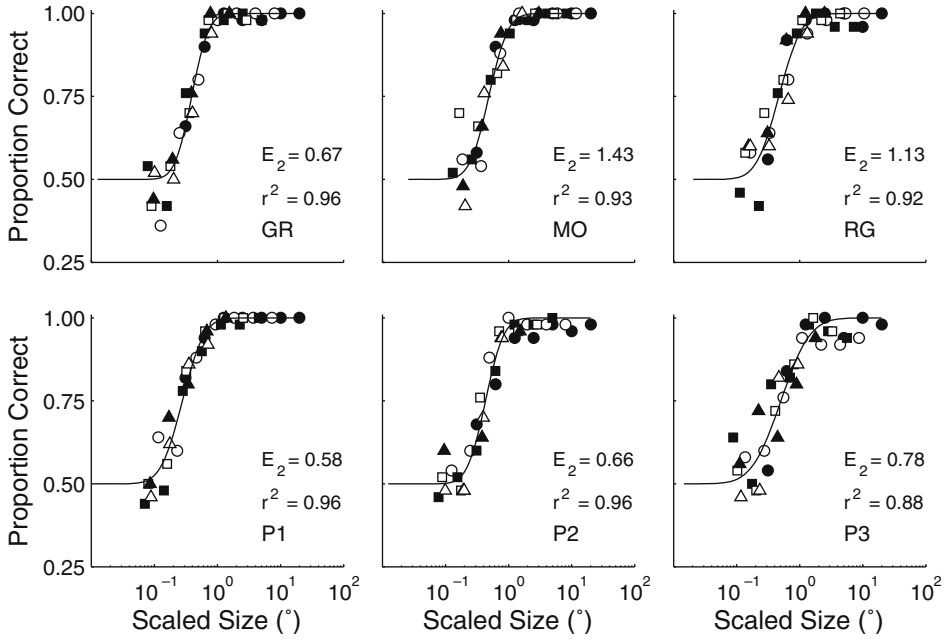

Fig. 3. Data from the direction discrimination experiment collapsed onto the best fitting function for each participant; 0° (filled circles), 1° (unfilled circles), 2° (filled squares), 4° (unfilled squares), 8° (filled triangles), 16° (unfilled triangles). The E_2 value and proportion of explained variance are shown for each participant.

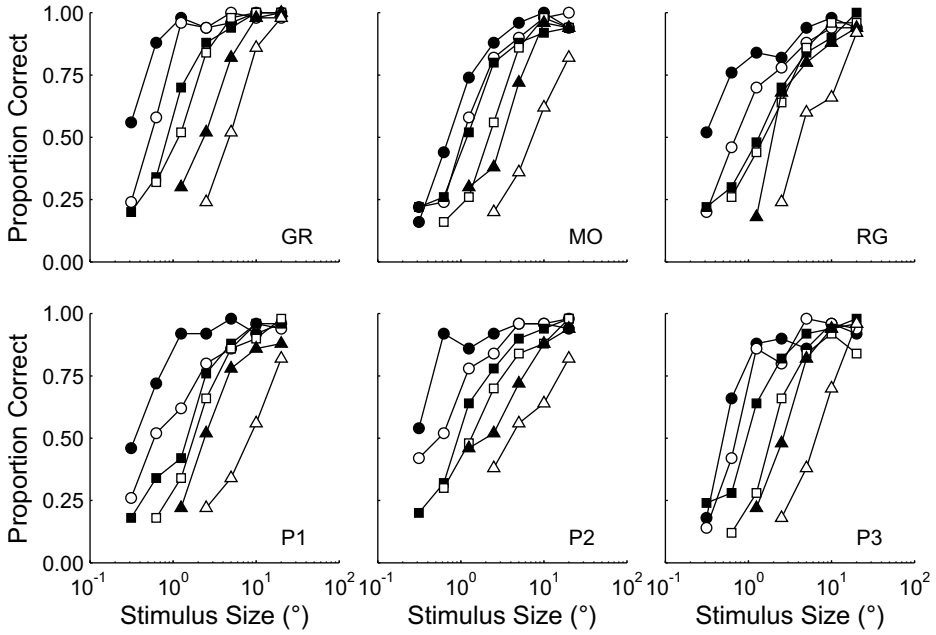

Fig. 4. Raw data from the walker identification experiment; 0° (filled circles), 1° (unfilled circles), 2° (filled squares), 4° (unfilled squares), 8° (filled triangles), 16° (unfilled triangles).

nification compensates for eccentricity-dependent sensitivity loss in this case as well.

The average E_2 value determined by this analysis was 1.27 with an estimated *SEM* of .196. The fits explained 96% of the variance in the data, on average. The 95% confidence interval ranges from .76 to 1.77. The difference between the average E_2 values in the two experiments was statistically significant, $t(5) = 4.12$, $p = .009$, $R^2 = .21$ (Fig. 5).

The size-scaling method employed here assumes that the accuracy vs. size functions differ only in terms of a shift on the log-size axis and that their positions change linearly with eccentricity. To assess these assumptions we computed the best fitting Gaussian integrals (defined by μ_E and σ_E) at each eccentricity, for each subject and each experiment. The results, averaged across six subjects, are summarized in Fig. 6. A statistically significant, main effect of σ would be inconsistent with the assumptions of size scaling, as would a statistically significant, non-linear trend in μ.

For the identification and direction tasks linearity explained 90% and 93% of the variability in the μs for the respective datasets, $F(1,5) = 115$ and 137, respectively, both $p < .001$. For the identification data there were also statistically significant quadratic and cubic trends in the m data, $F(1,5) = 13$ and 12.2, $p = .015$ and .017,

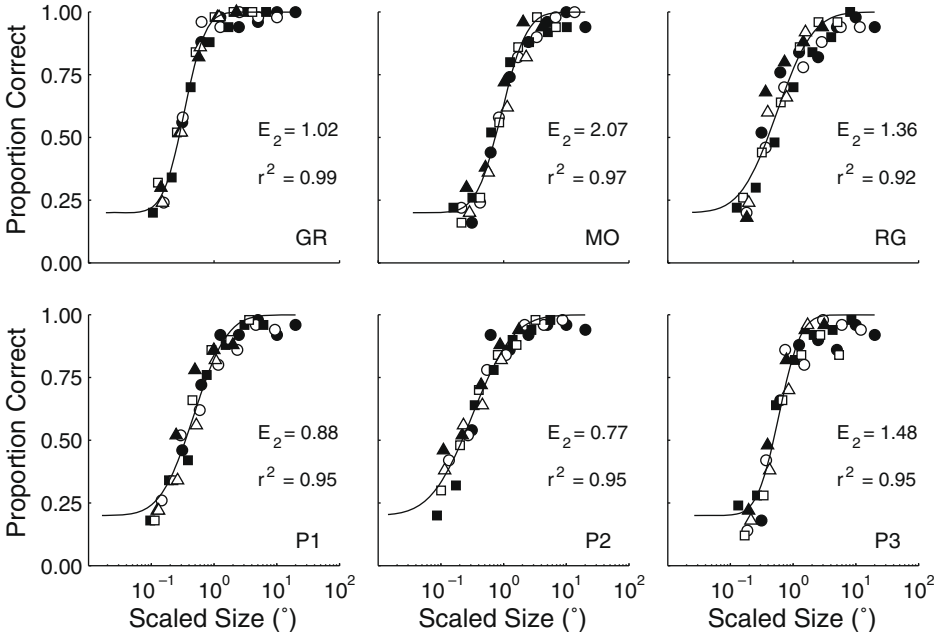

Fig. 5. Data from the walker identification experiment collapsed onto the best fitting function for each participant; 0° (filled circles), 1° (unfilled circles), 2° (filled squares), 4° (unfilled squares), 8° (filled triangles), 16° (unfilled triangles). The E_2 value and proportion of explained variance are shown for each participant.

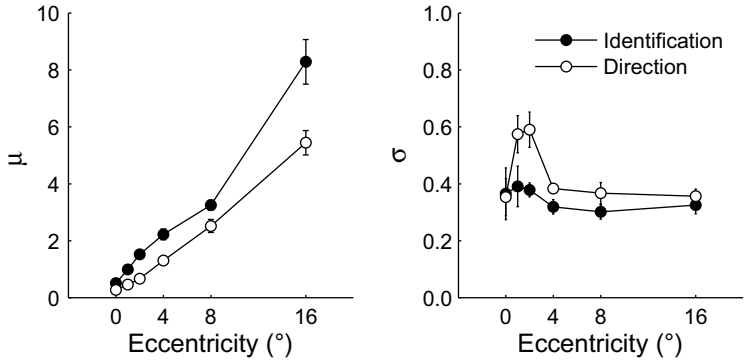

Fig. 6. Plots of the average *m* (left) and *s* (right) values for fit to the accuracy vs. size data at each eccentricity for both tasks. Error bars represent ± estimated *SEM*.

respectively. However, these trends explained only 1.6% and .68% of the variability in the dataset, respectively; i.e., $R^2 = .016$ and .0068, respectively. Therefore, although statistically significant, these differences are of little practical consequence. For the direction discrimination task there was a statistically significant quadratic trend, $F(1,5) = 15.3$, $p = .012$, $R^2 = .0045$. Again, this represents a statistically significant but unimportant difference.

For the walker identification task there was no statistically significant main effect of eccentricity for the σ values, $F(5,25) = 0.74$, $p = .6$, $R^2 = .075$. However, for the direction discrimination task there was a statistically significant main effect of eccentricity for the σ values, $F(5,25) = 6.9$, $p < .001$, $R^2 = .46$. The right panel of Fig. 6 shows a clear divergence of the σ values for eccentricities of 1° and 2°. The mean σ at these eccentricities (.58) was 41% greater than the average of the remaining four eccentricities (.41). The larger slopes at 1° and 2° mean that performance increased more slowly with stimulus size than at the remaining eccentricities; however this did not induce an important non-linearity in the means (μs) of the psychometric functions. Previously we have reported systematic changes in the slopes of psychometric functions with eccentricity (Gurnsey et al., 2006) but the present results do not show a consistent change with eccentricity. There is no obvious explanation for this result, however, the reported E_2 values for the direction discrimination task must be qualified by the finding that the assumptions of the size-scaling method were not perfectly met.

4. General discussion

4.1. Eccentric perception of biological motion is not unscalably poor

The studies described here were motivated by an apparent discrepancy between the results of Ikeda et al. (2005) and those of Gibson et al. (2005), Gurnsey et al. (2006), and Thompson et al. (2007). From the present results we conclude that eccentric perception of biological motion is not unusual because with sufficient magnification peripheral and foveal performance can be equated. This is true for walker-direction discrimination and walker identification, both of which required subjects to discriminate rather subtle differences between point-light walkers. In contrast, the five actions (walking, running, jumping, kicking, throwing) employed by Ikeda et al. differ substantially. It seems likely that in the absence of noise they too would have found that size scaling compensates for eccentricity-dependent sensitivity loss. In fact very large E_2 values would be expected because E_2 seems to increase as task difficulty decreases (cf. Gibson et al. and the present results).

It might be argued that the tasks in the present study could be performed using local motion signals of individual dots, whereas the use of noise dots in the Ikeda et al. (2005) study forced subjects to rely on the global motions of the stimuli because local motions were unreliable. We can't rule this out entirely. However, we made efforts to control for this in the direction discrimination task by generating a different walker on each trial. In this way there would be variability in the local motions from trial to trial and this would work against a strategy that relies on monitoring single dots. Furthermore, in both of the present experiments the walkers began their strides at different points in the gait cycle, again making any single dot an inconsistent cue from trial to trial. (In fact, Ikeda et al. do not report randomizing the onset phase of the stimuli so subjects may have been able to use specific motions in specific locations as cues to the presence of the target stimuli.) It remains to be seen in future work if local motions can support the levels of discrimination achieved in the present work. However, preliminary studies in our lab have shown that walker-direction discrimination at fixation is far worse when walkers are inverted, suggesting that global form and not just local motions contribute to performance.

Our view is that the use of scrambled-walker noise to limit performance in the case of Ikeda et al. (2005) did not reveal a limitation related to biological motion *per se* but a limitation related to noise. Clearly, there may be more than one eccentricity-dependent limitation at play in any psychophysical task (Latham & Whitaker, 1996; Poirier & Gurnsey, 2002; Strasburger, Rentschler, & Harvey, 1994). Indeed, the results of Ikeda et al. are similar in some ways to a recent report (Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000) showing that size scaling alone was not sufficient to equate contrast sensitivity functions for face identification across the visual field. The highest contrast sensitivity was found at fixation and peak sensitivity dropped with eccentricity. Therefore, to equate contrast sensitivity functions at different eccentricities both size and contrast had to be scaled. In a similar way it may be that when noise is used to limit performance both size and noise have to be scaled with eccentricity (Gurnsey et al., 2006). Poirier and Gurnsey (2002) considered the general issue of detecting multiple eccentricity-dependent limitations in detail and Poirier and Gurnsey (2005) showed that a number of odd results in the literature could be explained by multiple eccentricity-dependent limitations.

4.2. Relation of E_2 values to previous research

In the walker-direction discrimination task the average E_2 value of .87 differs substantially from the average E_2 value of 3.5 reported by Gibson et al. (2005). We noted in the introduction that the Gibson et al. task had a direction difference of ±90° and thus might not require extraction of global form from point-light walkers. In fact, in a control experiment Gibson et al. showed that subjects could reliably discriminate walker directions for stimulus sizes at which they could not identify the stimulus as a point-light walker. Fur-

thermore, Gibson et al. concluded that subjects were probably using signals in the local motions of individual dots. Support for this idea comes from recent work (Troje & Westhoff, 2006) showing that the motion of the feet of an animal in locomotion could indeed be used to derive direction from biological motion—even in the absence of any coherent global form. The mechanisms underlying this ability are considered to be entirely different from the ones that mediate the form of a walker. The difference in the E_2 value measured here and the one measured by Gibson et al. may reflect distinct visual mechanisms.

In contrast, the average E_2 value of .87 in the direction discrimination task is rather similar to the average E_2 value of .61 reported by Gurnsey et al. (2006) in a structure-from-motion task. This similarity may reveal that certain aspects of structure-from-motion may involve mechanisms similar to those engaged by biological motion stimuli.

4.3. Interpreting E_2 values

Levi et al. (1985) suggested that E_2 values of 2.5–3.5 compensate for eccentricity-dependent limitations imposed by ganglion cell density and that E_2 around .77 compensates for the cortical magnification factor (viz., the number of millimeters of cortex devoted to 1° of visual angle). To a limited extent one may attempt to identify the anatomical origin of an eccentricity-dependent limitation in a psychophysical task by estimating the E_2 that characterizes the task and relating it to retinal or cortical E_2 values, roughly 3 and .77, respectively. For example, Levi et al. reported that an E_2 of about 3 equated grating acuity across the visual field and that an E_2 of about .7 equated vernier acuity across the visual field (cf. Whitaker, Rovamo, MacVeigh, & Mäkelä, 1992). From this they concluded that grating acuity is limited by retinal factors and vernier acuity by cortical factors. On this crude scale the E_2 values characterizing the present tasks (.87 and 1.27) are closer to the cortical than retinal E_2. The confidence limits around these two estimates include .77 but not 3. Therefore, this line of reasoning suggests that retinal factors are not the principle limitations in the present tasks.

However, such inferences must be made with extreme caution because the E_2 recovered in a given task may depend on many things. For example, the relative contribution of retinal and cortical limitation may change with eccentricity (e.g., Poirier & Gurnsey, 2002) and non-anatomical factors (such as contrast) may also affect E_2 (e.g., Sally & Gurnsey, 2007). As well, Latham and Whitaker (1996) showed that E_2 values change systematically with stimulus manipulations (i.e., target/flanker separation). Therefore, knowing the E_2 value associated with a single task does little to constrain the anatomical or physiological locus of the eccentricity-dependent limitation.

Efforts to establish connections between E_2 values derived from psychophysical and brain-imaging experiments are made more difficult by the tremendous variability in the estimates in both cases. In early imaging work (Sereno et al., 1995) the cortical magnification factor for V1 was extremely steep (corresponding to an E_2 much less than 1, with the specific value depending on the assumptions one is prepared to make in the calculations) whereas more recent work (Dougherty et al., 2003) estimated the corresponding E_2 value to be 3.67. Both of these estimates differ substantially from the estimate of $E_2 = .75$ by Horton and Hoyt (1991). Therefore, without agreement about the E_2 value that characterizes human V1 it is impossible link the psychophysically measured E_2 values to those based on imaging or other data.

Psychophysical estimates of E_2 can be highly variable across tasks (Beard, Levi, & Klein, 1997; Whitaker, Mäkelä, et al., 1992) and within tasks. For example, in the present study the average E_2 value for walker identification is 1.27 is about 46% larger than the average E_2 value for walker-direction discrimination (.87), and this difference is statistically significant. However, the 95% confidence limits around these average values show about 37% overlap. Clearly, individual differences make psychophysical estimates of E_2 highly variable and thus difficult to relate to physiological and anatomical estimates, which are also highly variable. Therefore, questions about the connections between E_2 values derived from psychophysical and brain-imaging experiments are probably best addressed within subjects (e.g., Duncan & Boynton, 2003), as are questions about E_2 values associated with different tasks (Gurnsey et al., 2006; Sally & Gurnsey, 2004).

It has been reported that visual areas such as the superior temporal sulcus (STS) respond to biological motion (Grossman & Blake, 2002) and that areas such as STS are in fact retinotopic (Saygin & Sereno, 2008). There is no way at present to determine whether or not brain regions selective for biological motion (Bonda, Petrides, Ostry, & Evans, 1996; Grossman et al., 2000) contribute to eccentricity-dependent sensitivity loss with respect to biological motion. Certainly the widely varying estimates of E_2 for V1 based on fMRI data highlight the challenges of relating an imaging estimate of E_2 to a psychophysical estimate of E_2.

In spite of the difficulties inherent in identifying the source of an eccentricity-dependent sensitivity loss, it is clear that the perception of biological motion in the visual periphery is unremarkable in that, with sufficient scaling, peripheral and foveal performance can be equated. A conservative view is that V1 is the source of this limitation, and once overcome, higher visual areas with less retinotopy are able to extract the information necessary to perform the tasks at hand.

References

Bach, M. (1996). The Freiburg Visual Acuity test—Automatic measurement of visual acuity. *Optometry and Vision Science, 73*, 49–53.

Barclay, C., Cutting, J., & Kozlowski, L. (1978). Temporal and spatial factors in gait perception that influence gender recognition. *Perception & Psychophysics, 23*, 145–152.

Barrett, B. T., Morrill, P., & Whitaker, D. (2000). Compound grating discrimination in extrafoveal and amblyopic vision. *Experimental Brain Research, 131*(2), 225–235.

Beard, B. L., Levi, D. M., & Klein, S. A. (1997). Vernier acuity with non-simultaneous targets: The cortical magnification factor estimated by psychophysics. *Vision Research, 37*(3), 325–346.

Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology, 58*, 47–73.

Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews: Neuroscience, 2*(8), 561–567.

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *The Journal of Neuroscience, 16*(11), 3737–3744.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433–436.

Cutting, J., & Koslowski, L. (1977). Recognizing friends by their walk: Gait perception without familiarity cues. *Bulletin of the Psychonomic Society, 9*, 353–356.

Dittrich, W. H., Troscianko, T., Lea, S. E., & Morgan, D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception, 25*(6), 727–738.

Dougherty, R. F., Koch, V. M., Brewer, A. A., Fischer, B., Modersitzki, J., & Wandell, B. A. (2003). Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *Journal of Vision, 3*(10), 586–598.

Duncan, R. O., & Boynton, G. M. (2003). Cortical magnification within human primary visual cortex correlates with acuity thresholds. *Neuron, 38*(4), 659–671.

Gibson, L. A., Sadr, J., Troje, N. F., & Nakayama, K. (2005). Perception of biological motion at varying eccentricity. *Journal of Vision, 5*(8), 24–28.

Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron, 35*(6), 1167–1175.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience, 12*(5), 711–720.

Gurnsey, R., Poirier, F. J., Bluett, P., & Leibov, L. (2006). Identification of 3D shape from texture and motion across the visual field. *Journal of Vision, 6*(5), 543–553.

Horton, J. C., & Hoyt, W. F. (1991). The representation of the visual field in human striate cortex. A revision of the classic Holmes map. *Archives of Ophthalmology, 109*(6), 816–824.

Ikeda, H., Blake, R., & Watanabe, K. (2005). Eccentric perception of biological motion is unscalably poor. *Vision Research, 45*(15), 1935–1943.

Latham, K., & Whitaker, D. (1996). Relative roles of resolution and spatial interference in foveal and peripheral vision. *Ophthalmic & Physiological Optics, 16*(1), 49–57.

Levi, D. M., Klein, S. A., & Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research, 25*(7), 963–977.

Mather, G., & Murdoch, L. (1994). Gender discrimination in biological motion displays based on dynamic cues. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 258*, 273–279.

Melmoth, D. R., Kukkonen, H. T., Mäkelä, P. K., & Rovamo, J. M. (2000). The effect of contrast and size scaling on face perception in foveal and extrafoveal vision. *Investigative Ophthalmology & Visual Science, 41*(9), 2811–2819.

Mullen, K. T., Sakurai, M., & Chu, W. (2005). Does L/M cone opponency disappear in human periphery? *Perception, 34*(8), 951–959.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Poirier, F. J., & Gurnsey, R. (2002). Two eccentricity-dependent limitations on subjective contour discrimination. *Vision Research, 42*(2), 227–238.

Poirier, F. J., & Gurnsey, R. (2005). Non-monotonic changes in performance with eccentricity modeled by multiple eccentricity-dependent limitations. *Vision Research, 45*(18), 2436–2448.

Pollick, F. E., Paterson, H. M., Bruderlin, A., & Sanford, A. J. (2001). Perceiving affect from arm movement. *Cognition, 82*(2), B51–B61.

Rentschler, I., & Treutwein, B. (1985). Loss of spatial phase relationships in extrafoveal vision. *Nature, 313*(6000), 308–310.

Runeson, S. (1994). Perception of biological motion: The KSD-principle and the implications of a distal versus proximal approach. In G. Jansson, W. Epstein, & S. S. Bergström (Eds.), *Perceiving events and objects* (pp. 383–405). Hillsdale, NJ: Erlbaum.

Sally, S. L., & Gurnsey, R. (2003). Orientation discrimination in foveal and extra-foveal vision: Effects of stimulus bandwidth and contrast. *Vision Research, 43*(12), 1375–1385.

Sally, S. L., & Gurnsey, R. (2004). Orientation discrimination across the visual field: Matching perceived contrast near threshold. *Vision Research, 44*(23), 2719–2727.

Sally, S. L., & Gurnsey, R. (2007). Foveal and extra-foveal orientation discrimination. *Experimental Brain Research, 183*(3), 351–360.

Saygin, A. P., & Sereno, M. I. (2008). Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex. *Cerebral Cortex, 18*(9), 2158–2168.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., et al. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science, 268*(5212), 889–893.

Strasburger, H., Rentschler, I., & Harvey, L. O. Jr., (1994). Cortical magnification theory fails to predict visual recognition. *The European Journal of Neuroscience, 6*(10), 1583–1587.

Thompson, B., Hansen, B. C., Hess, R. F., & Troje, N. F. (2007). Peripheral vision: Good for biological motion, bad for signal noise segregation? *Journal of Vision, 7*(10), 1211–1217.

Troje, N. (2002a). The little difference. Fourier based synthesis of gender-specific biological motion. In R. Würtz & M. Lappe (Eds.), *Dynamic perception* (pp. 115–120). Aka Press.

Troje, N. F. (2002b). Decomposing biological motion: A framework for analysis and synthesis of human gait patterns. *Journal of Vision, 2*(5), 371–387.

Troje, N. F. (2008). Retrieving information from human movement patterns. In T. F. Shipley & J. M. Zacks (Eds.), *Understanding events: How humans see, represent, and act on events* (pp. 308–334). Oxford University Press.

Troje, N. F., & Westhoff, C. (2006). The inversion effect in biological motion perception: Evidence for a ''life detector''? *Current Biology, 16*(8), 821–824.

Troje, N. F., Westhoff, C., & Lavrov, M. (2005). Person identification from biological motion: Effects of structural and kinematic cues. *Perception & Psychophysics, 67*(4), 667–675.

Vakrou, C., Whitaker, D., McGraw, P. V., & McKeefry, D. (2005). Functional evidence for cone-specific connectivity in the human retina. *The Journal of Physiology, 566*(Pt. 1), 93–102.

Westhoff, C., & Troje, N. F. (2007). Kinematic cues for person identification from biological motion. *Perception & Psychophysics, 69*(2), 241–253.

Weymouth, F. W. (1958). Visual sensory units and the minimal angle of resolution. *American Journal of Ophthalmology, 46*(1, Part 2), 102–113.

Whitaker, D., Mäkelä, P., Rovamo, J., & Latham, K. (1992). The influence of eccentricity on position and movement acuities as revealed by spatial scaling. *Vision Research, 32*(10), 1913–1930.

Whitaker, D., Rovamo, J., MacVeigh, D., & Mäkelä, P. (1992). Spatial scaling of vernier acuity tasks. *Vision Research, 32*(8), 1481–1491.