

Available online at www.sciencedirect.com



Vision Research 45 (2005) 1935-1943



www.elsevier.com/locate/visres

Eccentric perception of biological motion is unscalably poor

Hanako Ikeda^a, Randolph Blake^b, Katsumi Watanabe^{a,b,*}

^a National Institute of Advanced Industrial Science and Technology, Tsukuba, Japan ^b Department of Psychology, Vanderbilt University, Nashville, Tennessee, USA

Received 24 November 2004; received in revised form 31 January 2005

Abstract

Accurately perceiving the activities of other people is a crucially important social skill of obvious survival value. Human vision is equipped with highly sensitive mechanisms for recognizing activities performed by others [Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. Perception and Psychophysics, 14, 201; Johansson, G. (1976). Spatio-temporal differentiation and integration in visual motion perception: An experimental and theoretical analysis of calculus-like functions in visual data processing. Psychological Research, 38, 379]. One putative functional role of biological motion perception is to register the presence of biological events anywhere within the visual field, not just within central vision. To assess the salience of biological motion throughout the visual field, we compared the detectability performances of biological motion animations imaged in central vision and in peripheral vision. To compensate for the poorer spatial resolution within the periphery, we spatially magnified the motion tokens defining biological motion. Normal and scrambled biological motion sequences were embedded in motion noise and presented in two successively viewed intervals on each trial (2AFC). Subjects indicated which of the two intervals contained normal biological motion. A staircase procedure varied the number of noise dots to produce a criterion level of discrimination performance. For both foveal and peripheral viewing, performance increased but saturated with stimulus size. Foveal and peripheral performance could not be equated by any magnitude of size scaling. Moreover, the inversion effect—superiority of upright over inverted biological motion [Sumi, S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. Perception, 13, 283]—was found only when animations were viewed within the central visual field. Evidently the neural resource responsible for biological motion perception are embodied within neural mechanisms focused on central vision. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Biological motion; Eccentricity; Size; Spatial scaling

1. Introduction

Being able to recognize people and to perceive what they are doing are crucially important visual abilities. Indeed, these perceptual skills can be key to survival in some situations, and they are certainly skills we routinely utilize in our everyday social interactions. It is not surprising to learn, therefore, that our visual system is equipped with perceptual mechanisms exquisitely sensitive to the kinematics defining human activity and individual identity. These mechanisms are most dramatically revealed when those kinematics are portrayed by point-light animations which remove static form cues from the visual information available for perception. First popularized by Johansson (1973), point-light animation involves placing small light "tokens" to points of articulation of an individual who is then filmed while engaging in various activities. Despite the absence of recognizable form within individual frames of the film,

^{*} Corresponding author. Address: Visual Cognition Group, Institute for Human Science and Biomedical Engineering, National Institute of Advanced Industrial Science and Technology, AIST Tsukuba Central 6, 1-1-1 Higashi, Tsukuba, Ibaraki 305-8566, Japan. Tel.: +81 29 861 6150; fax: +81 29 861 6790.

E-mail address: katsumi.watanabe@aist.go.jp (K. Watanabe).

^{0042-6989/\$ -} see front matter @ 2005 Elsevier Ltd. All rights reserved. doi:10.1016/j.visres.2005.02.001

viewers can readily perceive what the actor is doing. Called "biological motion perception" this unique form of structure from motion has been widely studied in recent years, and several good reviews of this work are available (Giese & Poggio, 2003; Thornton, Pinto, & Shiffrar, 1998; Verfaillie, 2000). Moreover, there are converging lines of evidence suggesting that the human visual system contains specialized neural mechanisms for the registration of biological motion, including evidence from human brain imaging experiments and from neuropsychological studies of brain damaged people (for a recent review of this work, see Blake, Sekuler, & Grossman, 2004).

One can envisage several possible reasons why perception of biological motion may have acquired special status during the course of evolution. For one, this visual skill could allow us quickly to detect the presence of other creatures anywhere within our field of view. Befitting this role, it is known that viewers can accurately perceive biological motion from animations as brief as 200 ms (Johansson, 1976), although longer exposures afford considerably better sensitivity (Neri, Morrone, & Burr, 1998). Moreover, people can perceive biological motion from point light animations embedded in dense arrays of dynamic noise (Bertenthal & Pinto, 1994; Cutting, Moore, & Morrison, 1988), suggesting that in the natural environment biological motion might be readily detectable because of relative immunity to camouflage. It is also possible, however, that biological motion perception comes into play primarily after visual motion has been detected, with its primary role involving recognition of a given activity or a given individual. Befitting this more refined role, it is known that observers viewing point light animations can reliably discriminate the gender of an actor (Kozlowski & Cutting, 1977; Mather & Murdoch, 1994; Murray, Yong, & Rhodes, 2000; Pollick, Lestou, Ryu, & Cho, 2002), the identity of a familiar individual (Cutting, 1978; Cutting & Kozlowski, 1977; Hill & Pollick, 2000), and the affective connotation of an action (Dittrich, Troscianko, Lea, & Morgan, 1996; Pollick, Paterson, Bruderlin, & Sanford, 2001).

Although these two functional roles—rapid detection and reliable recognition—certainly are not mutually exclusive, the former leads to a prediction that the latter necessarily does not. If biological motion perception plays an important role in detecting biologically relevant events anywhere within the field of view, then perception of biological motion should be salient throughout the visual field. After all, the sudden, unexpected appearance of another person rarely originates at the point of fixation; instead, we detect most objects and events within more peripheral regions of the visual field and then shift our attention to them for further scrutiny. This, then, represents the question that motivated the present experiment: How good are we at perceiving biological motion appearing within the peripheral visual field?

To answer this question, we cannot simply compare foveal viewing with peripheral viewing, for nearly all aspects of visual performance deteriorate with increasing eccentricity from the fovea (e.g., Beard, Levi, & Klein, 1997; Levi, Klein, & Aitsebaomo, 1985; Levi, McGraw, & Klein, 2000; Westheimer, 1982). The fundamental reasons for this deterioration are the lower spatial sampling of the retina and the reduced cortical representation of the peripheral visual field (Daniel & Whitteridge, 1961). Hence, performance deteriorates in the periphery for most tasks when the size of a stimulus remains constant. However, by "magnifying" a stimulus imaged within the peripheral visual field, it is possible to learn whether that stimulus can be placed on more even footing with its foveally viewed counterpart. In fact, when this spatial-scaling is done, performance in the fovea and performance in the periphery are indeed equated for a number of visual tasks including motion detection of slowly drifting gratings (Johnston & Wright, 1986; Wright, 1987) and contrast detection of Gabor micropatterns (Watson, 1987). Importantly, however, there are other visual tasks, including letter recognition (Melmoth & Rovamo, 2003) and face perception (Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000), for which spatial scaling does not equate performance. For those tasks, foveal performance remains superior despite all magnitudes of size increase in the periphery. This failure of magnification implies that the resources required for these tasks are concentrated within neural mechanisms primarily subserving the central region of the visual field.1

In the present study, we applied the spatial scaling paradigm to the perception of biological motion. Biological motion animations were shown at various eccentricities and at various sizes. They were presented within noise masks made up of dots with the same spatio-temporal properties as the dots portraying the biological motion event (Bertenthal & Pinto, 1994; Cutting et al., 1988). Detectability of biological motion was indexed in terms of the number of noise dots required to produce a criterion level of performance on a two-alternative, forced choice task (2AFC). Our aim was to learn whether performance in the periphery could be matched to foveal performance by magnifying the animations. A positive outcome (i.e., matching performance) would imply that human vision can rapidly and efficiently detect the presence of biological relevant events throughout the visual field. A negative outcome (i.e., inability to match foveal and peripheral viewing), however, would suggest that the neural resources for perception

¹ Note that "spatial scaling" is a purely functional approach. This is a major advantage of spatial scaling, compared to cortical scaling, because it does not require any assumption about underlying physiological processes. However, a failure of spatial scaling inevitably indicates a failure of cortical magnification for the function examined.

of biological motion are concentrated within central vision where they are brought into play only after potentially relevant events have been detected by relatively unrefined motion analyses. For purposes of comparison we also measured detection performance using inverted biological motion sequences.

2. Methods

2.1. Subjects

Six subjects (two female, four male), including two of the authors (HI, KW), participated in the study. Except for the authors, the participants were uninformed about the purpose of the study. The two authors and one subject (KY) took part in the entire set of experiments. The other subjects were tested on a subset of the conditions. All subjects had normal or corrected-to-normal vision.

2.2. Stimuli

Point-light biological motion sequences were created from videotapes of an individual performing five activities (jumping, running, walking, kicking, and throwing a ball) while wearing dark clothing with reflective tape on the 12 major joints. The videotapes were digitized at 25 Hz, and the joint positions were encoded as initial positions and vector motions from those starting positions. Biological motion was expressed as a motion of



Fig. 1. Schematic of the visual display. (a) Upright biological motion stimuli were composed of 12 black dots on a white background. The lines connecting the dots were not visible in the actual experiment. (b) Biological motion stimuli were presented embedded in noise dots with the same properties as signal dots composing the motion being masked (Cutting et al., 1988). (c) Dimensions of the biological motion stimuli and the noise area. (d) Inverted biological motion stimuli were created by mirror-reflecting the upright biological motion stimuli about the horizontal axis. (e) Scrambled biological motion stimuli were made by randomizing the starting positions of the signal dots.

12 black (0.4 cd/m^2) dots on a white (58 cd/m^2) background (Fig. 1a). The duration of each biological motion was 800 ms (i.e., 20 frames). Mirror-reversed images of each biological motion were also used, resulting in a total of 10 types of biological motion stimuli. The visual stimuli were presented on a 21-in. CRT display (refresh rate 75 Hz) controlled by an Apple Macintosh G4 computer. The effective frame rate was adjusted to 25 Hz by presenting the same frame three times before proceeding to the next frame.

To manipulate the difficulty of perceiving biological motion sequences, the sequences were embedded in masking noise comprising dots equivalent in size and dynamics to the dots comprising the biological sequences (Cutting et al., 1988). The motion trajectory of each noise dot was randomly chosen from the trajectories of the 12 dots of the biological motion sequence embedded in that noise. The starting position of each noise dot was determined randomly within a virtual square area centered on the biological motion dots (Fig. 1b).

The mean height-width ratio of the biological motion stimuli was 2:1 (Fig. 1c). The height and width of the noise area were set to 1.4 times and 2.8 times greater than those of the biological motion stimuli, respectively (therefore, the shape of the noise area was square). Stimulus size was defined as the side length of the noise area.

The animations (bio-motion plus noise) were presented at seven sizes (0.5, 1, 2, 4, 8, 12, or 16 deg visual angle) and at three eccentricities (0, 4, or 12 deg). The stimulus size was changed by magnifying all spatial dimensions of the visual stimulus, including the dot size. The eccentricity was varied by shifting a fixation cross $(0.4 \text{ cd/m}^2, 0.4 \text{ deg size})$ to the left of the screen while the stimulus always remained at the centre of the screen, so that the visual stimulus would be imaged in the right of the visual field. Eccentricity is defined as the angular distance between the center of the fixation mark and the center of the dot animation. The biological motion sequence was jittered within the noise square.

In addition to the upright biological motion sequences, we also measured masked thresholds for perceiving inverted biological motion sequences. These were created by mirror-reflecting the upright biological motion dots about the horizontal axis (Fig. 1d). For the inverted biological motion sequences, the trajectories of the noise dots were selected from the dots defining inverted biological motion.

2.3. Procedure

While comfortably seated, subjects binocularly viewed the video display from a distance of 57 cm; ambient room illumination was low photopic in a lit room. Head movements were minimized using a head and chin rest. Subjects were instructed to maintain strict gaze on the fixation cross during each trial. Subjects initiated a trial by pressing a key on a computer keyboard, an action that triggered presentation of two successive 800-ms stimulus presentations separated by a blank period of 500 ms. One of the two intervals, randomly determined for each trial, contained one of the ten biological motion sequences and the other interval contained a scrambled version of that same sequence created by randomizing the starting positions of the dots defining the biological motion sequence for that trial (Fig. 1e). Each of the ten biological motion sequences was equally likely on each trial. The biological motion sequence always started with the same frame. Note that on each trial local motion cues were identical for normal and scrambled sequences. After viewing the two sequences, subjects pressed one of two keys to indicate which interval contained the normal, unscrambled biological sequence, guessing if necessary. Responses were not timed, and auditory feedback was given immediately after each response. Upright and inverted biological motion were tested in separate staircases, so subjects always knew which category of animation (but not which exemplars) was being presented.

A staircase procedure was used to vary the number of noise dots to a level associated with 84% correct performance on this 2AFC task. To implement this staircase, a three-up/one-down staircase rule was implemented: following three consecutive correct responses 4 noise dots were added to the noise level of the current trial, and a single incorrect response reduced the noise level by 4 dots. After 12 reversals of the staircase, the noise level step-size was reduced to 2 dots in both ascending and descending directions. When the number of reversals reached 18, the staircase was terminated, and the noise resistance (i.e., performance) was calculated by averaging the noise levels of the last 5 reversals (i.e., a noise level associated with approximately 84% correct detection). For the very difficult conditions, the staircase occasionally dictated a negative noise level, in which case the biological sequence alone was presented until the staircase dictated the addition of noise dots. Each staircase always started with zero noise dots and took anywhere from 8 to 15 minutes to complete. Trials were self-paced, and subjects were encouraged to rest whenever desired.

Subjects HI, KW, and KY were tested with all combinations of stimulus types (upright and inverted), stimulus sizes (0.5, 1, 2, 4, 8, 12, and 16 deg), and eccentricities (0, 4, and 12 deg) [42 conditions]. All conditions were blocked. For the other four subjects, the largest stimulus size (16 deg) and three eccentricities (0, 4, and 12 deg) were used [6 conditions]. Each subject performed four sessions of staircase for each conditions (168 sessions for HI, KW, and KY; 24 sessions for the others). If the calculated performance in a session had a negative value, conditions with those parameters were not used for data analysis.

3. Results

Results for HI, KW, and KY are shown in Fig. 2, which plots average noise levels required to yield a criterion level of performance on the biological motion detection task-higher values of noise indicate superior detectability of biological motion in noise. Data are plotted as a function of stimulus size, with eccentricity as the parameter; each data point is the average of four staircase estimates. As expected, detection performance improved with increasing stimulus size, more so for the upright sequences than for the inverted ones. This improvement with size was most dramatic for the foveally viewed, upright sequences (0 eccentricity), where there was an initial threefold increase in sensitivity. Although the smallest dots were indeed visible at 0 and 4 deg eccentricity, it proved relatively difficult to discern their global coherence in the presence of noise dots. At 12 deg eccentricity, the task was simply impos-



Fig. 2. Results for subject HI, KW, and KY. Performances (averaged for four sessions) are plotted as a function of the stimulus size, with bars indicating 1 standard error of the mean. A larger stimulus size and a smaller eccentricity produced better performance, reaching asymptotes in all eccentricity conditions. The asymptotes differed for different eccentricities. In general, the upright conditions led to a better performance than the inverted condition.

H. Ikeda et al. / Vision Research 45 (2005) 1935–1943

45

sible for the smallest stimulus size because the individual dots were unresolvable. There is a tendency for performance to decline slightly at larger stimulus sizes, probably because the dots comprising the animations were spread over a relatively large extent of both hemifields. Based on the 0 deg eccentricity data, one could conclude that global spatial integration underlying perception of biological motion reaches its maximum at about 4 deg, which would imply receptive fields on the order of 16 deg² (keeping in mind that the 4 deg value is the dimension of one side of the virtual stimulus window). This represents a relatively large sized region of spatial integration, suggesting the involvement of neural mechanisms outside of early visual areas where receptive fields are smaller than this.

It is also noteworthy that variations in performance with stimulus size and eccentricity were much less pronounced for the inverted biological sequences. This represents one more piece of evidence for the uniqueness of upright biological motion and its apparent dependence on global contextual processing that is disrupted by inversion (e.g., Pavlova & Sokolov, 2000).

Of most immediate relevance for our purpose is the inability to match foveal and peripheral performance using stimulus size scaling.² For the upright sequences, it is abundantly clear that performance levels saturated at given stimulus sizes at all eccentricities tested. Most importantly, the maximum performance level was not the same for different eccentricities; simply shifting the stimulus 4 deg away from fovea considerably degraded the detection performance, and the stimulus magnification did not compensate for the reduced performance. This discrepancy of saturation levels among different eccentricities was particularly conspicuous in the upright condition: performance was generally higher in the upright condition than in the inverted condition (i.e., inversion effect; Pavlova & Sokolov, 2000, 2003; Shipley, 2003; Sumi, 1984; Troje, 2003; Verfaillie, 1993). However, the inversion effect was diminished in magnitude within the peripheral visual field.

To generate a data sufficiently large to justify performing analysis of variance (ANOVA), three new subjects performed the task with the stimulus size of 16 deg at 0, 4, and 12 deg eccentricities; their results were averaged with the appropriate values from Fig. 2 to produce the plots shown in Fig. 3. These data confirm performance was higher at smaller eccentricities, especially for the upright conditions. A two-way ANOVA with repeated measures revealed significant main effects of



Fig. 3. Averaged results from all six subjects with stimulus size of 16 deg. The data are plotted as a function of eccentricity. Bars indicate 1 standard error of the mean. At the 0 and 4 deg eccentricities, the inversion effect was evident, but not at the 12 deg eccentricity.

eccentricity (F(2, 10) = 27.93, p < 0.05) and stimulus type (upright vs. inverted, F(1, 5) = 18.65, p < 0.05). The interaction was also significant (F(2, 10) = 7.0, p < 0.05). Post-hoc Tukey HSD tests indicated that the inversion effect was significant at the 0 and 4 deg eccentricities (p < 0.05) but not at the 12 deg eccentricity.

One of the new subjects performed the task while his eye movements were monitored (Eye-link II tracker, SR Research, Ontario, Canada). The pattern of his results was similar to those of the others, and there was virtually no eye deviation during single trials. We are confident, therefore, that subjects were able to maintain careful fixation while performing this demanding task.

4. Discussion

The ability to perceive biological motion appearing within the peripheral visual field was always poorer compared to performance at the fovea. This relative deficit cannot be accounted for by the periphery's relatively poorer spatial resolution because the maximum performance at the fovea remained superior to those at the peripheral fields, irrespective of the spatial scaling. Moreover, the inversion effect of biological motion perception depended on stimulus eccentricity; the advantage of upright biological motion disappeared when the stimulus was viewed at the 12 deg periphery. These results suggest that the neural resources for keen biological motion perception are concentrated on the central region of the visual field. As we point out below, however, this limitation may apply to situations where the viewer is uncertain about what biological activity is being performed and where an explicit response is required.

Upright

 $^{^2}$ It may appear that peripheral performance was still improving with the 16 deg stimulus size in some conditions. This may leave a possibility that peripheral performance might eventually reach foveal performance in principle. However, the rate of improvement was negligible, with which any realistic size of the visual stimulus will not compensate for peripheral performance.

4.1. Why do not size and eccentricity scale?

Spatial scaling has been used extensively in visual psychophysics, the strategy being to discover the amount by which a stimulus must be enlarged to equate visual performance across the visual field (Barrett, Whitaker, McGraw, & Herbert, 1999; Johnston & Wright, 1986; Kelly, 1984; Koenderink, de Bouman, Mesquita, & Slappendel, 1978; Mäkelä, Rovamo, & Whitaker, 1997; Rovamo & Virsu, 1979; Saarinen, Rovamo, & Virsu, 1989; Watson, 1987; Whitaker, Mäkelä, Rovamo, & Latham, 1992; Whitaker, Rovamo, MacVeigh, & Mäkelä, 1992). Results show that spatial scaling (i.e., stimulus magnification) often can compensate for lower performance in the periphery. There are some tasks, however, for which spatial scaling cannot reestablish equity between foveal and peripheral performance. Included among these tasks are recognition of numerals (Strasburger & Rentschler, 1996; Strasburger, Rentschler, & Harvey, 1994; Strasburger, Harvey, & Rentschler, 1991), identification of faces (Mäkelä, Näsänen, Rovamo, & Melmoth, 2001; Melmoth et al., 2000), letter perception (Melmoth & Rovamo, 2003), and discrimination of phase shifts in compound gratings (Bennett & Banks, 1991; Bennett & Banks, 1987; but see Morrone, Burr, & Spinelli, 1989 for contradictory results). Our results indicate that the perception of biological motion also falls in this category of visual tasks where central vision is essential for good performance.³

There are important differences in the processing capabilities of central and peripheral vision. For spatial vision, the periphery has reduced acuity, reduced sensitivity (Pointer & Hess, 1989; Robson & Graham, 1981) and reduced positional accuracy (Westheimer, 1982). The site of these limitations seems to be a level between photoreceptors (Anderson, Mullen, & Hess, 1991; Hess & Hayes, 1994) and an early stage of visual processing (Hess & Dakin, 1999). Hess and Dakin (1997, 1999) reported that, with peripheral viewing (beyond 10 deg), subjects could detect paths of same-phase Gabors that were embedded in randomly positioned and randomly oriented Gabors, but they could not detect paths of alternating-phase Gabors. Based on this finding, they suggested a "fundamental difference" between central and peripheral visual processing (but see Nugent, Keswani, Woods, & Peli, 2003; for opposing results). This type of global spatial task is analogous to biological motion perception in the sense that both require integration of multiple stimuli to perceive a visual object or event. It is thus possible that increased spatial and/or temporal uncertainty in the periphery underlies the eccentricity dependency of biological motion perception.

Spatial and temporal uncertainty also may increase with task complexity. Melmoth et al. (2000) proposed that task complexity-not simply stimulus complexity-determines whether spatial scaling can equate performance over the visual field. There is no arguing that perception of biological motion entails more refined, global analysis than does simple motion detection. Indeed, our subjects volunteered that they could readily perceive dot motion in nearly all conditions but had trouble discerning whether or not those moving dots formed a coherent, biological event. In other words, what makes the task difficult in our study is not perceiving the dot motions defining biological kinematics but, rather, grouping those dots over space and time and, then, segregating those grouped dots from noise. And, obviously, this challenge is much more difficult when viewing these animations in the periphery, regardless of their size. So our results are congruent with the idea that task complexity determines the success of size scaling (Melmoth et al., 2000).

4.2. Inversion effects in the perception of biological motion

Our results agree with previous studies showing that display inversion impedes accurate perception of point-light biological motion (Pavlova & Sokolov, 2000, 2003; Shipley, 2003; Sumi, 1984; Troje, 2003). This inversion effect (i.e., perception of "upright" superior to perception of "inverted") is often construed as a hallmark of configural processing, defined as analytic mode focused on relational structure among component visual parts rather than on the separate parts themselves. In our study we found that the inversion effect is most conspicuous when biological motion is viewed in central vision. In fact, the inversion effect was not observed with the 12 deg peripheral viewing in the present experiment.

An inversion effect is also found in face processing (Carey & Diamond, 1977; Farah, Tanaka, & Drain, 1995; Murray et al., 2000; Pavlova & Sokolov, 2003; Yin, 1969). Although the inversion effect for face processing is a robust phenomenon, Sekuler, Gaspar, Gold, and Bennett (2004) have recently demonstrated that there is no qualitative difference in perception of upright and inverted faces by using noisy face stimuli. Likewise, in the present study, we found that biological motion sequences were processed less efficiently in the peripheral visual field than in the fovea visual field, irrespective of the orientation of the stimulus (upright or inverted; Fig. 2). Thus, there may be only a quantitative difference

³ On at least some other tasks, boosting stimulus contrast can partially compensate for incomplete spatial scaling. In our study, stimulus contrast was high for all conditions. Of course, one could construe our dependent variable (signal/noise ratio) as an index of contrast, and for no value of contrast was peripheral performance equivalent to central performance.

between upright and inverted biological motion, which requires further empirical investigation.⁴

4.3. Central resource for biological motion perception: active and passive processes

The main implication of the present study is that resources for biological motion perception are concentrated within the central visual field. The subjective ease and robustness in perceiving point-light biological motion could be construed to imply that biological motion perception is an automatic, data-driven bottom-up process, and evidence pointing to bottom-up processes does exist (Ahlstrom, Blake, & Ahlstrom, 1997; Mather, Radford, & West, 1992; Thornton et al., 1998). However, accumulating evidence also suggests that perception of complex dynamic visual events (including biological motion) also requires "top-down" attentional resources (Battelli, Cavanagh, & Thornton, 2003; Cavanagh, Labianca, & Thornton, 2001; Chatterjee, Freyd, & Shiffrar, 1996; Thornton et al., 1998, Thornton, Rensink, & Shiffrar, 2002). Do our findings bear on the extent of involvement of these two alternative modes of processing?

The experimental paradigm used in the present study may well favor an active, top-down processing strategy. The use of multiple actions in the detection task, rather than a single action (e.g., walking) typically used in other studies of biological motion might force subjects to access stored representations of the alternative exemplars. In addition, our use of masks comprising scrambled biological-motion probably makes this task more attentionally demanding. These masks, unlike purely random motion, may more effectively block lower-level, local to global strategies that could be operating in bottom-up fashion (Thornton et al., 1998; Thornton et al., 2002). It is feasible, therefore, that automatic, bottomup processing of biological motion can be achieved with reasonable efficiency within the peripheral visual field given appropriate stimulus conditions (see, for example, Thornton & Vuong, 2004).

5. Conclusion

Perception of biological motion has been studied rather extensively in recent years, and nearly all that work has entailed viewing animations imaged in the central visual field. If one of the important functions of biological motion perception is to register the presence of biological events anywhere within the field of view, perception of biological motion should be salient across the visual field. According to our results, however, this is not the case: efficient processing of point-light biological motion is confined to the central visual field. Moreover, the hallmark of configural processing—an inversion effect—is also limited to the central visual field. These results suggest that the primary function of biological motion perception may be to carefully and quickly analyze dynamic visual stimuli in a way enabling an individual to retrieve detailed information about the identity, intentions, and affective state of another individual (Troje, 2003).

For the perception of biological motion to be advantageous, various cues must be used so that the judgment can be optimized in any situation. Faced with such complex tasks, the visual system may handle biological motion with flexible mechanisms that have adjustable efficiency (Beintema & Lappe, 2002; Giese & Poggio, 2003; Neri et al., 1998) and not by a specialized, hardwired detector. Selective attention may contribute to the assumed flexibility of mechanisms for biological motion perception (Battelli et al., 2003; Cavanagh et al., 2001; Thornton et al., 2002).

Acknowledgments

This work was supported by US National Institutes of Health grant EY 07760 and by National Institute of Advanced Industrial Science and Technology, Japan. Part of this work was completed while RB was a Fellow of the Japan Society for the Promotion of Science.

References

- Ahlstrom, V., Blake, R., & Ahlstrom, U. (1997). Perception of biological motion. *Perception*, 26, 1539–1548.
- Anderson, S. J, Mullen, K. T., & Hess, R. F. (1991). Human peripheral spatial resolution for achromatic and chromatic stimuli: Limits imposed by optical and retinal factors. *Journal of Physiology* (London), 442, 47–64.
- Barrett, B. T., Whitaker, D., McGraw, P. V., & Herbert, A. M. (1999). Discriminating mirror symmetry in foveal and extra-foveal vision. *Vision Research*, 39, 3737–3744.
- Battelli, L., Cavanagh, P., & Thornton, I. M. (2003). Perception of biological motion in parietal patients. *Neurophycologia*, 41, 1808–1816.
- 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, 325–346.
- Beintema, J. A., & Lappe, M. (2002). Perception of biological motion without local image motion. *Proceedings of the National Academy* of Sciences of the United States of America, 99, 5661–5663.
- Bennett, P. J., & Banks, M. S. (1991). The effects of contrast, spatial scale, and orientation on foveal and peripheral phase discrimination. *Vision Research*, 31, 1759–1786.
- Bennett, P. J., & Banks, M. S. (1987). Sensitivity loss in oddsymmetrical mechanisms and phase anomalies in peripheral vision. *Nature*, 326, 873–876.

⁴ Additionally, assuming that there is an overlap between mechanisms for face perception and biological motion perception (Troje, 2003), another interesting prediction would be that the inversion effect for face perception also depends on stimulus eccentricity.

- Bertenthal, B. I., & Pinto, J. (1994). Global processing of biological motions. *Psychological Science*, 5, 221–225.
- Blake, R., Sekuler, R., & Grossman, E. (2004). Human brain areas involved in visual motion perception. In J. Kaas & C. Collins (Eds.), *The primate visual system*. CRC Press.
- Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science*, 195, 312–314.
- Cavanagh, P., Labianca, A. T., & Thornton, I. M. (2001). Attentionbased visual routines: Sprites. Cognition, 80, 47–60.
- Chatterjee, S. H., Freyd, J. J., & Shiffrar, M. (1996). Configural processing in the perception of apparent biological motion. *Journal* of Experimental Psychology: Human Perception and Performance, 22, 916–929.
- Cutting, J. E. (1978). Generation of synthetic male and female walkers through manipulation of a biomechanical invariant. *Perception*, *7*, 393–405.
- Cutting, J. E., & Kozlowski, L. T. (1977). Recognizing friends by their walk: Gait perception without familiarity cues. *Bulletin of the Psychonomic Society*, 9, 353–356.
- Cutting, J. E., Moore, C., & Morrison, R. (1988). Masking the motions of human gait. *Perception Psychophysics*, 44, 339–347.
- Daniel, P. M., & Whitteridge, G. (1961). The representation of the visual field on the cerebral cortex in monkey. *Journal of Physiology*, 159, 203–221.
- Dittrich, W. H., Troscianko, T., Lea, S., & Morgan, D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception*, 25, 727–738.
- Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception Performance*, 21, 628–634.
- Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, 4, 179–192.
- Hess, R. F., & Dakin, S. C. (1997). Absence of contour linking in peripheral vision. *Nature*, 390, 602–604.
- Hess, R. F., & Dakin, S. C. (1999). Contour integration in the peripheral field. *Vision Research*, 39, 947–959.
- Hess, R. F., & Hayes, A. (1994). The coding of spatial position by the human visual system: Effects of spatial scale and retinal eccentricity. *Vision Research*, 34, 625–643.
- Hill, H. H., & Pollick, F. E. (2000). Exaggerating temporal differences enhances recognition of individual from point light displays. *Psychological Science*, 11, 223–228.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics*, 14, 201–211.
- Johansson, G. (1976). Spatio-temporal differentiation and integration in visual motion perception: An experimental and theoretical analysis of calculus-like functions in visual data processing. *Psychological Research*, 38, 379–393.
- Johnston, A., & Wright, M. (1986). Matching velocity in central and peripheral vision. Vision Research, 26, 1099–1109.
- Kelly, D. H. (1984). Retinal inhomogeneity. I. Spatiotemporal contrast sensitivity. *Journal of the Optical Society of America A*, 1, 107– 113.
- Koenderink, J. J., de Bouman, A. E., Mesquita, B., & Slappendel, S. (1978). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. *Journal of the Optical Society of America*, 68, 854–856.
- Kozlowski, L. T., & Cutting, J. E. (1977). Recognizing the sex of a walker from dynamic point-light display. *Perception and Psychophysics*, 21, 575–580.
- Levi, D. M., Klein, S. A., & Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research*, 25, 963–977.
- Levi, D. M., McGraw, P. V., & Klein, S. A. (2000). Vernier and contrast discrimination in central and peripheral vision. *Vision Research*, 40, 973–988.

- Mäkelä, P., Näsänen, R., Rovamo, J., & Melmoth, D. (2001). Identification of facial images in peripheral vision. *Vision Research*, 41, 599–610.
- Mäkelä, P., Rovamo, J., & Whitaker, D. (1997). The effects of eccentricity and stimulus magnification on simultaneous performance in position and movement acuity tasks. *Vision Research*, 37, 1261–1270.
- Mather, G., & Murdoch, L. (1994). Gender discrimination in biological motion displays based on dynamic cues. *Proceedings of* the Royal Society of London B, 259, 273–279.
- Mather, G., Radford, K., & West, S. (1992). Low-level visual processing of biological motion displays based on dynamic cues. *Proceedings of the Royal Society of London B*, 258, 273–279.
- Melmoth, D. R., Kukkonen, H., Mäkelä, P., & Rovamo, J. M. (2000). Scaling extrafoveal detection of distortion in a face and grating. *Perception*, 29, 1117–1126.
- Melmoth, D. R., & Rovamo, J. M. (2003). Scaling of letter size and contrast equalizes perception across eccentricities and set sizes. *Vision Research*, 43, 769–777.
- Morrone, M. C., Burr, D. C., & Spinelli, D. (1989). Discrimination of spatial phase in central and peripheral vision. *Vision Research*, 29, 433–445.
- Murray, J. E., Yong, E., & Rhodes, G. (2000). Revisiting the perception of upside-down faces. *Psychological Science*, 6, 492–496.
- Neri, P., Morrone, M. C., & Burr, D. C. (1998). Seeing biological motion. *Nature*, 395, 894–896.
- Nugent, A. K., Keswani, R. N., Woods, R. L., & Peli, E. (2003). Contour integration in peripheral vision reduces gradually with eccentricity. *Vision Research*, 43, 2427–2437.
- Pavlova, M., & Sokolov, A. (2000). Orientation specificity in biological motion perception. *Perception and Psychophysics*, 62, 889–899.
- Pavlova, M., & Sokolov, A. (2003). Prior knowledge about display inversion in biological motion perception. *Perception*, 32, 937–946.
- Pointer, J. S., & Hess, R. F. (1989). The contrast sensitivity gradient across the human visual field: Emphasis on the low spatial frequency range. *Vision Research*, 29, 1133–1151.
- Pollick, F. E., Lestou, V., Ryu, J., & Cho, S. B. (2002). Estimating the efficiency of recognizing gender and affect from biological motion. *Vision Research*, *42*, 2345–2355.
- Pollick, F. E., Paterson, H., Bruderlin, A., & Sanford, A. J. (2001). Perceiving affect from arm movement. *Cognition*, 82, B51–B61.
- Robson, J. G., & Graham, N. (1981). Probability summation and regional variation in contrast sensitivity across the visual field. *Vision Research*, 21, 409–418.
- Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Research*, 37, 495–510.
- Saarinen, J., Rovamo, J., & Virsu, V. (1989). Analysis of spatial structure in eccentric vision. *Investigative Ophthalmology and Visual Science*, 30, 293–296.
- Sekuler, A. B., Gaspar, C. M., Gold, J. M., & Bennett, P. J. (2004). Inversion leads to quantitative, not qualitative, changes in face processing. *Current Biology*, 14, 391–396.
- Shipley, T. F. (2003). The effect of object and event orientation on perception of biological motion. *Psychological Science*, 14, 377–380.
- Strasburger, H., Harvey, L. O., & Rentschler, R. I. (1991). Contrast thresholds for identification of numeric characters in direct and eccentric view. *Perception and Psychophysics*, 49, 495–508.
- Strasburger, H., & Rentschler, I. (1996). Contrast-dependent dissociation of visual recognition and detection fields. *European Journal of Neuroscience*, 8, 1787–1791.
- Strasburger, H., Rentschler, I., & Harvey, L. O. (1994). Cortical magnification theory fails to predict visual recognition. *European Journal of Neuroscience*, 6, 1583–1588.
- Sumi, S. (1984). Upside-down presentation of the Johansson moving light-spot pattern. *Perception*, 13, 283–286.

- Thornton, I. M., Pinto, J., & Shiffrar, M. (1998). The visual perception of human locomotion. *Cognitive Neuropsychology*, 15, 535–552.
- Thornton, I. M., Rensink, R. A., & Shiffrar, M. (2002). Active versus passive processing of biological motion. *Perception*, 31, 837–853.
- Thornton, I. M., & Vuong, Q. C. (2004). Incidental processing of biological motion. *Current Biology*, 14, 1084–1089.
- Troje, N. (2003). Reference frames for orientation anisotropies in face recognition and biological-motion perception. *Perception*, 32, 201–210.
- Verfaillie, K. (1993). Orientation-dependent priming effects in the perception of biological motion. *Journal of Experimental Psychology: Human perception and performance*, 19, 992–1013.
- Verfaillie, K. (2000). Perceiving human locomotion: Priming effects in direction discrimination. *Brain and Cognition*, 44, 192–213.

- Watson, A. B. (1987). Estimation of local spatial scale. Journal of the Optical Society of America A, 4, 1579–1582.
- Westheimer, G. (1982). The spatial grain of the perifoveal visual field. *Vision Research*, 22, 157–162.
- 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, 1913–1930.
- Whitaker, D., Rovamo, J., MacVeigh, D., & Mäkelä, P. (1992). Spatial scaling of vernier acuity tasks. *Vision Research*, 32, 1481–1491.
- Wright, M. (1987). Spatiotemporal properties of grating motion detection in the center and the periphery of the visual field. *Journal of the Optical Society of America A*, 8, 1627–1633.
- Yin, R. K. (1969). Looking at upside-down faces. Journal of Experimental Psychology, 81, 141–145.