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Necessary but not sufficient: Motion perception is required for perceiving biological motion

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Abstract

Researchers have argued that biological motion perception from point-light animations is resolved from stationary form information. To determine whether motion is required for biological motion perception, we measured discrimination thresholds at isoluminance. Whereas simple direction discriminations falter at isoluminance, biological motion perception fails entirely. However, when performance is measured as a function of contrast, it is apparent that biological motion is contrast-dependent, while direction discriminations are contrast invariant. Our results are evidence that biological motion perception requires intact motion perception, but is also mediated by a secondary mechanism that may be the integration of form and motion, or the computation of higher-order motion cues.

Keywords: Vision; Motion perception; Biological motion; Isoluminance

1. Introduction

Human observers are able to extract surprising detail from the kinematics of body actions as depicted in the movements of the joints alone. Identity, gender, emotions, deception and vulnerability can all be portrayed effectively via point-light animations of human body actions (Cutting, 1978; Dittrich, Troscianko, Lea, & Morgan, 1996; Gunns, Johnston, & Hudson, 2002; Pollick, Lestou, Ryu, & Cho, 2002; Runeson & Frykholm, 1983). Many studies have been devoted to understanding how these simple animations give rise to such complex interpretations and meanings. It is generally believed that the interpretation of point-light animations is derived from visual analysis of dynamic cues, such as local motion, relative motion or local rigidities (Casile & Giese, 2005; Johansson, 1977; Troje, 2002). These hypotheses are based on the observations that point-light animations appear disorganized until set into motion (Johansson, 1973), and that disrupting the timing or temporal succession of frames renders point-light animations "unnatural" and difficult to discriminate (Mather, Radford, & West, 1992).

Perhaps counter-intuitively, however, some researchers have suggested that biological motion perception is instead a form-driven process, and recognition of the human body structure in these sequences can be constructed from stationary snapshots alone, even when depicted as point-lights (Lange & Lappe, 2006). This assertion is based on the findings that destroying the frame-to-frame local motion correspondences, such as by limiting dot lifetime and shuffling the dot position between the joints, does not impair biological motion perception (Beintema & Lappe, 2002).

We thus ask the question: Is motion analysis necessary for the perception of biological motion? To evaluate this, we have created point-light animations designed to be ineffective for perceptual processing by low-level motion mechanisms. These animations are constructed from yellow dots that are perceptually isoluminant with the gray background (i.e. the dots in the displays are differentiated from the background by wavelength, but not by luminance). Visual motion detectors are most efficiently driven by changes in luminance, contrast or texture over space (Adelson & Bergen, 1985; Sperling, 1989). Color-defined motion,

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and in particular yellow–violet color contrast, is extremely ineffective for driving these motion detectors (Cavanagh & Anstis, 1991; Ruppertsberg, Wuerger, & Bertamini, 2003; Teller & Lindsey, 1993). Isoluminant motion displays constructed from drifting sinewave gratings or random dot motion are reported to have slower perceived speed and often an apparent lack of perceived motion (so-called "motion standstill", (Lu, Lesmes, & Sperling, 1999; Ramachandran & Gregory, 1978), and motion discrimination thresholds for displays defined solely by color are typically an order of magnitude worse than for luminance defined displays (Bilodeau & Faubert, 1997; Wuerger & Landy, 1993).

We reasoned that if motion analyses are critical for biological motion perception, the impact of short-circuiting this system should be apparent at isoluminance. The results from these experiments indeed find biological motion sensitivity to fail at isoluminance, evidence that intact motion analysis is necessary for biological motion perception. However when performance is measured as a function of contrast, we revealed biological motion perception to benefit from additional luminance contrast beyond that predicted from the simple motion tasks. We take this as evidence for a secondary mechanism mediating biological motion perception.

2. Method

2.1. Participants

Only individuals with normal color vision (as measured by 22/24 correct on the Ishihara color test) participated in these experiments of which there were four (two authors: S1, S2). Observers gave informed, written consent as approved by the University of California, Irvine Institutional Review Board.

2.2. Stimuli

Schematics of the stimuli can be seen in Fig. 1. Animations were viewed within an 8.7° aperture positioned 2.2° parafoveally. Subjects monocularly viewed the displays either in the right visual field (S3, S4) or left visual field (S1, S2). All animations were displayed as yellow dots (.17° of visual angle) on a gray background with mean intensity of 8.0 cd/m^2. While there is some debate as to whether red–green isoluminant motion is computed via the same perceptual mechanisms as luminance defined motion, it is generally agreed that animations defined along the yellow–violet axis are extremely ineffective for perceiving motion (Bilodeau & Faubert, 1997; Ruppertsberg et al., 2003). Animations were displayed using Matlab (Mathworks, Inc.) in conjunction with the Psychophysics Toolbox.

2.2.1. Biological motion (BIO)

Point-light biological motion and scrambled motion animations were created from digitized video of an actor performing various activities (e.g. running, walking, kicking, throwing) with reflective tape on the joints. Animations were clipped to 500 ms and scaled to approximately 3 × 1.5° visual angle. Scrambled motion was created by randomizing the starting positions of the biological motion dots (within a 3 × 1.5° virtual window) but retaining the motion trajectories. The location of the target figure within the stimulus aperture jittered 1.5° from trial-to-trial to prevent single dots or small clusters of dots from being predictive of the target identity. Observers were asked to report whether each short animation depicted a biological or non-biological target. The biological and scrambled signal dots were embedded in motion-matched noise dots (i.e. spatially scrambled "walker" dots masked walkers, scrambled "kicker" dots masked kickers). The number of noise dots was adjusted using two interleaved 3–1 staircases. The staircases increased the number of noise dots after three sequential correct responses and reduced the number of noise dots following a single incorrect response, converging on 79.4% accuracy (the noise tolerance threshold). The staircases terminated after 30 reversals in performance (added or subtracted noise dots) and threshold noise tolerance was calculated as the average number of noise dots over the last 15 reversals of both staircases. At perceptual isoluminance the staircases failed to converge or appeared to converge at zero noise dots, because observers could not perform the task with even 79.4% accuracy. These instances are noted in the text, and in such cases accuracy was calculated from those same trials making up the last 15 staircase reversals.

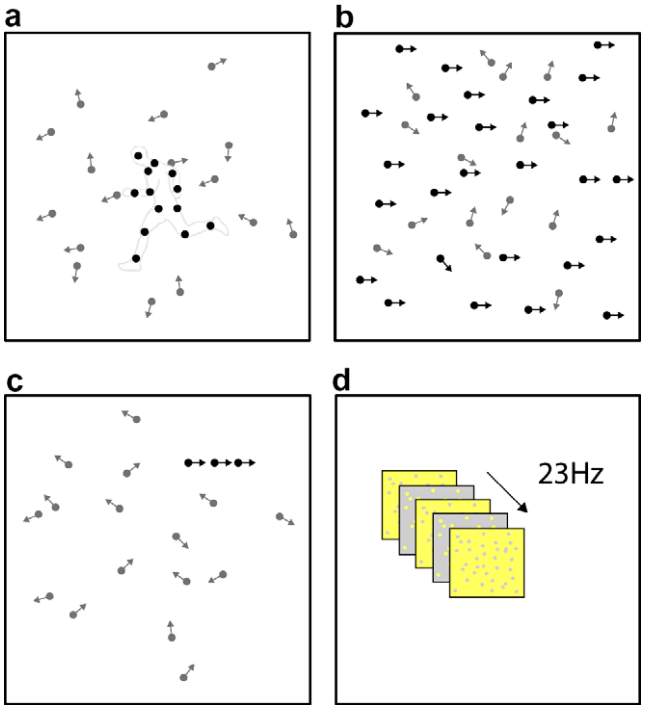

Fig. 1. Schematic of stimuli with signal dots denoted as black and noise dots as gray. All dots were yellow against a gray background in the experiments. (a) Single frame of a point-light biological actor embedded in noise. The outline of the actor is provided, but was not visible in our experiments. (b) Single frame of the coherent motion RDKs. On each frame some proportion of dots moved either left or right ('signal dots'), and the remaining dots moved in a random direction (c) Single frame of the collinear triad embedded in noise. (d) Schematic of the minimum flicker procedure. Observers monocularly viewed a stationary random dot image (a single frame of the RDK stimulus) that alternated between gray and yellow at 23 Hz. Subjects adjusted the brightness of the yellow until the perceived flicker was minimized. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2.2. Coherent motion (COH)

Observers viewed 500 ms random-dot kinematograms (RDKs) consisting of 100 dots with a speed of 8.5°/s. On each frame, some proportion of the dots was selected to move coherently (signal dots) while the remaining dots moved in independent directions (random path motion). Subjects were asked to report the direction of the coherent signal (left or right). The signal dots were randomly selected on each frame, preventing any single dot from being predictive of the coherent direction. Discrimination

accuracy was measured using the method of constant stimuli for each contrast level. Psychometric functions were fitted with a Weibull function and the proportion of coherent signal required for 79.4% accuracy (threshold performance) was estimated.

2.2.3. Collinear triads (3DOT)

Observers viewed 500 ms animations of three horizontally collinear dots moving left or right (speed fixed at 6.8°/s). The horizontal extent of the dots subtended 1.35° visual angle, with .43° separating each dot (approximately the size of a biological motion limb). The collinear triads were embedded in noise dots moving with the same speed but in random directions, and the position of the triad was randomly spatially jittered 2.2° from the center of the aperture on each trial. Observers were asked to report the motion direction of the target dots (left or right). The number of noise dots that could be tolerated while maintaining threshold performance (noise tolerance thresholds) was measured using a 3–1 double interleaved staircase. One subject was not able to discriminate the two types of animations, even without noise, and so the staircase failed to converge. For this individual, accuracy is calculated as mean performance over the trials making up the last 15 staircase reversals (no threshold).

2.3. Procedure

All experiments were displayed on a ViewSonic Graphics Series 220fp 21 in. monitor controlled by a G4 dual-processor Macintosh computer equipped with Matlab and the Psychophysics Toolbox. Participants were seated 50 cm from the screen with their chin comfortably situated on a headrest to minimize movement during data collection. Participant responses were collected on a standard keyboard.

2.3.1. Minimum flicker

The point of perceptual isoluminance, the intensity at which two wavelengths are perceived to have equal luminance, was measured for each individual. Because perceptual isoluminance is rarely equivalent to 0% physical luminance contrast, varies from individual to individual, and even between eyes of the same individual, we used the minimum flicker procedure to equate the luminance intensity of the yellow and gray (Anstis & Cavanagh, 1983; Cavanagh & Anstis, 1991). Briefly, observers monocularly viewed a stationary random dot image (a single frame of the COH stimulus) alternating counterphase between yellow and gray. Subjects pressed keys to adjust (increase or decrease) the brightness of the yellow until the perceived flicker of the 23 Hz display was minimized. This procedure was repeated 10 times, and the mean yellow intensity adjustment was calculated. Subjects repeated this procedure prior to starting each session (different days) with consistent adjustments from day to day.

Psychophysical measurements of observer thresholds were measured for a range of contrasts, from isoluminance to 20% contrast. Michelson contrast was calculated as $(\mu_Y - \mu_G)/(\mu_Y + \mu_G)$, where μ_Y is the mean contrast for the yellow foreground and μ_G is the mean contrast or the gray background. Trials were blocked by contrast and task type (BIO, COH, 3DOT). Subjects were given feedback.

3. Results

For all tasks, discrimination performance at isoluminance was significantly impaired compared to performance at high contrasts ($p < .05$), and sensitivity decreased with decreasing luminance contrast (Fig. 2). Subjects were able to tolerate fewer masking noise dots at the lowest contrast in both the biological motion and collinear triad tasks. Subjects also required a higher proportion of signal dots to discriminate the moving direction of coherent RDK at the lowest contrast levels. These results are not surprising given previous reports of poor sensitivity to color-defined motion (Bilodeau & Faubert, 1997; Troscianko, 1987; Wuerger & Landy, 1993).

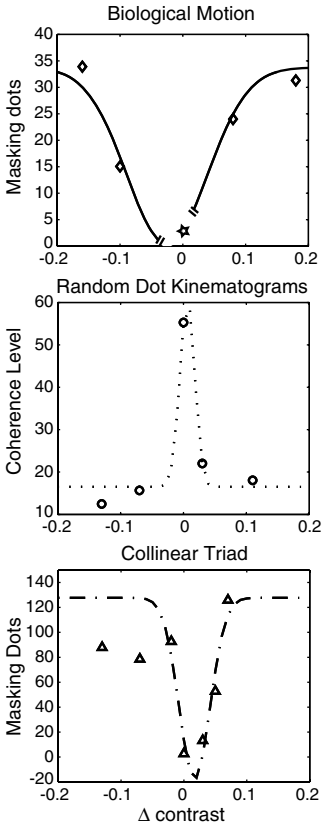

Fig. 2. Single subject performance (S1). Numbers of masking noise dots (biological motion and collinear triad) and percent coherence (RDK) required for threshold discrimination performance at each level of contrast. Abscissa is plotted as percent contrast relative to perceptual isoluminance (perceived 0% contrast). ☆ indicates subject performed at chance levels.

For the point-light animations only, discriminations failed entirely at isoluminance (Table 1). Performance on this task was significantly worse than in the simple motion tasks ($p < .01$), for which three of four subjects were able to maintain threshold performance, albeit with reduced sensitivity. Recovery of biological motion perception (measured as the slope of threshold versus contrast) was also quite

Table 1
Performance at Isoluminance

Subject	Bio (%)	3Dot (%)	Coh[a] (%)
S1	48.08	72.73	55.274
S2	66.67	78.31	65.887
S3	63.16	83.93	58.326
S4	52.54	81.36	100

For biological motion and collinear triad, computed as the mean performance over those final trials of the staircase that determines noise tolerance thresholds. For the coherence task, performance is measured as the proportion of coherent motion required for threshold direction discrimination. Subject S4 was unable to discriminate the RDK directions at isoluminance.

[a] Indicates 79.4% performance threshold at isoluminance.

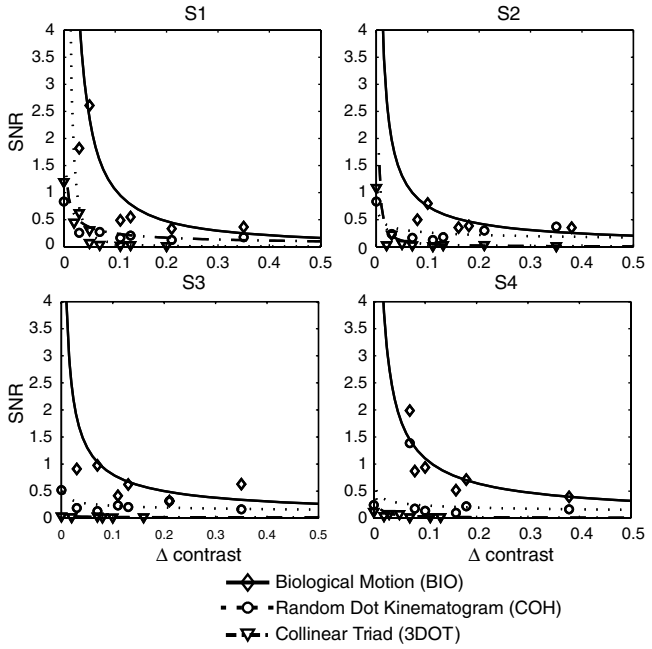

Fig. 3. Performance thresholds. Data from all four subjects, plotted on the common axis of signal-to-noise (SNR). For the biological motion and collinear triad conditions, SNR is calculated as number of signal dots/masking dots. For the COH (RDK) condition, SNR is the proportion of coherent dots. Performance is fit by a standard two-parameter power function. Note that no subjects were able to discriminate the biological from scrambled motion at perceptual isoluminance.

slow (Fig. 3). RDK and collinear direction discrimination thresholds recovered to optimal levels by 5% contrast, but performance on the point-light animations did not reach asymptotic levels until greater than 20% contrast. Although simple direction discriminations recovered completely at low contrast, biological motion perception was still impaired.

We do not attribute poor psychophysical sensitivity to biological motion at isoluminance to physical attributes of the display such as dot size or eccentricity, which were matched across the three tasks. Nor do we attribute performance to limitations on spatial resolution (e.g. spatial pooling) or the presence of masking noise, because subjects were able to discriminate the small, collinear triads embedded in dense arrays of motion-matched noise. These psychophysical findings are evidence for an additional perceptual mechanism mediating biological motion perception that is not recruited for simple direction discriminations, either local or global.

It is interesting to note that the collinear triad task may have benefited from the spatial proximity and common velocity (i.e. Gestalt grouping), creating near 'pop-out' conditions (typically measured with reaction time, but here would be reflected in the signal-to-noise ratios). In this case, one could interpret our data as some secondary mechanism, namely grouping, as benefiting the local motion tasks. The mechanism for motion pop-out is thought to be motion-energy detectors (Kastner, Nothdurft, & Pigarev, 1997), and neurons with these response characteristics have firing rates that saturate at very low contrasts (similar to levels at which our psychophysical measurements saturate, (Sclar, Maunsell, & Lennie, 1990). Also, contrast-defined complex stimuli, such as optic flow patterns, require longer duration or more contrast energy to discriminate at the same levels of efficiency as luminance defined versions (Allen & Derrington, 2000). Together this evidence suggests biological motion to be mediated by a slower, more complex pathway, likely the same mechanism mediating the complex optic flow patterns.

4. Discussion

In some sense, point-light biological motion is a highly contrived stimulus that we rarely experience in natural viewing (analogous, perhaps, to viewing someone camouflaged by a tree or a bush). Nonetheless, our visual system is equipped to organize these unusual animations into recognizable sequences of human actions. Our experiments are evidence that this awareness is achieved via perceptual mechanisms that are not nearly as sensitive as has been previously suggested. Humans require better signal, or less noise, to recognize biological motion than we do to discriminate simple motion patterns.

At isoluminance, our direction discrimination measurements were significantly impaired, but the subjects were able to reach threshold performance. In contrast, biological motion discriminations failed entirely. The mechanism mediating biological motion sensitivity is relatively quick (point-light animations are recognized within ~200 ms in robust viewing situations) and sums over a long temporal window (greater than 1 s, Neri, Morrone, & Burr, 1998. Our findings demonstrate that this mechanism also benefits from higher luminance contrast. While simple motion discriminations are achieved with optimal sensitivity by 5% contrast, sensitivity to biological motion continues to improve for contrast levels greater than 20%. Together these results are evidence that motion analyses are necessary, but not sufficient, for intact biological motion perception, and are evidence that biological motion is mediated by an additional, contrast-dependent mechanism.

Broadly speaking, vision research has characterized motion as belonging to one of several different classes. Initially characterized as short- and long-range, most researchers now classify motion as first- or second-order (Sperling, 1989), and motion that requires tracking (sometimes referred to as third-order, (Cavanagh, 1992; Lu & Sperling, 2001). First-order motion is characterized by changes in luminance across space and can be easily captured by a Reichardt detector, motion-energy filter, or the like (Adelson & Bergen, 1985; Egelhaaf, Borst, & Reichardt, 1989; van Santen & Sperling, 1985). Typical point-light biological motion animations, with black dots against a white background, are easily detected by first-order motion systems.

Second-order motion is invisible to motion-energy models. These stimuli have differences in relative contrast or texture across space, with no differences in mean luminance. Second-order point-light animations specially constructed from texture-defined tokens against an identically textured background are blind to first-order motion mechanisms but nonetheless are easily recognized when the tokens are in motion (Ahlström, Blake, & Ahlström, 1997).

Contrast-dependent motion sensitivity is reminiscent of a special class of motion analyses that are sometimes referred to as third-order (Sperling, 1989), or attention-based motion (Cavanagh, 1992). These higher-order motion mechanisms require attention to track moving features, and are sometimes considered form based in the sense that apparent structure may guide figure-ground segregation of the relevant moving objects (e.g. shape, color, orientation). Structure-from-motion as a class of visual phenomena and isoluminant chromatic motion are both thought to be analyzed, in part, by this higher-order motion mechanism (Lu et al., 1999). The contrast required to track third-order motion is much higher than that required to make simple direction discriminations (Cavanagh, 1992). Thus one interpretation of our results is that third-order motion is the necessary and sufficient mechanism for biological motion perception.

Alternatively, one could argue that the low contrast visual displays in conjunction with the complex biological motion stimuli create visual conditions that tax attentional resources. Although biological motion perception appears effortless, organizing these point-light displays demands attentional resources (Thornton, Rensink, & Shiffrar, 2002). Patients with lesions in the parietal lobe that have difficulty on a number of high-level motion tasks known to demand attention also have great difficulty discriminating biological motion sequences (Battelli, Cavanagh, & Thornton, 2003; Battelli, Pascual-Leone, & Cavanagh, 2007). In these patients, it appears that the temporal ordering of events is disorganized, leading to deficits in a wide range of tasks including apparent motion, motion tracking, and biological motion (Battelli et al., 2007). By this interpretation, it is the temporal integration of the motion signals in biological motion that suffers from low contrasts. One could speculate that the visual system seeks to obtain more reliable information through integrating over larger contrast intervals or over extended temporal ranges.

Cortical processing of high-level motion in normal individuals has also been linked to the parietal lobe, specifically the inferior parietal lobule (IPL, Claeys, Lindsey, De Schutter, & Orban, 2003. Biological motion, on the other hand, is associated with cortical activity on the posterior superior temporal sulcus, near the temporal, occipital and parietal junction (Bonda, Petrides, Ostry, & Evans, 1996; Grossman et al., 2000; Pelphrey et al., 2003; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). The relationship between the IPL and the posterior STS is yet unclear.

Models of STS function propose this region to be the integration site of visual motion and form analyses computed in the dorsal and ventral streams, respectively (Cusick, 1996; Giese & Poggio, 2003). Individual neurons in the monkey STS code both body form and action (Oram & Perrett, 1996), and the human STS best activated by natural body articulation (Beauchamp, Lee, Haxby, & Martin, 2003; Grossman & Blake, 2001; Grossman & Blake, 2002; Thompson, Clarke, Stewart, & Puce, 2005). Thus, on the basis of the physiological and neuroimaging findings, it appears that motion computations play a critical role in biological motion perception.

The contrast dependency we observe may reflect the computing of local motion features that has been demonstrated as critical for recognition of point-light animations. Casile and Giese (Casile and Giese, 2005) created artificial biological motion animations from clusters of local opponent motion features, and found that observers spontaneously recognized these as biological. As long as the artificial point-light animations contained underlying body structure, observers were able to learn to discriminate them at a rate similar to that for learning to discriminate novel human point-light animations. These results suggest that the mechanisms mediating perception of these point-light displays may reflect more general computations imposed on analyzing complex, articulating structures.

Finally, our results speak directly to the ongoing debate over the computational importance of motion analyses in point-light biological motion perception. While computational models using only stationary form templates may be able to discriminate point-light animations (Lange and Lappe, 2006), human observers cannot achieve this without intact motion processing. Because simple motion mechanisms recover at very low contrasts while biological motion perception does not, motion analyses can not be the complete story. Motion is necessary, but not sufficient, for biological motion perception. These complex stimuli benefit from the additional saliency achieved by added contrast, which may reflect the dependence on attention-based processes.

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References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*(2), 284–299.

Ahlström, V., Blake, R., & Ahlström, U. (1997). Perception of biological motion. *Perception, 26*, 1539–1548.

Allen, H. A., & Derrington, A. M. (2000). Slow discrimination of contrast-defined expansion patterns. *Vision Research, 40*(7), 735–744.

Anstis, S., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In *Colour vision: physiology and psychophysics* (pp. 155–166). London: Academic Press.

Battelli, L., Cavanagh, P., & Thornton, I. M. (2003). Perception of biological motion in parietal patients. *Neuropsychologia, 41*, 1808–1816.

Battelli, L., Pascual-Leone, A., & Cavanagh, P. (2007). The 'when' pathway of the right parietal lobe. *Trends in Cognitive Science, 11*(5), 204–210.

Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2003). FMRI responses to video and point-light displays of moving humans and manipulable objects. *Journal of Cognitive Neuroscience, 15*(7), 991–1001.

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*(8), 5661–5663.

Bilodeau, L., & Faubert, J. (1997). Isoluminance and chromatic motion perception throughout the visual field. *Vision Research, 37*(15), 2073–2081.

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.

Casile, A., & Giese, M. A. (2005). Critical features for the recognition of biological motion. *Journal of Vision, 5*(4), 348–360.

Cavanagh, P. (1992). Attention-based motion perception. *Science, 257*(5076), 1563–1565.

Cavanagh, P., & Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research, 31*(12), 2109–2148.

Claeys, K. G., Lindsey, D. T., De Schutter, E., & Orban, G. A. (2003). A higher order motion region in human inferior parietal lobule: Evidence from fMRI. *Neuron, 40*(3), 631–642.

Cusick, C. G. (1996). The superior temporal polysensory region in monkeys. In K. S. Rockland, J. H. Kaas, & A. Peters (Eds.). *Extrastriate cortex in primates* (Vol. 14, pp. 435–468). New York: Plenum Press.

Cutting, J. E. (1978). Generation of synthetic male and female walkers through manipulation of a biomechanical invariant. *Perception, 7*(4), 393–405.

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

Egelhaaf, M., Borst, A., & Reichardt, W. (1989). Computational structure of a biological motion-detection system as revealed by local detector analysis in the fly's nervous system. *Journal of the Optical Society of America A, 6*(7), 1070–1087.

Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience, 4*(3), 179–192.

Grossman, E. D., & Blake, R. (2001). Brain activity evoked by inverted and imagined biological motion. *Vision Research, 41*, 1475–1482.

Grossman, E., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron, 35*(6), 1157–1165.

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.

Gunns, R. E., Johnston, L., & Hudson, S. M. (2002). Victim selection and kinematics: A point-light investigation of vulnerability to attack. *Journal of Nonverbal Behavior, 26*(3), 129–158.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics, 14*(2), 201–211.

Johansson, G. (1977). Studies on visual perception of locomotion. *Perception, 6*(4), 365–376.

Kastner, S., Nothdurft, H. C., & Pigarev, I. N. (1997). Neuronal correlates of pop-out in cat striate cortex. *Vision Research, 37*(4), 371–376.

Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *Journal of Neuroscience, 26*(11), 2894–2906.

Lu, Z. L., Lesmes, L. A., & Sperling, G. (1999). Perceptual motion standstill in rapidly moving chromatic displays. *Proceedings of the National Academy of Sciences of the United States of America, 96*(26), 15374–15379.

Lu, Z. L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America A, 18*(9), 2331–2370.

Mather, G., Radford, K., & West, S. (1992). Low-level visual processing of biological motion. *Proceedings of Biological Sciences, 249*(1325), 149–155.

Neri, P., Morrone, M. C., & Burr, D. C. (1998). Seeing biological motion. *Nature, 395*(6705), 894–896.

Oram, M. W., & Perrett, D. I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the Macaque monkey. *Journal of Neurophysiology, 76*(1), 109–129.

Pelphrey, K. A., Mitchell, T. V., McKeown, M. J., Goldstein, J., Allison, T., & McCarthy, G. (2003). Brain activity evoked by the perception of human walking: Controlling for meaningful coherent motion. *Journal of Neuroscience, 23*(17), 6819–6825.

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.

Ramachandran, V. S., & Gregory, R. L. (1978). Does colour provide an input to human motion perception? *Nature, 275*(5675), 55–56.

Runeson, S., & Frykholm, G. (1983). Kinematic specification of dynamics as an informational basis for person-and-action perception: Expectation, gender recognition, and deceptive intention. *Journal of Experimental Psychology: General, 112*, 585–615.

Ruppertsberg, A. I., Wuerger, S. M., & Bertamini, M. (2003). The chromatic input to global motion perception. *Visual Neuroscience, 20*(4), 421–428.

Sclar, G., Maunsell, J. H., & Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Research, 30*(1), 1–10.

Sperling, G. (1989). Three stages and two systems of visual processing. *Spatial Vision, 4*(2–3), 183–207.

Teller, D. Y., & Lindsey, D. T. (1993). Motion at isoluminance: motion dead zones in three-dimensional color space. *Journal of the Optical Society of America A, 10*(6), 1324–1331.

Thompson, J. C., Clarke, M., Stewart, T., & Puce, A. (2005). Configural processing of biological motion in human superior temporal sulcus. *Journal of Neuroscience, 25*(39), 9059–9066.

Thornton, I. M., Rensink, R. A., & Shiffrar, M. (2002). Active versus passive processing of biological motion. *Perception, 31*(7), 837–853.

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

Troscianko, T. (1987). Perception of random-dot symmetry and apparent movement at and near isoluminance. *Vision Research, 27*(4), 547–554.

Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences of the United States of America, 98*(20), 11656–11661.

van Santen, J. P., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A, 2*(2), 300–321.

Wuerger, S. M., & Landy, M. S. (1993). Role of chromatic and luminance contrast in inferring structure from motion. *Journal of the Optical Society of America A, 10*(6), 1363–1372.