Biological motion perception is cue-invariant

Craig Aaen-Stockdale McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

Benjamin Thompson McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

Robert F. Hess McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

Nikolaus F. Troje Department of Psychology, Queen's University, Kingston, Ontario, Canada

Previous work investigating whether biological motion is supported by local second-order motion has been contradictory, with different groups finding either a difference or no difference in performance compared to that obtained with first-order stimuli. Here we show psychophysically, using randomized-polarity and contrast-modulated stimuli, that detection of second-order biological motion walkers *is* worse for stimuli defined by second-order cues, but this difference is explained by a difference in visibility of the local motion in the stimuli. By mixing first-order and second-order dots within the same stimulus, we show that, when the two types of dot are equally visible, first-order noise dots can mask a second-order walker, and vice-versa. We also show that direction-discrimination of normal, inverted and scrambled walkers follow the same pattern for second-order as that obtained with first-order stimuli. These results are consistent with biological motion being processed by a mechanism that is cue-invariant.

Keywords: biological motion, second-order, motion, cue-invariance

Citation: Aaen-Stockdale, C., Thompson, B., Hess, R. F., & Troje, N. F. (2008). Biological motion perception is cue-invariant. *Journal of Vision, 8*(8):6, 1–11, http://journalofvision.org/8/8/6/, doi:10.1167/8.8.6.

Introduction

Our ability to perceive and interpret the movements of other people and animals is referred to in the literature as "biological motion perception" and is often studied using point light walkers. These stimuli are constructed from dynamic dots, with each dot representing an anatomical landmark, often the major joints (Johansson, 1973). Detailed information can be extracted from these displays, such as the nature of the specific action that is being conducted (Dittrich, 1993), the gender of the actor (Jordan, Fallah, & Stoner, 2006; Mather & Murdoch, 1994; Pollick, Kay, Heim, & Stringer, 2005; Troje, 2002; Troje, Sadr, Geyer, & Nakayama, 2006) and their identity (Jokisch, Daum, & Troje, 2006; Troje, Westhoff, & Lavrov, 2005; Westhoff & Troje, 2007).

These stimuli have several benefits for experimental designs. Firstly, point light walkers can be embedded in dot masks, the properties of which can be manipulated to control the sources of information that are available to the visual system. For example, placing a point light walker in a mask constructed from other scrambled point light walkers renders the local motion of the individual dots uninformative and forces the visual system to rely on global, configural, information (Bertenthal & Pinto, 1994; Cutting, Moore, & Morrison, 1988; Thompson, Hansen, Hess, & Troje, 2007). In addition, point light walkers can be spatially scrambled to remove configural information and force a reliance on individual dot trajectory information for task performance (Troje & Westhoff, 2006).

Imaging studies (Grèzes et al., 2001; Grossman et al., 2000; Peelen, Wiggett, & Downing, 2006; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Servos, Osu, Santi, & Kawato, 2002) and repetitive transcranial magnetic stimulation (rTMS) studies (Grossman, Battelli, & Pascual-Leone, 2005) have shown that biological motion perception recruits a specialized network of neural regions including posterior superior temporal sulcus (pSTS) and V3. Biological motion is sufficiently salient to override contradictory depth information (Bülthoff, Bülthoff, & Sinha, 1998; Lu, Tjan, & Liu, 2006) and appears to be processed efficiently in both central and peripheral vision (Thompson et al., 2007).

First- and second-order biological motion

Local motions can be defined by changes in luminance (first-order motion) or other characteristics such as flicker,

doi: 10.1167/8.8.6 Received January 15, 2008; published June 6, 2008 ISSN 1534-7362

texture and contrast. Motion that is defined by modulation of some property other than luminance is referred to as 'second-order' motion (Cavanagh & Mather, 1989) and local second-order motion is invisible to first-order motion sensors (Chubb & Sperling, 1988).

Mather, Radford, and West (1992) established that the second-order system could support biological motion, but at a reduced level. Using walking figures defined by dots that reversed their polarity randomly on each frame, they demonstrated that observers could discriminate coherent vs. positionally scrambled biological motion and could identify walker direction. However, performance was much poorer with second-order dots than for first-order dots. To prevent the use of static form cues and to reduce performance from ceiling, the walker was masked by 60 noise dots, which were randomly re-plotted on each frame. Bellefeuille and Faubert (1998) showed that animal species can be discriminated from each other in second-order biological motion sequences in which the dots on the joints are regions of flickering noise travelling across a static noise background. However, due to the nature of their stimulus, they did not have a comparable first-order version to establish whether discrimination was better or worse in second-order stimuli.

Ahlström, Blake, and Ahlström (1997), in a study that investigated several properties of biological motion perception, presented evidence which suggested that the second-order system was just as good as the first-order system at detection of biological motion. They investigated discrimination of coherent vs. phase-scrambled versions of a variety of actions. However, as the authors themselves acknowledged, ceiling effects were present in their data, which made the relative performance of first- and second-order systems difficult to quantify. In addition, a close examination of their methods suggests that a subset of their stimuli contained motion signals of both a first- and second-order nature.

Given the increased appreciation of second-order vision in the last ten years it is important to revisit this issue.

It is likely that first-order and second-order motion are initially analyzed in parallel by separate processing streams (Ledgeway & Smith, 1994; Nishida, Ledgeway, & Edwards, 1997; Smith & Ledgeway, 1997), but models of motion processing (Lu & Sperling, 1995, 2001; Wilson, Ferrera, & Yo, 1992) usually integrate these two streams at, or before, the level of global motion analysis. It is therefore unlikely that there should be any qualitative difference between the configural processing of biological motion defined by first- or second-order motion.

Work by Badcock and Khuu (2001) and Edwards and Badcock (1995) suggested that the two processing streams could remain segregated up to the level of global motion and optic flow analysis. However, Ledgeway, Hess, and McGraw (2002) demonstrated that those findings were dependent upon the relative visibility of the local elements in the stimulus. They highlighted the importance of ensuring equal visibility of local first-order and second-order motion when comparing the two systems. It may be possible to unify the findings regarding second-order biological motion with a model of biological motion in which the motion of the figures are processed by a mechanism or *mechanisms* that are "cue-invariant," but in which the local motions are weighted by their visibility.

In Experiment 1 we show, using randomized-polarity stimuli analogous to those used by Mather et al. (1992) and Ahlström et al. (1997), and stimuli composed of luminance- or contrast-modulated noise, that observers can detect the presence of a second-order walker in noise that masks the local motions of the dots, but performance is consistently worse than for first-order. In Experiment 2, we combine first- and second-order dots within the same stimulus and show that, when the luminance of the first-order dots is reduced, a point is reached where first-order noise dots effectively mask a second-order walker, and vice-versa. This finding strongly implicates a cue-invariant mechanism in the processing of biological motion. In Experiment 3, we show that subjects can discriminate walker direction in second-order stimuli. We also show that scrambling the global configuration has little effect on direction-discrimination, but a substantial inversion effect holds for both normal and scrambled walkers. These results replicate those found with first-order stimuli (Troje & Westhoff, 2006) and also suggest that the same mechanism is processing both types of stimulus.

General methods

Observers

For Experiment 1, the observers were two of the authors (CAS and BST) and three observers naive to the hypothesis (YXU, JS and GM). For Experiment 2 the observers were one of the authors (CAS) and two observers naive to the hypothesis (JS & GM).

In the direction discrimination task (Experiment 3), knowledge of the crucial role of the feet could potentially contaminate the results (Troje & Westhoff, 2006), therefore eight observers were recruited who were unfamiliar with biological motion experiments. All observers were experienced with psychophysical tasks and were compensated for their time.

Apparatus

Stimuli were presented on a CRT monitor (*Mitsubishi Diamond Pro 2070SB*) with a screen resolution of 1024 × 768. From the viewing distance of 80 cm, the screen subtended 28° × 21°. Stimulus presentation was controlled by a 1.25 GHz Macintosh G4 computer (Experiment 1) or a 2.33 GHz MacBook Pro (Experiments 2 and 3), on

which the color look-up table was gamma-corrected. Stimuli were programmed in Matlab 7.2 using the Psychophysics Toolbox routines (Brainard, 1997; Pelli, 1997).

Stimuli

Stimuli consisted of two components, a walker and a mask. The walker stimulus was constructed using the average motion capture data of 50 male and 50 female walkers. For a full explanation of the generation and representation of the stimuli, see Troje (2002). Participants viewed the stimuli binocularly and centrally at a viewing distance of 80 cm. The mask was presented within an area that subtended 8.6 × 8.6° visual angle. The walker was presented within the mask area and was made up of 11 dots. The height of the walker subtended 6.4°.

Walkers were presented facing left or right with no translation, as if walking on a treadmill. They were presented upright or inverted, and spatially scrambled or coherent. In the scrambled condition, the phase relationships between the dots were left intact, but the spatial position of each dot was randomly relocated within half the mask area. From trial to trial, walker position was jittered within the noise display up to 0.6 of the mask area left or right and 0.4 of the mask area above or below central presentation. In the inverted conditions, walkers were mirror flipped about a horizontal axis.

In Experiments 1 and 2, the mask was composed of scrambled walkers and was constructed from the same dot elements as the walker stimuli. The mask was generated by scrambling the spatial positions of dots taken from additional walker stimuli, within the stimulus area. The phases of the mask dots were also scrambled to provide a mask constructed of individual elements moving along the same trajectories as the target walker, but with no coherent spatial or temporal relation to one another. By embedding the point light displays in masks constructed of scrambled point light stimuli, the individual dot trajectory information in the display is rendered progressively less useful (Bertenthal & Pinto, 1994; Cutting et al., 1988). The ability to detect biological motion in a scrambled walker mask therefore requires global integration of the dots constituting the walker and subsequent segregation of the resulting figure from the noise dots. The global processes involved in biological motion perception are therefore isolated and the observer cannot complete the task by simply spotting the motion of any particular part of the walker. In central vision, masks composed of linearly moving or flickering dots have very little effect except at very high noise densities—probably a simple effect of obliterating the walker dots (Cutting et al., 1988; Thompson et al., 2007).

In Experiment 3, in which we used a direction-discrimination paradigm instead of the detection paradigm used in other experiments, the mask was a static flickering noise mask of 100 dots. The mask dots were randomly positioned within the mask area, and did not move. They had a lifetime of 200 ms, after which they were erased and replotted. Their phases were randomized so that they did not appear and disappear at the same time. Using this flicker mask allowed us to investigate the effects of local motions of biological motion perception, while eliminating static form cues and bringing performance down off ceiling.

Experiment 1

Two different types of second-order stimulus were used in this study. The first stimulus was a random-polarity (RP) stimulus similar to that used by Mather et al. (1992) and Ahlström et al. (1997). The background was a mean luminance gray and the polarity of the walker and mask dots were randomly assigned to be either maximum or minimum luminance on each new frame. This produced a *maximum* flicker frequency of 37.5 Hz, which is higher than that used by Mather et al. (1992) (14 Hz) and Ahlström et al. (1997) (9.5 Hz), but still within the visible range (Kelly, 1961). The dots were 4 pixels in diameter, which subtended 0.11° of visual angle. This was compared to a similar (first-order) display in which the polarity of the dots was randomly assigned before the beginning of the trial and did not change throughout the stimulus presentation (fixed polarity or FP). As previous reports have compared an RP stimulus to one in which the dots were all the same polarity, observer CAS also completed a control condition in which all the dots in the display were the same polarity, to control for any grouping effect that this may have had.

The luminance- and contrast-modulated stimuli used in Experiment 1 are similar to those used by Ahlström et al. (1997), but their stimuli consisted of uniform gray dots on a background of full-contrast binary noise, which would have meant that their LM stimuli contained a contrast-modulation in addition to a luminance-modulation.

We used a differently modulated stimulus. In this stimulus, the contrast of the background noise was 10% and the contrast within the luminance-modulated dots was the same as the background contrast, rather than a uniform gray, which eliminated the contrast-modulation artifact. The LM dots differed from the background only in their mean luminance. The depth of the luminance modulation of the LM dots is calculated by

$$\text{Luminance modulation depth} = (DL_{mean} - BL_{mean})/(DL_{mean} + BL_{mean}), \quad (1)$$

where DL_{mean} is the mean luminance of the noise within the dots.

For the contrast-modulated stimuli, the Michelson contrast $[(L_{max} - L_{min}) / (L_{max} + L_{min})]$ of the 2D binary

noise within the dots was increased above that of the background. The depth of the contrast modulation of the CM dots is calculated by

$$\text{Contrast modulation depth} = (\text{DC} - \text{BC})/(\text{DC} + \text{BC}), \quad (2)$$

where DC is the Michelson contrast of the noise within the dots and BC is the contrast of the background noise.

Procedure

We used the method of constant stimuli to construct a psychometric function sampled at nine logarithmically spaced mask densities (from 20 to 200 noise dots), with 50 observations per point. In each trial, two stimuli (a normal coherent walker and a spatially scrambled walker) were shown one after the other within a noise mask. Each was presented for 800 ms. The two-interval forced choice (2IFC) task was to report in which interval the coherent walker had appeared, the other interval contained a scrambled walker, which simply became part of the mask and was therefore undetectable.

For the FP and RP conditions, a trial started with presentation of a fixation cross for 500 ms followed by presentation of the first stimulus. After an inter-stimulus interval of 500 ms the second stimulus was presented. After the second interval, a prompt appeared on the screen and the subject reported whether the coherent walker had appeared in the first or second interval. Responding triggered the next trial.

For the LM and CM conditions, each trial began with the presentation of a new static noise field for 500 ms. After this waiting period the dots appeared and began moving against the background, after which they disappeared leaving only the background noise. After an inter-stimulus interval of 500 ms, the dots for the second stimulus were displayed on top of the same noise background. After the subject responded, the background noise was immediately replaced by a new noise sample ready for the next trial.

Results

Signal-to-noise was calculated for any particular condition as the number of signal dots divided by the number of noise dots. Threshold (75% correct) signal-to-noise ratios were obtained from psychometric functions fitted to the data using the psignifit toolbox version 2.5.6 for Matlab, which implements the maximum-likelihood

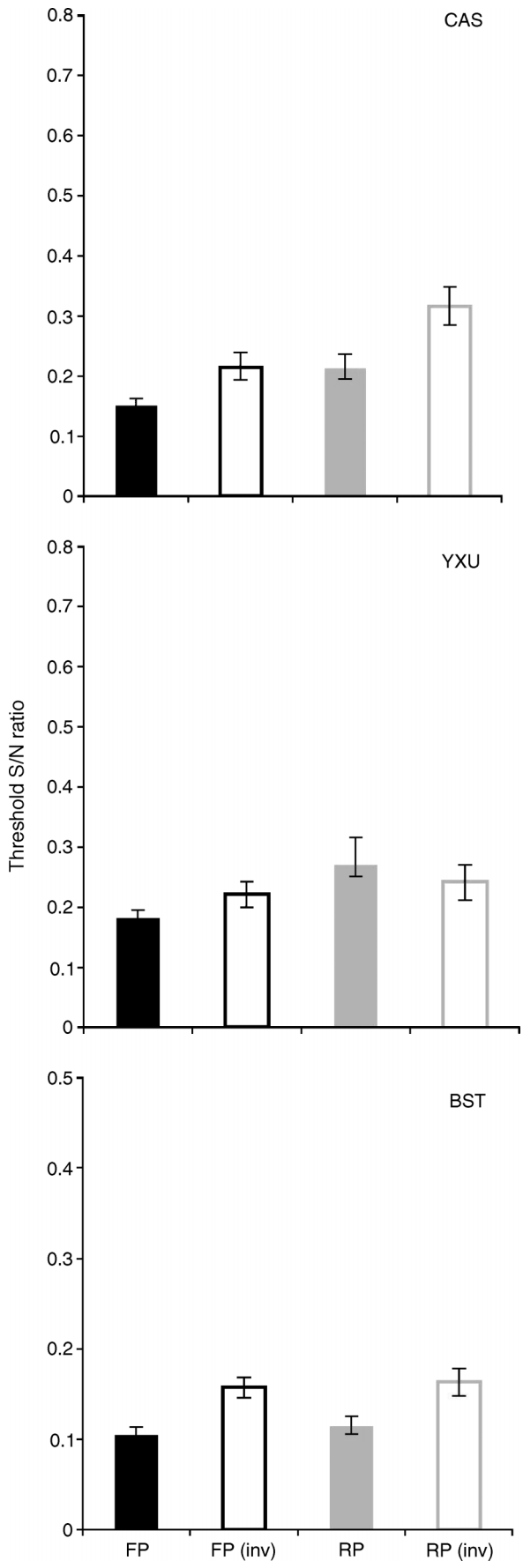

Figure 1. Detection thresholds for normal and inverted fixed- and randomized-polarity walkers in scrambled walker noise. Error bars show 68% confidence intervals.

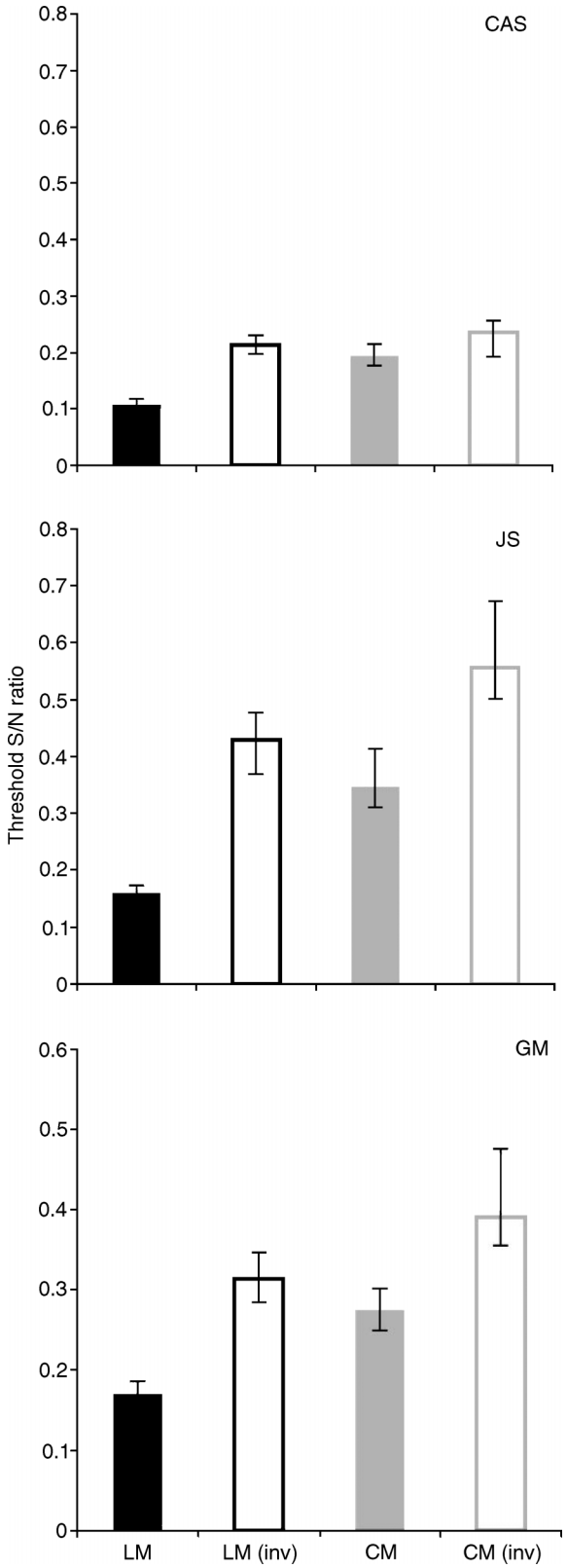

Figure 2. Detection thresholds for normal and inverted luminance- and contrast-modulated walkers in scrambled walker noise. Error bars show 68% confidence intervals.

method described by Wichmann and Hill (2001a). Confidence intervals (68%) were found by the BCa bootstrap method implemented by psignifit, based on 1999 simulations (Wichmann & Hill, 2001b). Results are shown in Figures 1 and 2.

Detection thresholds for first-order walkers (LM and FP) were consistently lower than detection thresholds for second-order walkers (CM and RP). The FP stimuli used in both the current and previous studies (Ahlström et al., 1997; Mather et al., 1992) were composed of dots of similar polarity. As the second-order (RP) stimulus changed polarity, some dots would be white when others were black. It is possible therefore that the impaired performance for the RP stimuli demonstrated here and also found by Mather et al. (1992) was due to a failure of grouping between the on- and off-pathways rather than second-order motion *per se*. Observer CAS, therefore, ran a control condition in which all the dots in the FP stimulus (walker and mask) were always the same polarity. There was no difference between thresholds for similar polarity dots versus dissimilar polarity dots suggesting that the second-order nature of the stimulus, rather than a failure to group black and white dots, was responsible for the poorer performance in the RP conditions.

An inversion effect was found for all conditions, although it was marginally less convincing for second-order conditions (see observer CAS in condition CM and observer YXU in condition RP).

The difference between discrimination thresholds for first- and second-order stimuli could result from a difference in sensitivity to the dots rather than qualitative differences in global integration between the first- and second-order pathways. It would certainly be more parsimonious to postulate a single biological motion system combined with differential sensitivity to local first- and second-order motion. If this is the case, then the two types of motion should interact when equal in visibility. Experiment 2 tested this hypothesis.

Experiment 2

A direct test of cue invariance in biological motion processing would be to combine first- and second-order dots within the same stimulus and see whether one interacts with the other. Experiment 2 aimed to demonstrate that, if of similar visibility, first-order biological motion could be masked by second-order noise and vice-versa.

Procedure

We used the same LM and CM stimuli as used in Experiment 1. The task was a two-interval forced choice

where the observer had to detect which of two intervals contained a walker. The other interval contained a scrambled walker and both were masked by scrambled walker noise dots. The total number of noise dots was varied from 29 to 349 in nine logarithmically spaced steps to extract a psychometric function. Fifty observations were collected per point. There were two separate populations of dots in the stimulus. One population contained the walker and some noise dots. The other population contained just noise dots. There was *always* the same number of dots in each population, but the total number of noise dots was varied (an example of the stimulus can be viewed here: [http://journalofvision.org/8/8/6/images/movie01.mov]). Threshold signal-to-noise ratios were

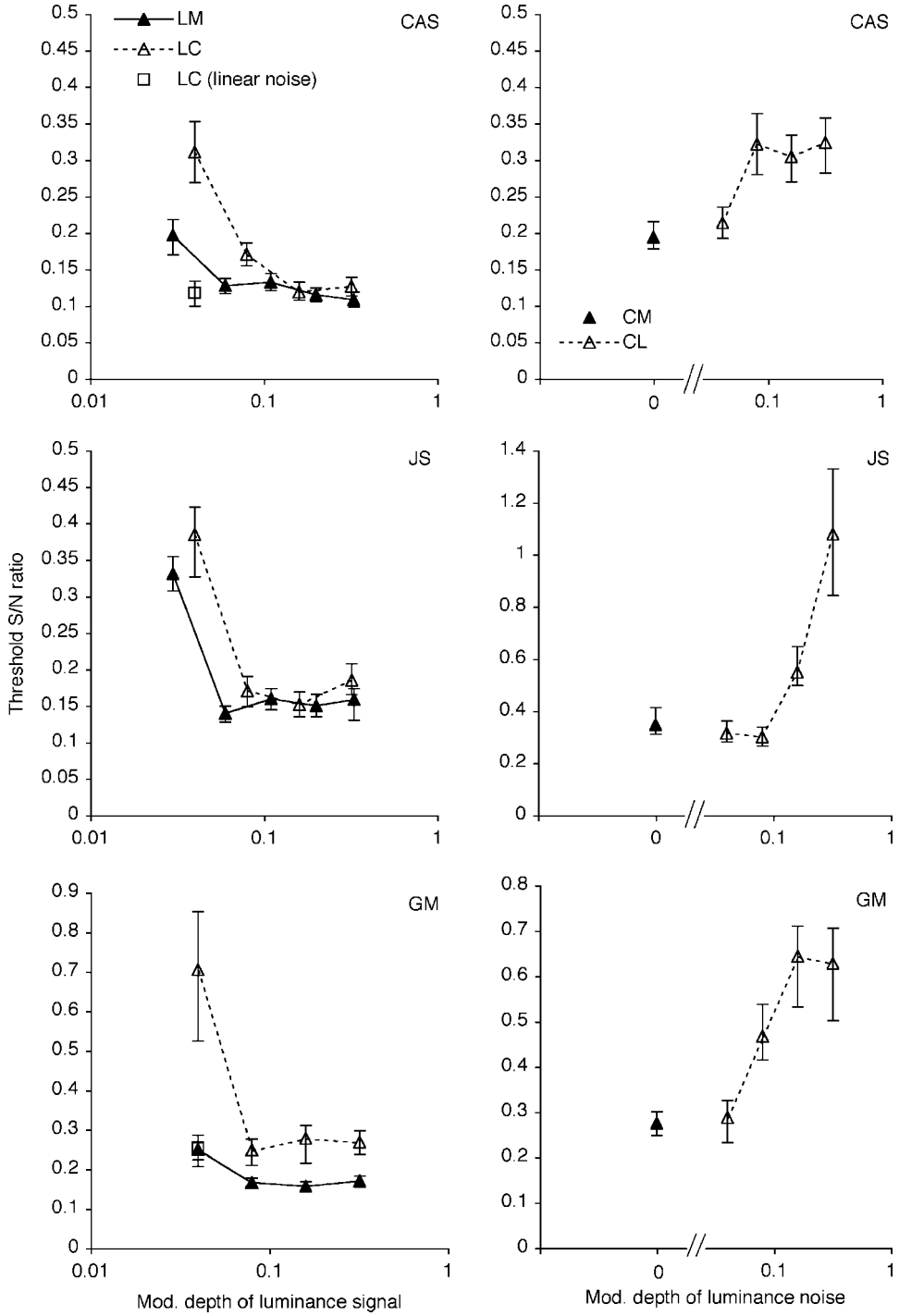

Figure 3. Interactions between first- and second-order dots in a biological motion stimulus are crucially dependent upon the relative visibility of the local motions. Closed symbols show thresholds for LM or CM stimuli. Without additional noise dots. Open symbols show performance with additional noise dots of a different type. Error bars show 68% confidence.

obtained with first-order dots of varied luminance in the absence/presence of an additional population of second-order noise dots. Thresholds were also obtained for full contrast second-order dots in isolation, or with an additional population of first-order noise dots of varied luminance.

Participants CAS and JS were tested at slightly different modulation depths with/without second-order dots to obtain the whole shape and extent of the LM and LC functions. Participant GM was tested at exactly the same modulation depths with/without second-order dots.

Results

The results for three observers are presented in Figure 3 for a first-order walker (left) and a second-order walker (right). When the walker was first-order and was presented with only first-order masking dots (LM), signal-to-noise ratios were good across most of the range (left, solid line). If an additional population of second-order dots was added to the stimulus (LC), they had no effect when the first-order dots were high luminance, but when the luminance of the first-order population—which contained the walker—was reduced, the second-order dots began to interfere with detection, raising thresholds dramatically (left, dashed line). If the walker was second-order and the additional population of noise dots was first-order (CL), they interfered strongly at high luminance (right, dotted line), but as the luminance of the first-order dots was reduced, performance dropped to a level equal to that obtained when there were no extra dots at all (right, CM).

Moving contrast-modulations contain first-order motion signals as well as second-order information, but the first-order signals are drift-balanced and therefore useless for extracting the motion of the contrast modulation. It is possible that this first-order "noise" was masking the signal carried by the luminance-modulated dots when the signal was low visibility, rather than anything related to impairment of a biological motion system. We believe that this is unlikely, since it has been repeatedly demonstrated that random linear motion signals (such as would result from a drift-balanced contrast modulation) have very little masking effect on biological motion, with its very distinctive circular and pendulous motion trajectories (Cutting et al., 1988; Thompson et al., 2007). However, two of the subjects (CAS and GM) carried out a control condition, at the lowest modulation depth tested for the combined (LC) condition, but in which the additional CM noise dots were moving linearly, rather than being taken from scrambled walkers. If performance was impaired in this condition, it would have been likely that first-order noise generated by the CM dots was masking the LM signal. However, this turned out not to be the case. The results for observer GM fell exactly on top of those for the LM condition, while the results for observer CAS fell very close to the LM function, although slightly below their expected level. This condition (LC linear noise) was completed last and a learning effect may explain this slight discrepancy. On the whole, the addition of CM dots only impaired detection of LM biological motion if the CM dots were of similar visibility *and if they were moving biologically*.

Experiment 3

Experiment 1 demonstrated that detection thresholds for a variety of second-order stimuli show an inversion effect akin to that found with first-order stimuli. Experiment 2 showed that detection thresholds (signal/noise ratios) can be impaired by dots of a different type when visibility of the local elements comprising the walker stimuli was varied. The goal of Experiment 3 was to establish whether the direction of second-order biological motion could be discriminated and whether direction-discrimination was dependent upon configural or local motion cues. Troje and Westhoff (2006) found that the inversion effect for direction-discrimination also occurred if the positions of the dots in the walker stimulus were scrambled, entirely removing form information. Previously, the inversion effect had been ascribed to a disruption of configural processing. Troje and Westhoff went on to show that inversion of just the feet in a walker stimulus resulted in an inversion effect suggesting that the local motions of the feet, specifically, were used to discriminate walker direction and the inversion effect can result from a disruption of this signal.

Procedure

This experiment was a partial replication of Troje and Westhoff (2006), but the contrast-modulated stimuli were generated in the manner outlined for Experiment 2. Walkers were presented walking right or left, upright or inverted and either scrambled or coherent. The mask was a static flickering noise mask of 100 dots. The mask dots were randomly positioned within the mask area, and did not move. They had a lifetime of 200 ms, after which they were erased and replotted. Their phases were randomized so that they did not appear and disappear at the same time. The observers' task was to indicate the direction in which the walker appeared to walk.

Results

The average proportions of correct responses for eight naive observers are presented in Figure 4. As can be seen, inversion of the stimulus drastically impaired performance. However, scrambling the stimulus did not seem to have much of an effect unless the stimulus was also

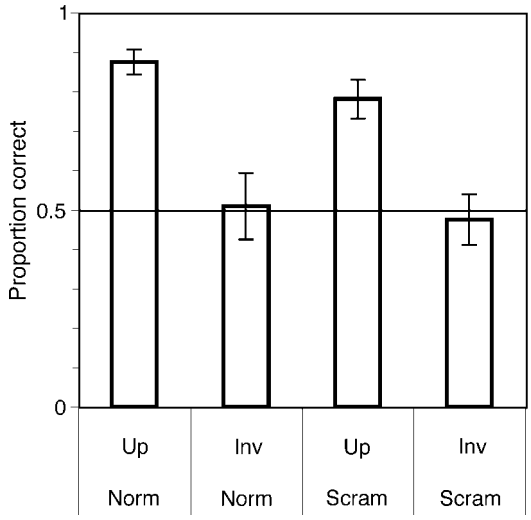

Figure 4. The average proportion of correct responses in a direction-discrimination task. N = 8 naive observers. Error bars show 68% confidence limits.

inverted. A 2 × 2 ANOVA carried out on the data showed a highly significant main effect of inversion ($F(1,28)$ = 29.34, $p < 0.001$), but no main effect of scrambling ($F(1,28) = 0.82$, NS) and no interaction ($F(1,28) = 0.3$, NS). This implies that the second-order inversion effect for direction-discrimination, like that for first-order, is not only a result of a global configural inversion effect, but an inability to reliably use the cues provided by the local dot motions. This pattern of results is identical to that obtained for first-order stimuli and suggests that the same mechanism is processing both types of stimulus.

Discussion

Although second-order biological motion appears to be weaker than performance for first-order when both stimuli are presented at maximum contrast (Experiment 1), we hypothesized that this was a result of differential visibility of the local motions in the stimulus, resulting in differential weighting at higher stages of the motion system, rather than any qualitative difference between the pathways or a preference for first-order input to the biological motion system. We directly tested this idea by combining both first- and second-order dots within the same stimulus (Experiment 2). This technique has previously been used to show cue-invariance in global motion processing (Ledgeway et al., 2002). We show in this paper that there are visibility-dependent interactions between the two pathways for biological motion, strongly supporting the idea of a cue-invariant biological motion system.

In addition, naive observers could discriminate the direction of both normal and scrambled second-order walkers, provided the stimuli were not inverted (Experiment 3). This pattern of results is identical to that obtained for first-order motion and suggests that biological motion of either type is subject to an inversion effect that operates on the local motion of individual dots, particularly those of the feet (Troje & Westhoff, 2006).

Our results suggest that biological motion is carried out by cue-invariant mechanisms and that differences in performance reported between first- and second-order biological motion are a result of the differential sensitivity of the visual system to these two different types of local motion, rather than any difference in first- or second-order biological motion processing *per se*. This is consistent with the level at which biological motion analysis is thought to be taking place in the visual system. Several imaging and rTMS studies have highlighted the importance of posterior superior temporal sulcus (pSTS) to biological motion perception (Grèzes et al., 2001; Grossman et al., 2000, 2005; Pelphrey et al., 2005). This is an area that is likely to receive input from V5. One study has suggested a role for area VP/V3v (Servos et al., 2002) an extrastriate area with connections to V5. Area V5 appears to be active during biological motion perception, but not preferentially. There is much evidence for cue-invariance in V5/MT (Albright, 1992; Stoner & Albright, 1992) and MST (Aaen-Stockdale, Ledgeway, & Hess, 2007; Geesaman & Andersen, 1996) so it would be surprising if biological-motion selective areas higher than this, such as pSTS, responded differentially to first- and second-order motion.

This leaves open the question of why exactly second-order local motion is weaker than first-order. The difference in sensitivity could result from the fact that second-order detectors respond to first-order motion in addition to second-order motion. This would mean that there are more mechanisms detecting first-order motion than second-order motion. First-order thresholds may therefore reflect a pooling of the responses from both first-order and second-order mechanisms and may be lower due to probability summation.

It has been suggested that the differences between first- and second-order processing could be the result of a delay in processing second-order motion, caused by the additional rectification necessary (Yo & Wilson, 1992). Other authors suggest that it is a result of more severe low-pass temporal filtering of second-order motion (Derrington, Badcock, & Henning, 1993). However, neither of these explanations fully explain the data. A more complete explanation may be that second-order motion mechanisms are simply less direction selective. Ledgeway and Hess (2002) showed that second-order mechanisms have poorer direction selectivity than first-order mechanisms.

Our study does not really contribute to this debate, as we are dealing with processing at a global level, by which point it appears that first- and second-order signals have been combined. The direction-selectivity hypothesis may, however, explain the relative weight of motion signals

from first- and second-order stimuli. It is entirely possible that by reducing the luminance of the first-order dots, we are smearing the temporal energy in the first-order dots to the point where discrimination of their motion direction is equivalent to that obtained for second-order dots.

Both first- and second-order stimuli show an inversion effect for detection and discrimination. The inversion effect was originally considered to be caused by a failure of configural processing (Dittrich, 1993; Proffitt & Bertenthal, 1990; Reed, Stone, Bozova, & Tanaka, 2003), but the fact that an inversion effect occurs with scrambled stimuli suggests that, in addition to global form inversion effects, there is a second inversion effect mediated by local motion trajectories, which reveals a mechanism tuned to the distinctive motion of the lower extremities of an animal in locomotion (Troje & Westhoff, 2006). Previous studies have used the presence of inversion effects to infer intact biological motion processing in clinical populations (Neri, Luu, & Levi, 2007; Thompson, Troje, Hansen, & Hess, 2008). Our data show the presence of both configural and local motion trajectory-based inversion effects for second-order biological motion, a pattern of results that is identical to that obtained with first-order stimuli. This suggests that the same mechanism is responsible for processing both types of stimulus.

Our results are consistent with, and substantially extend, the findings of Mather et al. (1992). There are, however, inconsistencies between our results (especially Experiment 1) and those of Ahlström et al. (1997). While Ahlström et al. (1997) argue that there is no difference in performance between first- and second-order, we have demonstrated that there is a difference, but this is dependent upon the relative visibility of the local motion signals. The difference between our data and theirs can be explained by differences in stimulus construction.

Our second-order stimuli are composed of dots within which the contrast of the noise background is increased. The comparable stimulus used by Ahlström et al. (1997) (the "texture human") was constructed from dots composed of patches of random noise that moved across a background noise field of the same average luminance. Whilst in any single frame, the dots were indistinguishable from the background, the movement of these regions across a background would still have generated first-order motion signals, making it difficult to separate the relative influences of the two systems.

A further consideration is the ceiling effect evident in the data presented by Ahlström et al. (1997). The d' scores reported for most conditions were ~3, which signifies near-perfect performance (Macmillan & Creelman, 1991). This high level of performance may have been due to the absence of masking dots, the use of stimuli in which actors were performing highly informative actions and long presentation durations (>1 sec).

In the present study, we demonstrated that the differences between first- and second-order motion evident in previous studies, and replicated here (Experiment 1), can be explained by differential visibility of first- and second-order motion signals to an otherwise cue-invariant biological motion mechanism. When the visibility of local motion signals are equated, the two pathways interact predictably.

Acknowledgments

We would like to thank Shin'ya Nishida, Michael Landy, and one other anonymous reviewer for their very useful comments. This research was supported by CIHR grant number MOP 10808 to RFH, NSERC grant number 298198-05, and CFI project grant number 201705 to NFT.

Commercial relationships: none.
Corresponding author: Craig Aaen-Stockdale.
Email: craig.aaenstockdale@mcgill.ca.
Address: McGill Vision Research, 687 Pine Avenue West, Montreal, Quebec, Canada H3A 1A1.

References

Aaen-Stockdale, C., Ledgeway, T., & Hess, R. F. (2007). Second-order optic flow deficits in amblyopia. *Investigative Ophthalmology & Visual Science, 48,* 5532–5538. [PubMed]

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

Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science, 255,* 1141–1143. [PubMed]

Badcock, D. R., & Khuu, S. K. (2001). Independent first- and second-order motion energy analyses of optic flow. *Psychological Research, 65,* 50–56. [PubMed]

Bellefeuille, A., & Faubert, J. (1998). Independence of contour and biological-motion cues for motion-defined animal shapes. *Perception, 27,* 225–235. [PubMed]

Bertenthal, B. I., & Pinto, J. (1994). Global processing of biological motions. *Psychological Science, 5,* 221–225.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Bülthoff, I., Bülthoff, H., & Sinha, P. (1998). Top-down influences on stereoscopic depth-perception. *Nature Neuroscience, 1,* 254–257. [PubMed]

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision, 4,* 103–129. [PubMed]

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, Optics and Image Science, 5,* 1986–2007. [PubMed]

Cutting, J. E., Moore, C., & Morrison, R. (1988). Masking the motions of human gait. *Perception & Psychophysics, 44,* 339–347. [PubMed]

Derrington, A. M., Badcock, D. R., & Henning, G. B. (1993). Discriminating the direction of second-order motion at short stimulus durations. *Vision Research, 33,* 1785–1794. [PubMed]

Dittrich, W. H. (1993). Action categories and the perception of biological motion. *Perception, 22,* 15–22. [PubMed]

Edwards, M., & Badcock, D. R. (1995). Global motion perception: No interaction between the first- and second-order motion pathways. *Vision Research, 35,* 2589–2602. [PubMed]

Geesaman, B. J., & Andersen, R. A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *Journal of Neuroscience, 16,* 4716–4732. [PubMed] [Article]

Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *Neuroimage, 13,* 775–785. [PubMed]

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,* 711–720. [PubMed]

Grossman, E. D., Battelli, L., & Pascual-Leone, A. (2005). Repetitive TMS over posterior STS disrupts perception of biological motion. *Vision Research, 45,* 2847–2853. [PubMed]

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

Jokisch, D., Daum, I., & Troje, N. F. (2006). Self recognition versus recognition of others by biological motion: Viewpoint-dependent effects. *Perception, 35,* 911–920. [PubMed]

Jordan, H., Fallah, M., & Stoner, G. R. (2006). Adaptation of gender derived from biological motion. *Nature Neuroscience, 9,* 738–739. [PubMed]

Kelly, D. H. (1961). Visual response to time-dependent stimuli. I. Amplitude sensitivity measurements. *Journal of the Optical Society of America, 51,* 422–429. [PubMed]

Ledgeway, T., & Hess, R. F. (2002). Failure of direction identification for briefly presented second-order motion stimuli: Evidence for weak direction selectivity of the mechanisms encoding motion. *Vision Research, 42,* 1739–1758. [PubMed]

Ledgeway, T., Hess, R. F., & McGraw, P. V. (2002). Masking effects between local first-order and second-order motions in the extraction of global-motion direction depend critically on stimulus visibility. *Perception, 31* (ECVP Abstract Supplement).

Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research, 34,* 2727–2740. [PubMed]

Lu, H., Tjan, B. S., & Liu, Z. (2006). Shape recognition alters sensitivity in stereoscopic depth discrimination. *Journal of Vision, 6*(1):7, 75–86, http://journalofvision.org/6/1/7/, doi:10.1167/6.1.7. [PubMed] [Article]

Lu, Z. L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research, 35,* 2697–2722. [PubMed]

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, Optics, Image Science, and Vision, 18,* 2331–2370. [PubMed]

Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. Cambridge: Cambridge University Press.

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

Mather, G., Radford, K., & West, S. (1992). Low-level visual processing of biological motion. *Proceedings of the Royal Society B: Biological Sciences, 249,* 149–155. [PubMed]

Neri, P., Luu, J. Y., & Levi, D. M. (2007). Sensitivity to biological motion drops by approximately 1/2 log-unit with inversion, and is unaffected by amblyopia. *Vision Research, 47,* 1209–1214. [PubMed] [Article]

Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system. *Vision Research, 37,* 2685–2698. [PubMed]

Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron, 49,* 815–822. [PubMed] [Article]

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

Pelphrey, K. A., Morris, J. P., Michelich, C. R., Allison, T., & McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: An FMRI study of eye, mouth and hand movements. *Cerebral Cortex, 15,* 1866–1876. [PubMed] [Article]

Pollick, F. E., Kay, J. W., Heim, K., & Stringer, R. (2005). Gender recognition from point-light walkers. *Journal of Experimental Psychology: Human Perception and Performance, 31,* 1247–1265. [PubMed]

Proffitt, D. R., & Bertenthal, B. I. (1990). Converging operations revisited: Assessing what infants perceive using discrimination measures. *Perception & Psychophysics, 47,* 1–11. [PubMed]

Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science, 14,* 302–308. [PubMed]

Servos, P., Osu, R., Santi, A., & Kawato, M. (2002). The neural substrates of biological motion perception: An fMRI study. *Cerebral Cortex, 12,* 772–782. [PubMed] [Article]

Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: Fact or artifact? *Vision Research, 37,* 45–62. [PubMed]

Stoner, G. R., & Albright, T. D. (1992). Motion coherency rules are form-cue invariant. *Vision Research, 32,* 465–475. [PubMed]

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):12, 1–7, http://journalofvision.org/7/10/12/, doi:10.1167/7.10.12. [PubMed] [Article]

Thompson, B., Troje, N. F., Hansen, B. C., & Hess, R. F. (2008). Amblyopic perception of biological motion. *Journal of Vision, 8*(4):22, 1–14, http://journalofvision.org/8/4/22/, doi:10.1167/8.4.22. [PubMed] [Article]

Troje, N. F. (2002). Decomposing biological motion: A framework for analysis and synthesis of human gait patterns. *Journal of Vision, 2*(5):2, 371–387, http://journalofvision.org/2/5/2/, doi:10.1167/2.5.2. [PubMed] [Article]

Troje, N. F., Sadr, J., Geyer, H., & Nakayama, K. (2006). Adaptation aftereffects in the perception of gender from biological motion. *Journal of Vision, 6*(8):7, 850–857, http://journalofvision.org/6/8/7/, doi:10.1167/6.8.7. [PubMed] [Article]

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

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

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

Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63,* 1293–1313. [PubMed]

Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception & Psychophysics, 63,* 1314–1329. [PubMed]

Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9,* 79–97. [PubMed]

Yo, C., & Wilson, H. R. (1992). Perceived direction of moving two-dimensional patterns depends on duration, contrast, and eccentricity. *Vision Research, 32,* 135–147. [PubMed]