Seeing the world topsy-turvy: The primary role of kinematics in biological motion inversion effects

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Abstract. Physical inversion of whole or partial human body representations typically has catastrophic consequences on the observer’s ability to perform visual processing tasks. Explanations usually focus on the effects of inversion on the visual system’s ability to exploit configural or structural relationships, but more recently have also implicated motion or kinematic cue processing. Here, we systematically tested the role of both on perceptions of sex from upright and inverted point-light walkers. Our data suggest that inversion results in systematic degradations of the processing of kinematic cues. Specifically and intriguingly, they reveal sex-based kinematic differences: Kinematics characteristic of females generally are resistant to inversion effects, while those of males drive systematic sex misperceptions. Implications of the findings are discussed.

Keywords: biological motion, sex perception, inversion, point-light walkers, structural processing, kinematic processing.

1 Introduction

“Mister Squiggle”—the marionette namesake of a long-running Australian children’s show who happened to have a pencil for a nose—had a singular and delightful skill. It was to use his nose to draw images that were upside down. Only when his hapless human sidekick reoriented the image would its subject matter become clear: A car or tree or a human’s face would emerge from what just moments before had seemed a meaningless graphic jumble http://www.youtube.com/watch?v=HwNrG9a22nc.

In the field of human perception, this phenomenon is rather more formally known as the Inversion Effect. It manifests in a range of situations such that physical orientation of an image determines its interpretability: Images that easily are interpreted when presented right side up are rendered meaningless when presented upside down. In the case of the Thatcher Illusion (Thompson, 1980), for example, only when a previously inverted image is presented right side up does it become clear the well-known face actually has incorporated into it gross structural anomalies (see, for example, Bartlett & Searcy, 1993).

Whole body representations are similarly prone to the effects of physical inversion. Point-light walkers—usually a high-value stimulus from which observers can almost instantly interpret complex and detailed information (Johansson, 1973)—become a far less reliable source of information when presented upside down (Ikeda, Blake, & Watanabe, 2005; Pavlova & Sokolov, 2000; Proffitt & Bertenthal, 1990; Suni, 1984). Moreover, the consequences to interpretability of physical inversion seem to be generalized: They manifest across a range of tasks including detection of figures in visual noise (Bertenthal & Pinto, 1994; Pavlova & Sokolov, 2000; Troje, 2003), direction discrimination (Bertenthal & Pinto, 1994), action recognition (Dittrich, 1993; Shipley, 2003), and sex discrimination (Barclay, Cutting, & Kozlowski, 1978).

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Accounts of the mechanisms underlying these effects usually focus on the consequences of physical inversion for configural or structural processing (Bertenthal & Pinto, 1994; Dittrich, 1993; Proffitt & Bertenthal, 1990; Reed, Stone, Bozova, & Tanaka, 2003; Shiffrar, Lichtey, & Chatterjee, 1997). In the case of both faces and point-light walkers, the consensus view has been that mechanisms specialized for those respective types of body representations are so highly tuned to the “normal” or right-side-up structure that disruptions imposed by physical inversion undermine the entire stimulus processing sequence (Freire, Lee, & Symons, 2000; Leder & Bruce, 2000; Maurer, Le Grand, & Mondloch, 2002; Proffitt & Bertenthal, 1990; Reed et al., 2003).

More recently, however, evidence has emerged suggesting the story may be more complex. Troje and Westhoff (2006) argue that, in the case of biological motion perceptions at least, the explanatory power of the so-called “shape inversion effect” is insufficient. They posit an alternative account in which motion or kinematic processing also plays a role. According to their model, there is an hierarchy of contributions to the inversion effect such that disruption of structural processing plays a secondary role to disruption of kinematic processing. That is, while the processing of structural cues remains relatively uncompromised when point-light figures are presented upside down, the processing of kinematic cues is strongly compromised (Troje & Westhoff, 2006).

Interestingly, Johnson and Tassinary (2005) independently propose a model for the perception of sex cues that is consistent with Troje and Westhoff’s (2006) account of inversion effects. Like Troje and Westhoff, Johnson and Tassinary propose a structure/kinematic processing hierarchy, but one that mediates not biological motion perceptions generally but sex discriminations specifically. In particular, Johnson and Tassinary propose that, when discriminating the sex of an individual, structural cues are the primary and direct driver of sex perceptions and that kinematic cues are secondary, or indirect indicators. In the context of inversion effects, Johnson and Tassinary’s model is consistent with Troje and Westhoff’s: It predicts that under inversion conditions, perceptions arising from the processing of structural cues should be more robust to inversion than perceptions driven by the processing of kinematic cues.

There is some evidence to support those two models, but it is controversial. Barclay et al. (1978) first reported that inversion of point-light walkers leads to systematic misperceptions of the sex of the walkers such that inverted females look male, and inverted males look female. Mather and Murdoch (1994), investigating the mechanisms that give rise to perceived sex, proposed that kinematic cues (rather than structural cues) mediate sex perceptions. They argued that the inversion effects reported by Barclay et al. may have been mediated by confusions driven by the relative velocities of hip and shoulder markers in Barclay’s original point-light displays. While the idea that kinematic rather than structural cues drive sex perceptions contradicts the model proposed by Johnson and Tassinary (2005), Mather and Murdoch’s account of the effect is consistent with the idea that inversion disrupts the processing of kinematic rather than structural information.

With that in mind, the general aim of the experiments described here was to investigate the impact of inversion on biological motion processing. More specifically, the experiments reported here investigated the impact of inversion on sex discriminations made on the basis of structural and kinematic cues. Experiment 1 shows that sex discriminations made on the basis of structural cues alone are unaffected by inversion. Sex discriminations made on the basis of kinematic cues are disrupted by inversion, but only for male point-light walkers. Experiment 2 shows those effects persist when kinematic sex cues are paired with coherent structural sex cues. Together, these experiments confirm a sex cues processing hierarchy that is consistent with the models of biological motion processing proposed by both Troje and Westhoff (2006) and Johnson and Tassinary (2005). In that hierarchy, structural cues to sex are more resilient to orientation changes than are kinematic cues.

2 Methods

2.1 Participants

Participants comprised seven males and seven females (age-range: 21–56 years). All had normal or corrected-to-normal vision. Prior to testing, each participant received an information sheet explaining the experimental task and informed written consent was obtained. Experiments were conducted in accordance with the Helsinki Declaration (2008).

2.2 Design

A repeated-measures design was used in both experiments. Using a two-alternative forced-choice (2AFC) paradigm, participants discriminated each of a series of point-light walkers (presented in ran-
domized order) as “male” or “female.” The independent variables were strength of sex cues (structure model/kinematic model—see below) and point-light orientation (upright vs inverted). The dependent variable was proportion of “male” responses for each type of stimulus (model combination + orientation) shown. Analyses of the data were conducted by using the PSY statistical program (Professor Kevin Bird, University of NSW, Kensington NSW, Australia).

2.3 Apparatus
Stimuli were presented on a 19” monitor positioned 37 cm from each participant such that 1 cm subtended 1° of visual angle. Participants indicated their responses using a standard QWERTY keyboard (M and Z keys signalling female or male counterbalanced across participants). PointLightLab (Version 4.5.10), a custom-developed program, was used to generate point-light walker stimuli.

2.4 Stimuli
The point-light walker stimuli used for these experiments were adapted from 13 models constructed by Nikolaus Troje (2002, 2008). Those models were constructed from actual walkers (50 females, 50 males) using the techniques described elsewhere (Troje, 2008). The 13 models provided describe a gender continuum that steps from an extreme female model (continuum value −6) in single standard deviation units to an extreme male model (continuum value +6). The model at 0 on the continuum represents the average from all the walkers.

Each of Troje’s original models is composed of two sets of information. There are structural coordinates defining the starting locations of each of the 15 point-lights (structure cues) from which each walker is composed—see Figure 1. Those coordinates vary the locations of the point-lights as a function of the strength of the sex cues: The positions of the 15 points, with respect to each other, is different for each model on the original continuum. Paired with each of those points is also kinematic information that describes changes in location of each joint coordinate over time for each particular model. That path information is such that each joint travels a predictable track that returns to its original starting position each complete (two steps) walking cycle. In that way, in the original continuum, each of the 13 models varies simultaneously in both structural and kinematic cues to sex.

For the stimuli used here, we separated, for each point-light at each point along the continuum, the structural and kinematic cues and then recombined those separate cues in unique ways to create new walkers that vary in the strength of sex cues carried by structure, by kinematics, or by both. For example, the starting positions of the 15 point-lights used to describe the structure of the objectively sex-neutral walker (structural cues, model 0) can be paired with the kinematic (path) information from that same model in the standard configuration. Here, we describe that model in terms of its structure/kinematic components as 0/0. Similarly, it is possible to pair the sex-neutral model structural cues with the kinematic cues from the −5 female walker for a unique model described here as 0/−5. In those two examples, the structural information about the sex of the walker has been held constant while the kinematic cues to sex have changed. It is similarly possible to combine the -5 model structure with the 0 model kinematics (−5/0) and the +5 model structure with the 0 model kinematics (+5/0) for two walkers that vary in the strength of their structural sex cues but which simultaneously are equal in terms of their kinematic cues to sex. Those pairing manipulations for each experiment are detailed below.

Stimuli were in sagittal view and each walker subtended an average visual angle of 16.7° in height and 6.8° in width. All 15 points of light were depicted as white dots, each with a luminance level of 160 cd/m² and were presented on a gray background of 12.5 cd/m². The Michelson contrast [(Lmax − Lmin)/(Lmax + Lmin)] between the luminance level of the white points of light and background was 0.42.

2.5 Procedure
Participants were seated in a light and sound-attenuated room. Instructions were presented both orally and in written form on the computer screen before testing commenced. Participants were asked to respond as quickly and accurately as possible. Testing was completed in a single session. All participants completed an initial practice block comprising 10 trials for the purpose of task familiarization. During and after practice, participants were encouraged to ask questions of the observer. Stimuli were presented in blocks (see below) with block orders randomized between participants. Within each block, stimuli were presented in randomized orders within and across participants. Presentation duration for each stimulus was 1000 ms, which equates in this case to one point-light walker step. The interstimulus interval was 1000 ms. Participants indicated for each stimulus observed whether they believed the walker to be “male” or “female.”
Experiment 1

As already noted, Troje and Westhoff’s (2006) account of the inversion effect, which marries with the sex processing model of Johnson and Tassinary (2005), is that perceptual impairments are driven primarily by the impacts of inversion on kinematic, not structural, processing. While they note in their paper that inversion effects manifest with respect to multiple perceptual tasks, the paradigm via which they provide empirical support for their model focuses specifically on a direction discrimination task. The question arises whether the impact of inversion on kinematic processing will be observed in relation to other discrimination tasks.

Experiment 1 was designed specifically to address that question by asking observers to judge the sex of upright and inverted walkers. As already noted, Barclay et al. (1978) have previously demonstrated sex discriminations are subject to an inversion effect, but here the mechanism giving rise to those effects is unpacked. Specifically, the impact of inversion on structural and kinematic sex-cue processing was separately probed using two novel point-light continua. In the first, sex was differentiated only by structural cues. Kinematic cues did not distinguish between walkers. In the second continuum, the opposite was true: Kinematic cues were the only reliable cues to sex because structural cues were constant. It was predicted that inversion of the point-light models would affect sex perceptions based on kinematic cues, but not sex perceptions based on structural cues.

Figure 1. Stimuli were created using structural and kinematic (path) information derived from models of point-light walkers provided by Troje (2008). A. Each walker is composed of a set of point-lights at specific starting coordinates (top figure) and then motion is imposed along a specific kinematic path (bottom figure). B. Those two pieces of information can be separated to control for, in this example, structure while varying path. In both figures, the structural information is consistent with a 0 model walker from Troje’s original continuum. The top figure is the 0 structural model paired with the −5 (female) model motion path. The bottom figure is the 0 structural model paired with the +5 (male) model motion path. C. In these figures, motion is held constant while structure is varied. The top figure is the −5 structure paired with the 0 model motion path. The bottom figure is the +5 structure paired with the 0 model motion path. Inversion can be achieved by rotation of these figures through 180°.
3.1 Methods
Two different sets of 13 walkers were used here. In the first set, structural information varied: The coordinates for each of the original 13 point-light walker models were paired, in every case, with kinematic information from the sex-neutral (0) walker model (structure varies, kinematics constant). In the second set of walkers, structural cues to sex were held constant while kinematic cues varied: The structural coordinates for the 0 walker were paired with the 13 different sets of path information from each of the original 13 models (structure constant, kinematics vary). For each of the models thus produced, both upright and inverted exemplars were created. Two blocks of stimuli were presented such that the effects of structural and kinematic information could be tested separately. Each block comprised 260 trials with order randomized (13 exemplars × 2 orientations × 10 repeats).

3.2 Results
For each model tested, at each orientation, the mean proportion of “male” responses was calculated across participants. Those data are illustrated in Figure 2. As that figure shows, when kinematic (path) information is held constant (panel A.), changing structural information about sex leads to systematic changes in the proportion of times each model is judged as looking “male” and those changes are similar for both upright (solid line) and inverted (dashed line) walkers. Models with strong female structural cues almost never are judged as looking male. As the strength of the male structural cues increases, so do the proportions of times the models are judged as male at both orientations. That pattern is not replicated when holding structural cues constant. Varying the kinematic information about sex (panel B.) leads to a similar pattern of change in the proportion of “male” responses when walkers are upright. However, that pattern changes when walkers are inverted. For inverted walkers with only kinematic cues signalling sex, the proportion of “male” responses initially increases as the strength of the cues to femaleness decrease. The function peaks for the weakest male models. As the strength of the male cues continues to increase, the proportions of times the inverted walkers are judged as male systematically declines. That is, when information about sex is carried only by kinematic cues, inverted male walkers look increasingly female as cues to maleness increase.

Planned contrasts were run to test for a main effect of orientation on each of the two different model sets. Dealing first with the “Structure” condition, orientation had no effect on perceived sex ($F_{1,13} = 0.31, p = .59$). Conversely, and as predicted, orientation did have a systematic impact when walker sex was defined by kinematics ($F_{1,13} = 11.50, p = .005$). A post hoc t-test revealed that the 0/16 model (neutral structural cues to sex paired with strong kinematic cues) was judged as female at a rate almost at chance ($t_{13} = 1.67, p = .23$).

![Figure 2](image-url). Proportion of “male” responses for each model at each orientation tested. The two components comprising each walker are shown on the abscissa. Mean proportions are shown on the ordinate. A. Holding kinematic cues constant and varying structural cues to sex leads to predictable and systematic changes in the perceived sex of the 13 different walkers tested. As sex cues change systematically from extreme female structure (−6/0 model) to extreme male structure (+6/0 model), the proportions of “male” judgements increases for both upright (solid line) and inverted (dashed line) walkers. B. Holding structure constant and varying kinematic cues to sex gives a different result. In this case, inversion leads to the weakest male walkers (0/0, 0/+1, 0/+2, 0/+3) looking most male. Inversion reduces the perceived maleness of the most extreme male (0/+4, 0/+5, 0/+6) walkers. Error bars represent ±1 standard error.
Another way of representing those data are shown in Figure 3. For each participant, a difference score was calculated by subtracting the proportion of “male” responses for each upright model from the proportion of “male” responses for each inverted model. 95% confidence intervals were then constructed for each set of models. As shown in Figure 3, structural cues (blue) to sex were almost unaffected by orientation: Almost every interval captures 0. The pattern is very different for kinematic (red) cues. As maleness increases, there is a systematic decline in the difference scores, consistent with inverted walkers looking increasingly female.

3.3 Conclusion
Results of Experiment 1 support the hypothesis that inversion significantly affects sex perceptions based on kinematic cues but not sex perceptions based on structural cues. In particular, and as illustrated in Figures 2 & 3, inversion has little effect on sex perceptions generated by point-light models varying only in structural sex cues. Models with strong female cues are perceived as female, models with strong male cues are perceived as male. That pattern changes when sex cues are carried by kinematic information. In that case, and just as when structure carries sex information, upright walkers are reliably discriminated as female and male in a pattern consistent with the kinematic sex-cue information carried in each walker. When those walkers are inverted, female walkers generally are perceived as female. Male walkers with weak sex cues are perceived as male. However, as male sex cues increase in strength, walkers increasingly are perceived as female.

As such, present data tie together two key biological motion processing models. First, the present data suggest that of the two processing streams (Troje & Westhoff, 2006) contributing to perceptions of the sex of point-light walkers, the kinematic is more detrimentally affected by inversion than is the structural. Those effects could be mediated via an orientation-tuned disruption to match with the stored templates (see Troje & Westhoff, 2006). That is consistent too with Johnson and Tassinary (2005) sex processing-specific model. Johnson and Tassinary argue that structure-based discriminations are more robust to the detrimental impacts of inversion than are discriminations based on kinematic cues. The results reported here are consistent with their proposal that structure serves as the primary, direct, and therefore more inversion-resilient cue to sex, while kinematics play a secondary role that is more susceptible to inversion effects.

Figure 3. 95% Confidence Intervals (CIs) for difference scores for each model set. For each participant, a difference score was calculated by subtracting for each model tested their proportion of “male” responses to upright walkers from their proportion to inverted walkers. 95% CIs were then constructed for each model. A score of 0 means there were no differences between performances on upright and inverted walkers. Positive scores indicated inverted walkers look more male. Negative scores indicated inverted walkers look more female. The blue interval is for models where the sex cue is carried by structural cues. The red interval is for models where the sex cue is carried by kinematic cues. Models are shown on the colored labels on the abscissa.
These data are not without precedent. Barclay et al. (1978) has previously reported that observers reliably reported upside down male point-light walkers as female and vice versa for female walkers. While the present findings support only the first of those two outcomes, they are to our knowledge the first reported replication of Barclay et al.’s physical inversion/sex inversion relationship. Those differences may be associated with the effects of signal strength observed in these data. Quite clearly sex discriminations were most disrupted for those inverted walkers defined by strong male kinematics. Those walkers, like Barclay’s, were perceived as female when inverted, suggesting perhaps that at least for the male walkers used by Barclay, structural cues were not salient and their observers used kinematic information to make their sex discriminations. That account cannot explain why Barclay’s female walkers were judged by observers to be male.

In summary, data from Experiment 1 support the proposal that inversion has a greater detrimental impact on the processing of kinematic cues than it does on the processing of structural cues to sex. Most importantly, in that respect, these data are consistent with Troje and Westhoff’s (2006) suggestion that inversion effects are driven by a disruption to kinematic processing ahead of structure processing, and with Johnson and Tassinary’s (2005) sex processing-specific model in which structure is the primary cue to sex. That summary is based on a unique feature of the data reported here: Observers based their sex discriminations on either kinematic or structural cues. The question thus arises whether compatible patterns of responding would manifest for point-light walkers in which both carriers simultaneously were available. That is, if walkers varied in terms of both their structural and their kinematic cues to sex would the same effects be observed? That question is addressed by Experiment 2.

4 Experiment 2
In Experiment 1, the advantage of the methodological approach adopted was that it afforded the ability to isolate the inversion effects arising with respect to kinematic and structural processing individually. As noted above, that approach also has associated with it some limitations: In regular point-light walkers, sex typically is conveyed by the dual cues of structure and kinematics simultaneously. So, while data from Experiment 1 are consistent with the view that inversion has a more catastrophic impact upon the observer’s ability to exploit kinematic than structural cues to sex, at least for male walkers, the question does arise as to whether such effects would be maintained when both carriers simultaneously are available.

To that end, Experiment 2 was conducted to test the impact of inversion on perceptions of point-light walkers comprised simultaneously of structural and kinematic cues to sex. Specifically, two objectively sex-structured walkers (structure levels 2 female and 1 male) were paired with both female and male kinematic cues in combinations that were either complementary (female/female) or contradictory (male/female) in terms of sex cues. In Experiment 2a, combinations comprised female and male structural walkers onto which seven different levels of female kinematic cues were imposed. In Experiment 2b, the combinations comprised seven levels of male kinematics. Upright and inverted versions of each stimulus set were created.

Using those stimuli, and based on the data from Experiment 1, it was predicted that inversion effects would manifest only on walkers with male kinematics. In particular, it was predicted that systematically different performances for upright and inverted walkers would not manifest in sex discriminations for the stimuli used in Experiment 2a (where both female and male structures had female kinematics). It was predicted that differences between performances on upright and inverted walkers would be observed in Experiment 2b (where both female and male structures had male kinematics). A secondary aim was to investigate the tuning of structure-based supremacy in driving perceptual outcomes. Put simply, we tested the effect of signal strength on perceptual outcomes for each type of walker in each of the orientations in which they were presented.

4.1 Experiment 2a: Female kinematics
The aim of Experiment 2a was to test the impact of inversion on sex discriminations of point-light walkers in which the structural cues were female or were male and the kinematic cues all female. Based on the data from Experiment 1, it was predicted that, if inversion effects are driven by kinematic rather than structural cues, there would be no systematic effects of inversion on sex discriminations for female and male structural point-light walkers when those were paired with female kinematics.
4.1.1 Methods
Methods were as described above with the following changes: Two different sets of structural coordinates, those of the \(-1\) (female) model and those of the \(+1\) (male) model had paired with them seven different kinematic models, each carrying female sex cues of different strengths: \(-6, -5, -4, -3, -2, -1, \) \& \(0\). For each of those 14 models, an upright and an inverted version was created and the stimuli presented as a single randomized block comprised 280 trials (14 exemplars \(\times\) 2 orientations \(\times\) 10 repeats).

4.2 Results
As previously, results here are expressed as mean proportions of male responses across participants for each structure/kinematic sex cue combination—Figure 4. Proportions less than 0.5 are consistent with systematically “female” responses, proportions greater than 0.5 are consistent with systematically “male” responses. Female kinematic cues are represented along the x-axis from strongest on the left to weakest on the right (so in decreasing strength of female sex cue). As can be seen in Figure 4, when female kinematic cues were paired with a female structural cue, point-light walkers look female when the kinematic cues to sex are strong and look increasingly male as the strength of the female kinematic cues diminish. That pattern of discriminations is consistent for both upright and inverted walkers although it does appear, for the strongest kinematic cues, that inversion reduces the salience of the female cues to sex (see General Discussion). When female kinematic cues are paired with a male structural cue, the point-light walkers look more male as the female kinematic cues weaken in strength. Indeed, only when female kinematics were imposed on the objectively female \((-1)\) structure did participants reliably report the walkers as looking female. When paired with the objectively male structure \((+1)\), even the strongest female kinematic cue \((-6)\) did not give rise to perceptions that reliably were female: A post hoc \(t\)-test on the proportion of “male” responses for the \(+1/-6\) model showed the rate of responding not to be different from 0.5 \((t_{13} = 0.76, p = .40)\). Most importantly, from all these data, there seems to be no systematic effect of stimulus inversion.

Planned orthogonal contrasts tested the main effects of orientation (upright vs inverted walkers) and kinematic sex cue signal strength. As predicted, no main effect of orientation was observed for either the objectively female \((-1)\) structure \((F_{1,13} = 2.25, p = .16)\) or the objectively male \((+1)\) structure \((F_{1,13} = 0.67, p = .43)\). That is, no systematic effect of orientation was observed for either set of combinations when the kinematic sex signal was female. The strength of the female kinematic cues did influence perceptions: Perceived sex changed systematically as a function of female kinematic signal strength for both the female \((F_{1,13} = 43.7, p < .001\) for upright, \(F_{1,13} = 12.8, p = .003\) for inverted) and the male \((F_{1,13} = 16.64, p = .001\) for upright, \(F_{1,13} = 28.1, p < .001\) for inverted) structural cues. In summary, there were no systematic effects of stimulus inversion on the perceived sex of structurally female and structurally male point-light walkers when those walkers carried female kinematic cues.

4.3 Experiment 2b: Male kinematics
The aim of Experiment 2b was to test the impact of inversion on sex discriminations of point-light walkers in which the structural cues were female or were male and the kinematic cues all male. Based

![Figure 4](image-url)
on the data from Experiment 1, it was predicted that, if inversion effects are driven by kinematic rather than structural cues, there would be systematic effects of inversion on sex discriminations for female and male structural point-light walkers when those were paired with male kinematics.

4.3.1 Methods

The methods here were as for Experiment 2a except that instead of pairing the female and male structural models with female kinematics, male kinematics were used. That is, female (−1) and male (+1) structural models were paired with +6, +5, +4, +3, +2, +1, & 0 kinematic cues.

4.3.2 Results

Using the previous conventions, Figure 5 shows the mean sex discrimination performances for the stimuli tested here. The patterns of responding are very different from Experiment 2a: There is little effect of male kinematic sex cues strength, except when those were paired with the female structural cues. That is likely to be a ceiling effect. All the upright walkers tested here were very often perceived to be male. There was a strong and systematic effect of inversion and that effect was impacted by the strength of the male kinematic sex cue. In particular, inversion systematically reduced the proportions of times every stimulus tested was perceived to be male.

The main effect of orientation was significant for both the objectively female-structured walkers \((F_{1,13} = 8.43, p = .012)\) and for the objectively male-structured walkers \((F_{1,13} = 13.31, p = .003)\). In both cases, the proportion of “male” discriminations was significantly reduced by inversion, suggesting inversion made the walkers look more female. Male kinematic sex cue strength had no systematic effect on sex discrimination performances for upright walkers with female \((F_{1,13} = 0.02, p = .90)\) and male \((F_{1,13} = 0.1, p = .76)\) structures. Similarly, male kinematic sex cue strength had no effect on sex discrimination performances for inverted male structures \((F_{1,13} = 2.75, p = .12)\). However, male kinematics significantly affected performance when paired with female structure \((F_{1,13} = 6.09, p = .03)\). Specifically, and as in Experiment 1, stronger male kinematics, when presented upside down, looked less “male”, although even for the combination of female structure with the strongest male kinematic sex cue the walkers never were reliably reported as looking female \((t_{13} = 0.53, p = .48)\). In summary, and as predicted, when point-light walkers carry male kinematic cues to sex, inversion affects sex perceptions and does so when combined with both female and male structural cues.

4.4 Conclusion

Experiment 2 had two primary aims. Experiment 2a was designed to test the impact of female kinematics on sex discriminations of point-light walkers in which the structural cues were female or were male. Experiment 2b was designed to test, on the same structural cues, the impact of inversion on perceptions driven by male kinematic sex cues. It was predicted that systematic inversion effects would be seen only for walkers with male kinematics. The data confirm that prediction. While sex discriminations of walkers containing only female kinematic cues to sex were mediated by the strength of

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![Mean Proportion “male” Responses](image)

**Figure 5.** A. Mean proportions of “male” responses for upright (solid line) and inverted (dashed line) point-light walkers with female structure (−1) imposed on male kinematics (0 to +6). B. Mean proportions of “male” responses for upright (solid line) and inverted (dashed line) point-light walkers with male structure (+1) imposed on male kinematics (0 to +6). In both figures, error bars represent ±1 standard error of the mean.
those cues, there were no systematic differences in those effects produced by inversion. In comparison, sex discriminations of walkers containing only male kinematic cues showed only weak tuning for the strength of the cues (probably a ceiling effect) but strong effects of inversion. For every stimulus, the proportion of “male” responses elicited was reduced when the stimulus was inverted. In summary, Experiment 2 confirms that inversion effects are mediated by the effect of the change of orientation on the processing of kinematic sex cues when those cues are male. In addition, Experiment 2 shows that those effects on kinematic processes are, for the structural configurations used here, independent of the sex of the structural cues presented with them.

With that in mind, data from Experiments 2a and 2b provide further confirmation of the models of biological motion processing described by Troje and Westhoff (2006) and by Johnson and Tassinary (2005). Troje and Westhoff proposed that the inversion effect is due primarily to impairments, when figures are upside down, of the visual system’s ability to interpret task-relevant kinematics. In terms of sex discriminations, the data reported here confirm a critical role for kinematics in inversion effects. Similarly, these data are consistent with Johnson and Tassinary’s proposal that sex perceptions are driven directly by structural cues—a process these data suggest is not orientation-tuned—and indirectly by kinematic cues. These data suggest that kinematic signals can systematically influence sex perception, but only in a secondary relationship to more heavily weighted structural information.

5 General Discussion
This study was designed to investigate the mechanisms mediating inversion effects on biological motion perceptions. As noted above, traditional accounts of the mechanisms of those effects have focused on the impact of orientation changes on structural processing mechanisms (Bertenthal & Pinto, 1994; Dittrich, 1993; Proffitt & Bertenthal, 1990; Shiffrar et al., 1997). Turning a body representation upside down, it classically has been argued, catastrophically impacts upon the visual system’s ability to exploit learned structural relationships and that, in turn, impacts on myriad perceptual tasks (Bertenthal & Pinto, 1994; Reed et al., 2003; Shiffrar et al., 1997). Those effects include, but are not limited to, discriminations of biological sex (Barclay et al., 1978). More recently, however, the explanatory power of the so-called “shape inversion effect” has been called into question (Troje & Westhoff, 2006). At least in the case of biological motion processing, there is reason to believe the impacts on perception resulting from physical inversion may arise primarily as a consequence of resulting distortions in the visual system’s ability to process kinematic information (Troje & Westhoff, 2006). What is interesting about that proposal is that Johnson and Tassinary (2005) also developed an account of biological motion processing, this time for the mechanisms giving rise to sex perceptions specifically, that holds that sex perceptions arise primarily through structural processing. They propose that kinematic sex cues play a secondary role. In terms of inversion effects—turning their hypothesis on its head, so to speak—their model predicts that the weaker driver of sex perceptions, kinematics, will, when processing cues changed by orientation, be more deleteriously impacted than structural cues. That is, both models predict that sex perceptions mediated by structural cues will be more robust to orientation changes than sex perceptions mediated by kinematic cues.

The primary goal of the experiments reported here was to test that prediction. In Experiment 1, participants judged the sex of point-light walkers composed of independent structural and kinematic cues to sex. Sex cues were carried either by structural or by kinematic cues. The only systematic effects of inversion were observed for kinematic cues, and only for male kinematic cues. In those circumstances, the proportions of times walkers were judged to be male were reduced. The goal of Experiment 2 was to further test that relationship between orientation, structural cues, and kinematics. In Experiment 2, kinematic sex cues were paired with objective female or male structural cues. The data confirmed that orientation not only selectively impacts on the processing of kinematic cues, and that those effects are specific to male kinematics, but that those effects occur relatively independently of the structural cues that are present. In addition to that, signal strength did not, in the case of male kinematics at least, have an across-the-board impact—only for the inverted female-structured walkers did greater signal strength result in reduced male responses. No similar tuning effects were observed when male kinematics were paired with either female or male structures. In summary, the data are evidence that kinematic signals can influence sex perceptions even when sex-specific structural cues are available; while structural cues are primary when walkers are right side up, kinematic signals can drive perceptions when those same walkers are presented upside down.
In addition to those systematic effects, there were a number of point-light walker models that seem to give rise to different patterns of responding depending on their orientation. In Experiment 1, the proportions of “male” responses for the most sexually ambiguous models (using the structure/kinematic convention), the 0/0 and 1/0 models, were lower than might be expected given the systematic changes across the rest of the models. Similarly, in Experiment 2a, two models, \(-1/-6\) and \(-1/-5\), generated higher than expected proportions of “male” responses. In neither case is it clear why given the overall, and systematic, changes across all the point-light walker models. One possible interpretation of those patterns is that they reflect processes first described by Barclay et al. (1978). In that first description of point-light walker inversion effects, Barclay’s observers reported that turning the walkers upside down seemed to change their sex. The same is true here: For those four models that seem “out of pattern,” there is a tendency for observers more often to perceive the models as being of the opposite sex to the objective cues present when the cues are presented upside down. Whether those reports reflect a true perceptual reversal of the perceived sex, or perhaps a response bias (“it does not look female so it must be male”) requires further investigation.

The other effect that manifests in these data is the so-called “male bias.” Here, for both the structure (upright and inverted) and kinematics (upright only) continua, point-light walkers that actually carried weak female cues were misperceived as male. The male bias previously has been reported to manifest not only for point-light walkers (Troje, Sadr, Geyer, & Nakayama, 2006; Troje & Szabo, 2006), but also for hands (Gaetano, Brooks, & van der Zwan, 2012; Gaetano, Brooks, van der Zwan, Hayward, & Oxner, 2013; Gaetano, van der Zwan, Blair, & Brooks, 2014), and for faces (Hess, Adams, Grammer, & Kleck, 2009). That it manifests here in both conditions suggests that for point-light walkers at least, the bias is driven by both structure and kinematics processing mechanisms. Again, the mechanisms mediating that effect need systematic investigation.

While the outcomes reported here support the major existing models, they also give rise to at least one important additional question: Why does inversion selectively disrupt the processing of kinematics characteristic of males, to the point where in some cases sex is reliably misperceived (Experiment 1, supported by patterns in Experiment 2)? While physical/perceptual inversion relationships have previously been reported (Barclay et al., 1978), our data suggest they arise specifically in cases involving male kinematics. Because the effect arose with respect to two types of point-light walkers—one in which sex was defined by a single carrier (Experiment 1), and a second in which dual carriers were present (Experiment 2)—the effect seems unlikely to be a stimulus-based artifact. But the question of why the visual system is particularly susceptible to the effects of inverting male kinematics or perhaps conversely, why characteristically female motion shows no comparable effect, remains unanswered. Data from both orientations tested here show that the presence of female kinematics is factored into resulting sex perceptions. So, we know at least that the absence of an orientation effect with respect to female kinematics cannot be based on a complete reliance when processing those walkers on their sex-specific structural cues.

Overall then, the present data provide novel insight into an effect that has for many years interested psychophysicists and laypeople alike. Inversion, as we know from demonstrations like the Thatcher Illusion (Thompson, 1980) and the artistry of a pencil-nosed puppet, has a serious negative impact on the ability to process visual information, including in the case of human body representations. Here, we have shown that that impact is caused in large part by impairment of kinematic processing abilities. Simultaneously, our data show that kinematics do nonetheless feature into judgements of sex, even when structural information is available. As such, we provide support for the complimentary—with respect at least to inverted-figure processing—models proposed by Troje and Westhoff (2006) and Johnson and Tassinary (2005). Taken together, their models and our data suggest that in the case of biological motion processing structural and kinematic cues contribute hierarchically to sex perceptions. Specifically, mechanisms processing structural cues are relatively robust to inversion. Mechanisms processing kinematic cues are not.

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