

# Acceleration carries the local inversion effect in biological motion perception

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The ability to derive the facing direction of a spatially scrambled point-light walker relies on the motions of the feet and is impaired if they are inverted. We exploited this local inversion effect in three experiments that employed novel stimuli derived from only fragments of full foot trajectories. In [Experiment 1](#), observers were presented with stimuli derived from a single fragment or a pair of counterphase fragments of the foot trajectory of a human walker in a direction discrimination task. We show that direction can be retrieved for displays as short as 100 ms and is retrieved in an orientation-dependent manner only for stimuli derived from the paired fragments. In [Experiment 2](#), we investigated direction retrieval from stimuli derived from paired fragments of other foot motions. We show that the inversion effect is correlated with the difference in vertical acceleration between the constituent fragments of each stimulus. In [Experiment 3](#), we compared direction retrieval from the veridical human walker stimuli with stimuli that were identical but had accelerations removed. We show that the inversion effect disappears for the stimuli containing no accelerations. The results suggest that the local inversion effect is carried by accelerations contained in the foot motions.

Keywords: biological motion, inversion effect, local motion, acceleration, direction discrimination

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## Introduction

Visual perception of animal movement patterns, or biological motion patterns (Johansson, 1973), has traditionally been investigated with displays comprised of a number of light-points depicting the motions of an agent's major joints. When the points are organized coherently, such a display is sufficient to allow the recognition of an agent and its action. Moreover, higher-order characteristics such as gender (e.g., Barclay, Cutting, & Kozlowski, 1978; Kozlowski & Cutting, 1977; Mather & Murdoch, 1994; Troje, 2002) and identity (e.g., Cutting & Kozlowski, 1977; Hill & Pollick, 2000; Troje, Westhoff, & Lavrov, 2005) can also be extracted.

Orientation-specificity is a widely demonstrated characteristic of biological motion perception. Perceptual performance is generally impaired if the point-light displays are inverted. For example, observers in a study by Sumi (1984) reported that the perceived quality or naturalness of movement was degraded with inversion. Pavlova (1989) showed that observers were impaired in the recognition of a walking dog when the point-light sequence was inverted. Bertenthal and Pinto (1994) found that the detection of a coherent point-light target in a mask of additional walker point-lights dropped to chance when

the target was inverted. Observers' abilities to judge human action type (Dittrich, 1993), and the agent's gender (Barclay et al., 1978) were also disrupted upon inverting point-light displays. These inversion-related impairments in perceiving coherent point-light displays have often been attributed to impaired processing of global, configural information as conveyed by the display's overall spatiotemporal organization (e.g., Bertenthal & Pinto, 1994). Indeed, the importance of configural information for biological motion perception is supported by findings that walking persons can be perceived from point-light figures in which each point is reallocated to another randomly selected position on the limb in successive frames or successive sets of frames and thus have little or no local motion (Beintema & Lappe, 2002; Neri, Morrone, & Burr, 1998).

Notably, it has been shown recently that in addition to an inversion effect that may well be attributable to the inversion of global form, there is a second inversion effect in biological motion perception that cannot be attributed to configural processing and is inherent to properties of the local motion signals (Troje & Westhoff, 2006). In their study, Troje and Westhoff (2006) presented observers with walking animals that were organized coherently or spatially and temporally scrambled thereby rendering any global spatiotemporal information useless. All stimuli

displayed stationary walking; that is, both the coherent and scrambled variations of the walkers did not contain any overall translatory motion. The displays were presented at both upright and inverted orientations and observers were asked to indicate the direction in which the walkers were facing. For the coherent displays, they found that direction discrimination performance decreased at the inverted orientation relative to the upright orientation. This particular result is consistent with many previous studies demonstrating an inversion-related impairment for perceiving coherent point-light patterns (e.g., Pavlova, 1989; Sumi, 1984). Of particular relevance however, is their finding that from the spatially scrambled displays that contain solely local motion cues, observers could still discriminate facing direction reliably. Critically however, performances dropped to chance level when display orientation was inverted. As scrambled displays do not contain coherent structure, this inversion effect cannot be attributed to the processing of global configuration. An additional experiment where only specific parts of the display were inverted revealed that the cues for direction of motion and the associated inversion effect were carried by the dots representing the feet of the walkers. This finding corroborated an earlier study by Mather, Radford, and West (1992) that showed that performances on coherence and direction discrimination tasks were most affected by the omission of the wrist and ankle dots, as compared to the omission of the shoulder and hip, or elbow and knee dots.

The findings by Troje and Westhoff (2006) suggest that two inversion effects need to be considered in biological motion perception. While there seems to be an inversion effect which relies on the global configuration of the walker, there is also a second one, which relies on the local motion of the distal parts of the lower body. The authors suggested that this second inversion effect reflects a visual mechanism that sub-serves the ability to detect terrestrial, articulated animals in the visual environment (see also, Troje, 2008).

In support of the hypothesis put forth by Troje and Westhoff (2006), we have shown that the perception of animacy from spatially scrambled point-light displays is also orientation-specific (Chang & Troje, 2008). In this study, we presented observers with coherent and scrambled displays at both upright and inverted orientations and asked observers to rate each display on a six-point Likert scale according to whether it was a “living being.” Critically, we found that upright, scrambled displays were rated more animate than inverted, scrambled displays, suggesting that the mechanisms responsible for processing local biological motion signals not only retrieve locomotive direction but also aid in identifying animate agents in the environment.

According to Troje and Westhoff (2006), the critical invariant in local biological motions is based on the fact that gravitational acceleration imprints orientation-specific signatures on the movements of a terrestrial animal in

locomotion (see also, Shipley, 2003). Indeed, Bingham, Schmidt, and Rosenblum (1995) have shown a role for dynamics for the perception of both inanimate and animate events. In this study, observers were presented with point-light displays of events that reflected varying types of dynamics (i.e., biodynamics, hydrodynamics, aerodynamics, rigid body). Both the orientation of the display and observer orientation were manipulated and observers were asked to describe the events with free responses or by circling properties from a given list. Results indicated that observers were well able to identify the various events as depicted by point-light motions. Importantly, observers’ descriptive patterns reflected the various underlying types of dynamics. In addition, perception seemed to depend on the orientation of the event with respect to gravitational direction and seemed unaffected by the relative orientation of the observer with respect to the display. From these results, the authors concluded that underlying dynamics play a role in the perceptual significance of motions and specifically that variations in velocity contained in the motion, or *trajectory form*, contributes to event identification (for original work on event identification from motion or trajectory forms, see Bingham, 1987; Runeson, 1974).

Our previous finding that both the ability to discriminate walking direction and the perception of animacy from scrambled biological motion displays could be well elicited within stimulus durations as short as 200 ms (Chang & Troje, 2008) suggests that the visual system is able to exploit the relevant cues from only a fraction of the full gait cycle (~1100 ms for a human walker). Here, we ask whether all fragments of the gait cycle contain equally salient directional information and contribute equally to the associated inversion effect.

We present three experiments that investigated the cues underlying the local inversion effect by testing direction discrimination from novel biological motion stimuli that contain only small fragments of different types of foot trajectories. In [Experiment 1](#), we first asked if the cues contained in the local foot motion can be assessed from a single dot trajectory by isolating the local motion of the human foot and presenting displays derived from one foot dot tracing an individual fragment of the trajectory or displays derived from one pair of foot dots that trace counterphase fragments of the gait cycle (as in the case for the two feet of a full walker). We show that the inversion effect occurs only for displays derived from the paired fragments. In [Experiment 2](#), we investigated direction retrieval from displays derived from paired fragments of the gait cycle belonging to other foot types (human walker, human runner, cat, and pigeon) in order to gain insight into the type of cues that may be relevant for the inversion effect. Finally, in [Experiment 3](#), we investigated specifically the importance of acceleration for the local inversion effect by comparing direction discrimination for the human walker stimuli of [Experiment 2](#) and stimuli that were identical to these

naturally accelerating stimuli, but had accelerations removed along the trajectory fragments (i.e., moved with uniform speeds).

## Experiment 1

Troje and Westhoff (2006) showed that for full walker displays that are spatially scrambled, the cues for direction and the inversion effect are carried by the motion of the dots representing the feet. These cues are exploited by the visual system independently of the temporal relationships among the individual dots and can thus be thought to be completely local in nature. Additionally, we have shown that the relevant cues can be retrieved within as short as 200 ms (Chang & Troje, 2008). Together, these findings imply that observers can retrieve the facing direction of the display from a stimulus that exposes only a single 200 ms window of the foot trajectory. Yet, it is difficult to imagine that such a stimulus would be sufficient. Recall that a single moving dot if taken from a stationary walker, exhibits no net translatory motion if displayed for the duration of a full gait cycle. In contrast, a display consisting of an isolated short fragment (e.g., 200 ms) of the foot's trajectory contains a clear net displacement. Depending on the part of the trajectory it is sampled from, the translation is either coherent or incoherent with the facing direction of the walker. If observers base their decision on the displacement of the individual dots, they would perform at chance level on average and an inversion effect would not be expected. It is hard to imagine that observers would ignore displacement as a cue to direction, and it is hard to imagine what other could be left in the short fragments that would signal the facing direction of the walker.

Perhaps then, single short trajectory fragments do not provide the critical information—despite the finding that spatial and temporal structure is not critical. Perhaps it is necessary to present the trajectories within a context where the local translatory motion of the individual dots is equated by adding other dots with local translatory motion in the opposite direction, thus rendering these cues non-discriminative and forcing the observer to use intrinsic cues in order to determine the facing direction of a stationary walker.

In **Experiment 1**, we employed two sets of stimuli. We presented one group of observers with displays derived from a single foot dot that traced a particular individual fragment of the gait cycle, and a second group of observers with displays derived from a pair of foot dots that traced counterphase fragments of the gait cycle. According to the reasoning above, observers in the first group would be expected to use primarily translatory cues resulting in poor performance and no inversion effect in the direction discrimination task whereas observers in the second group would show behavior similar to that

obtained previously with full scrambled walker displays (i.e., elevated performance rates and a pronounced inversion effect).

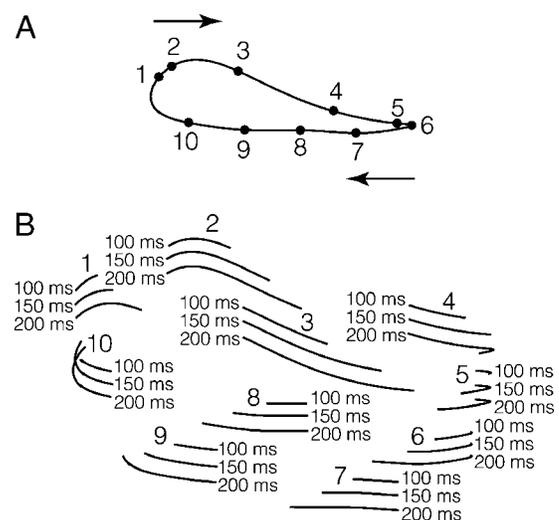
## Methods

### Participants

Two groups of naive observers participated in this experiment. Group 1 consisted of six observers that ranged in age from 18 to 26 years (mean age of 20.50 years; 2 males, 4 females). Group 2 consisted of 12 observers that ranged in age from 18 to 23 years (mean age of 19.03 years; 5 males, 7 females). All observers had normal or corrected-to-normal vision.

### Stimuli and apparatus

The motion of the foot of a human walker as defined by the point of one ankle isolated from the original human point-light sequence used in the study by Troje and Westhoff (2006) was used to derive two sets of stimuli for the current experiment. The foot's motion, shown at its veridical speed with a gait frequency of 0.93 Hz, was displayed in sagittal view either from the left or from the right side. The full gait cycle was sampled by specifying 10 start frames, spaced at approximately equal intervals along the cycle, from which the fragment could begin<sup>1</sup>. From these starting positions, fragments were created that extended 100 ms, 150 ms, or 200 ms in length. **Figure 1** depicts the 10 start frame positions along the full gait trajectory of the foot (A), and the individual trajectories of the 10 fragments at the three window lengths (B).



**Figure 1.** The trajectory of the human foot across a full gait cycle with the 10 starting positions (A), and the foot trajectories outlined for each fragment (1–10) at the three temporal lengths (B). Trajectories shown here are taken from a right-facing walker. Thus, while fragments 1–4 displace to the right, fragments 6–10 displace to the left. For fragment 5, the direction of displacement reverses as the window length increases.

Observers in Group 1 were presented with displays 1000 ms in duration that consisted of 10 copies of one specified foot fragment (identical start-frame and length) that were displayed at random positions within a  $3.6 \times 3.6$  deg area in the center of a computer screen. Each copy had its own randomly chosen onset time and was visible only during the specified time window. The stimuli were presented upright or inverted about the horizontal axis.

Observers in Group 2 were presented with stimuli derived from five fragment pairs created by pairing fragments labeled 1/6, 2/7, 3/8, 4/9, and 5/10 in Figure 1. Thus, each fragment pair consisted of two foot point motions, one of which traced a trajectory that was 180 deg phase-shifted relative to the other along the gait cycle. Each display consisted of 10 sets of a specified fragment pair (identical start-frame and length) that were displayed at random positions within a  $3.6 \times 3.6$  deg area in the center of the screen. Each set had its own randomly chosen onset time and was visible only during the specified time window. Again, stimuli were presented at both upright and inverted orientations.

The stimuli were generated using MATLAB (Mathworks, Natick, MA) with extensions from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), and were displayed on a 22 inch ViewSonic P220f CRT color monitor with 0.25 mm dot pitch,  $1280 \times 1024$  pixels spatial resolution, and 100 Hz frame rate. All stimuli appeared as white dots on a black background and each display subtended a visual angle of  $3.6 \times 3.6$  deg.

### Procedure

The stimuli were viewed binocularly at a distance of 80 cm as maintained by a chin-rest. A two-alternative, forced-choice direction discrimination paradigm was used where the observers' task was to decide the direction (left or right) in which the perceived entity (whatever it may be) seemed to face. Feedback was not given for observer responses.

For both groups, participants were first instructed on the task both verbally and by printed instructions on the computer screen. A practice block was then presented during which participants familiarized themselves with the task. After the practice block, participants completed the experiment proper.

For Group 1, the practice block comprised of 40 trials that consisted of left and right, and upright and inverted versions of the 10 gait cycle fragments of 200 ms length. The experiment proper consisted of 960 trials in total that were completed across two identical experimental blocks of 480 trials each. Each experimental block consisted of all possible combinations of the two directions, two orientations, 10 fragments, and three window lengths, repeated four times. Within each repetition, the 120 possible stimuli were presented in random order.

For Group 2, the practice block comprised of 20 trials that consisted of left and right, and upright and inverted

versions of the five fragment pairs of 200 ms length. A total of 960 trials were completed for the experiment proper across two identical experimental blocks of 480 trials each. A single experimental block consisted of all possible combinations of the two directions, two orientations, five fragment pairs, and three window lengths, repeated eight times. Within each repetition, the 60 possible stimuli were presented in random order.

The resulting design of this experiment for both groups was a within-subject test of factors orientation (i.e., upright or inverted), fragment (Group 1) or fragment pair (Group 2), and fragment length.

## Results

The data were analyzed both in terms of the proportions of responses consistent with the facing direction of the walker from which the stimuli were derived and in terms of  $d'$  sensitivity measures (Macmillan & Creelman, 2005) derived from these rates. The two sets of analyses yielded identical results. For greater clarity, data are presented here in terms of the proportions of responses consistent with walking direction.

### Single fragments

Results obtained from Group 1 are illustrated in Figure 2A. Overall performance was at chance level (0.45 proportion of responses consistent with the facing direction of the walker). It is evident that observers simply responded to the horizontal translatory displacement of the individual dots. For fragments 1–4 where dots moved in the direction in which the walker was originally facing, rates of responses that were consistent with the facing direction of the walker were high. For fragments 6–9 where dots moved in the opposite direction, observers consistently reported the opposing direction. For fragments 5 and 10 where the horizontal direction of the dot switches, responses depended on display length in a manner consistent with the assumption that observers based their responses on mere horizontal translation. Additionally, the data from this group show no inversion effect.

Statistics support the above observations. A 2 (test block)  $\times$  2 (orientation)  $\times$  10 (fragment)  $\times$  3 (length) repeated-measures analysis of variance (ANOVA) showed a significant main effect of fragment,  $F(9, 45) = 879.73$ ,  $p < 0.001$ , a significant fragment  $\times$  length interaction,  $F(18, 90) = 19.26$ ,  $p = 0.007$ , but no effect of orientation,  $F(1, 5) = 0.33$ ,  $p = 0.589$ , or length,  $F(2, 10) = 1.95$ ,  $p = 0.222$ . All other interactions were not significant and performance between the two test blocks did not differ,  $F(1, 5) = 0.64$ ,  $p = 0.460$ . Thus, data from the two blocks were pooled for all further analyses.

Tukey's post-hoc comparisons of the response rates of the 10 fragments, collapsed across orientation and length,

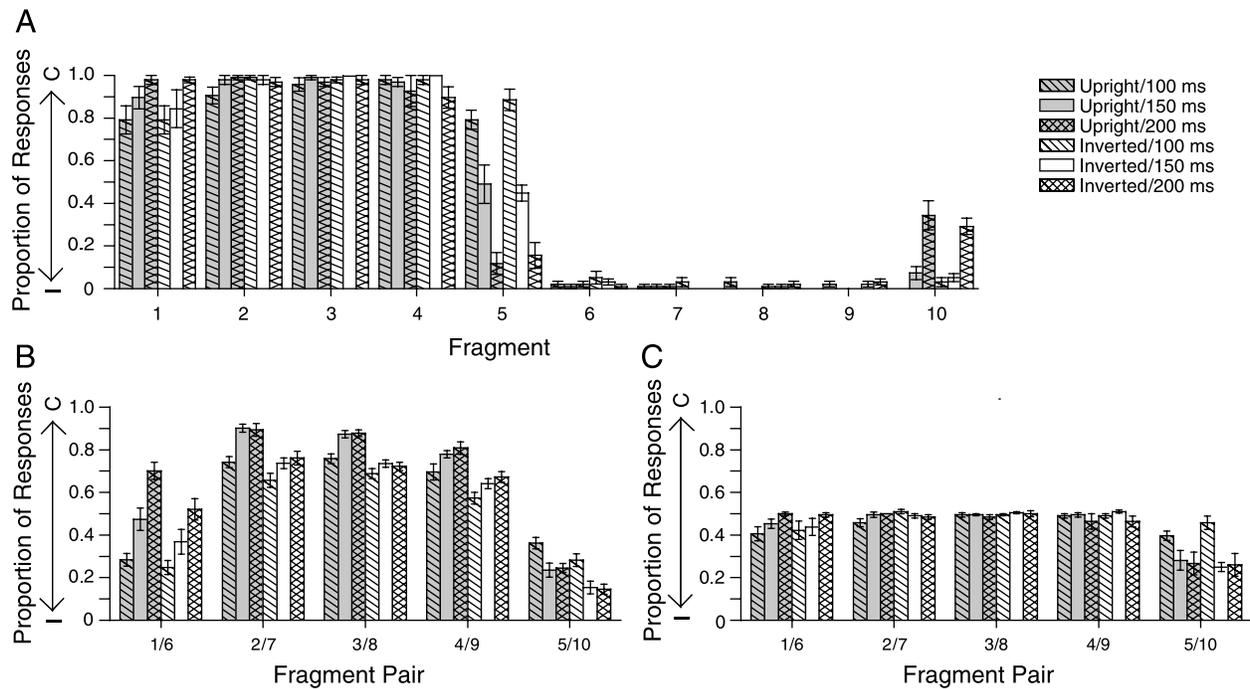


Figure 2. Performance expressed in terms of the mean proportion of responses consistent with the facing direction of the walker. Thus, response rates above and below 0.5 indicate larger proportions of responses that were consistent (C) and inconsistent (I) with walking direction, respectively. (A) Response rates for the 10 fragments across the three temporal lengths and between two orientations obtained for Group 1. (B) Response rates for the five fragment pairs across three fragment lengths and between two orientations for Group 2. (C) Response rates of five fragment pairs across three fragment lengths and between two orientations computed from the individual fragment response rates obtained for Group 1. Error bars represent  $\pm 1$  standard error of the mean.

indicated that the rates for fragments 2–4 did not differ ( $p > 0.900$  for all comparisons), but were higher than rates for all other fragments ( $p < 0.020$  for all). The rates of fragments 6–9 did not differ ( $p > 0.900$  for all), but were substantially lower than the rates of fragments 1, 5, and 10 ( $p < 0.001$  for all), which differed from each other ( $p < 0.001$  for all).

The fragment  $\times$  length interaction was investigated with individual one-way ANOVAs that compared the three lengths for each fragment. The analyses yielded a significant main effect of length for fragments 5,  $F(2, 10) = 38.25$ ,  $p < 0.001$ , and 10,  $F(2, 10) = 25.68$ ,  $p < 0.001$ , only. Post-hoc Tukey comparisons of the three lengths for fragment 5 showed that the rate at 100 ms was significantly higher than rates at 150 ms and 200 ms ( $p < 0.001$  for both), and the rate at 150 ms was significantly higher than the rate at 200 ms ( $p < 0.001$ ). Comparisons for fragment 10 showed that while rates at 100 ms and 150 ms did not differ ( $p = 0.574$ ), they were significantly lower than the rate at 200 ms ( $p < 0.001$  for both).

### Paired fragments

The results for Group 2 are displayed in Figure 2B. Overall performances were above chance level (0.59 proportion of responses consistent with facing-direction

of the walker) with rates generally higher for the upright (0.64 proportion of responses) than for the inverted displays (0.53 proportion of responses). Closer inspection reveals that at both orientations, observers perceived the direction consistent with the facing direction of the walker for pairs 2/7, 3/8, and 4/9 (0.57–0.90 proportion of responses) with rates increasing systematically with increasing window length, but perceived the opposite direction for pair 5/10 (0.15–0.36 proportion of responses) with the rate of responses in the opposite direction increasing systematically with increasing window length. For pair 1/6, the perceived direction changed with changes in window length (0.25–0.70 proportion of responses).

Response rates for Group 2 were analyzed with a 2 (test block)  $\times$  2 (orientation)  $\times$  5 (fragment pair)  $\times$  3 (length) repeated-measures ANOVA. The analysis showed significant main effects of orientation,  $F(1, 11) = 361.98$ ,  $p < 0.001$ , fragment pair,  $F(4, 44) = 158.00$ ,  $p < 0.001$ , and length,  $F(2, 22) = 62.89$ ,  $p < 0.001$ , a significant orientation  $\times$  length interaction,  $F(2, 22) = 16.10$ ,  $p < 0.001$ , and a significant fragment pair  $\times$  length interaction,  $F(8, 88) = 11.98$ ,  $p < 0.001$ . Performances between the two test blocks did not differ,  $F(1, 11) = 0.26$ ,  $p = 0.621$  and were thus pooled. A  $t$ -test using the pooled response rates confirmed that overall rates of responses consistent with the facing direction of the walker were higher than chance-level,  $t(11) = 7.712$ ,  $p < 0.001$ .

Tukey's post-hoc comparisons of the five fragment pairs, collapsed across orientation and length, indicated that the rates for pairs 2/7 and 3/8 did not differ ( $p = 0.820$ ), and were both higher than the rate for pair 4/9 ( $p < 0.005$  for both). The rates of pairs 1/6 and 5/10 differed from those of all other pairs ( $p < 0.001$  for all comparisons). Finally, Tukey's comparisons of the three lengths revealed that rates at all three lengths differed ( $p < 0.001$  for all). Specifically, rates increased with increasing length.

The orientation  $\times$  length interaction was analyzed with a one-way ANOVA that evaluated difference scores, obtained for each participant by subtracting rates of the inverted condition from those of the upright condition while collapsing for orientation and fragment pair, across the three lengths. The analysis showed a significant main effect of length,  $F(2, 22) = 16.16$ ,  $p < 0.001$ . Tukey's post-hoc comparisons revealed that the inversion effect, measured in terms of the difference in rates of responses consistent with walker direction between upright and inverted orientations, was smaller for length 100 ms than for 150 ms and 200 ms ( $p < 0.005$  for both), and the inversion effects for 150 ms and 200 ms did not differ ( $p = 0.194$ ).

The fragment pair  $\times$  length interaction was examined with individual one-way ANOVAs that compared the three lengths for each pair. The analyses showed a significant main effect of length for pair 1/6,  $F(2, 22) = 31.16$ ,  $p < 0.001$ , pair 2/7,  $F(2, 22) = 10.21$ ,  $p < 0.001$ , pair 3/8,  $F(2, 22) = 6.32$ ,  $p = 0.007$ , pair 4/9,  $F(2, 22) = 4.57$ ,  $p = 0.022$ , and pair 5/10,  $F(2, 22) = 13.31$ ,  $p < 0.001$ . Tukey's comparisons for pair 1/6 indicated that rates at all three lengths differed ( $p < 0.005$  for all) with rates increasing with increasing window length. Comparisons for pair 2/7 indicated that the rate for 100 ms was significantly lower than the rates for 150 ms and 200 ms ( $p < 0.003$  for both), and the rates for 150 ms and 200 ms did not differ ( $p = 0.967$ ). Similarly for pair 3/8, the rate for 100 ms was significantly lower than the rates for 150 ms and 200 ms ( $p < 0.017$  for both), which did not differ ( $p = 0.987$ ). Comparisons for pair 4/9 showed that the rate at 100 ms was statistically lower than the rate at 200 ms only ( $p = 0.020$ ), although the rates for 150 ms and 200 ms did not differ ( $p = 0.687$ ). Finally, pair 5/10 showed a reversed trend from that of pairs 2/7 and 3/8. Specifically, the rate of responses consistent with the direction of the walker for 100 ms was significantly higher than the rates for 150 ms and 200 ms ( $p < 0.001$  for both), which did not differ ( $p > 0.900$ ).

## Discussion

The results for Group 1 are qualitatively different from those of Group 2. As expected, observers in Group 1 who were presented with displays derived from a single fragment merely based direction judgments upon the horizontal displacement of the individual dot elements.

Across a full gait cycle, the displacement averages out and there is no net displacement. Accordingly, observers' overall response rates were at chance level. Interpreting the displays solely based upon dot translatory movement also explains the lack of an inversion effect in the results of Group 1.

In contrast to Group 1, the results for observers in Group 2 who were presented with displays derived from paired fragments show above chance-level response rates and a strong inversion effect. These results are consistent with the orientation-dependency for discriminating walking direction from scrambled displays derived from full walkers and corroborate the finding of the critical role of the foot motion (Troje & Westhoff, 2006). The response behavior of observers in Group 2 is qualitatively different from that of observers in Group 1 and cannot be explained by a simple linear integration of the responses given to the individual fragments. Figure 2C re-plots the results of Group 1 collapsing the data over fragment pairs. Average response rates for these pairs are close to chance level and there is no inversion effect when the fragments are shown in isolation (Group 1). These data are very different from the data obtained when the fragment pairs are presented simultaneously (Group 2).

Critically, these results suggest that retrieving direction of motion from scrambled biological motion displays involves more than processing the local spatiotemporal cues inherent to the isolated motion of the foot. Rather, we must conclude that even within the context of a full scrambled walker display that cannot be resolved into a percept of coherent form, the foot's elemental cues are evaluated with respect to the motions of other elements, or at least to other parts of the same element's trajectory, as we have shown here. But, why are additional reference dots important?

Critical to the discussion of this question is the distinction between the direction of explicit translatory motion of an object (or a walker, in our case), and the implicit cues contained in the deformation of the body. We call the former extrinsic motion and the latter intrinsic motion (see also, Kersten, 1998, who used these terms in a slightly different, yet analogous context). In his early work, Johansson (1973, 1974) demonstrated how the human visual system decomposes the kinematics of the display of a rolling wheel into common translatory (i.e., extrinsic) motion and deviant circular (i.e., intrinsic) motion in order to understand the mechanics of the scene. Presented alone, a point representing the rim of a rolling wheel is interpreted as moving along a cycloidal path (i.e., a path resembling periodic arches). Only when a second point is added (e.g., on the axle of the wheel) can observers perceive the rolling wheel. In the context of our stimuli, subtraction of the common translatory (extrinsic) component of the motion results in the absolute cyclic motion of the foot and retains the walker's intrinsic motion, but only if the full gait cycle can be considered. The qualitative difference in response behavior between

the two groups in the present experiment is most likely due to a switch from the perception of solely extrinsic motion with the single fragments in Group 1 to the use of intrinsic motion cues with the paired fragments in Group 2. Only the latter matches the reality from which the stimuli were derived: the stationary walker that lacks any extrinsic motion but contains intrinsic motion cues revealing its facing direction.

It should be noted at this point that participants in this experiment were not informed as to the nature of the stimuli (i.e., that they were derived from a human walker). It is clear then, that the cues that are relevant for retrieving direction are independent of higher-level knowledge of the nature of the stimuli and particularly, of whether they derive from animate or inanimate objects. The exact nature of these cues however, and their contributions to the observed effects remain unclear.

Most of the fragment pairs employed in this experiment consist of a fragment that represents a fraction of the foot trajectory's stance phase and a fragment that represents a fraction of its swing phase. During the stance phase, the foot is planted on the ground and is more or less motionless. The motion of the dots that correspond to the stance phase is rather due to the motion of a panning camera that keeps the walker in the center of the display, or alternatively, to the motion of the belt of an invisible treadmill. The velocity of the dot is approximately constant and identical to the translatory (extrinsic) motion of the walker, but points in the opposite direction. The other dot, which represents a fragment from the swing phase exhibits a velocity profile that is much more variable. During the swing phase, the foot accelerates along both the horizontal and vertical dimensions due to muscle activity and gravitational acceleration. If the visual system could reliably identify stance-phase fragments and discriminate them from other types of fragments, it could safely assume that the walker is facing in the direction opposite to the direction in which the stance phase fragments move.

What, then, accounts for the inversion effect? Inversion, that is, the mirror flipping of stimulus about the horizontal axis, affects only vertical components of the trajectory. The linear, horizontal motion of the stance phase fragments is largely unaffected by inversion. We must conclude then that the observed inversion effect is due to vertical asymmetries in the swing phase segments. In principle, such asymmetries can be due to the polarity of vertical velocity, vertical acceleration, or even higher order derivatives. It is unlikely that the visual system is merely differentially sensitive to downward and upward vertical motion. In fact, this possibility is precluded by our results. For example, a superior sensitivity for downward vertical motion would predict higher rates of responses consistent with the facing direction of the walker for the paired displays containing an inverted fragment 1 than for displays containing its upright version. The results reflected the opposite pattern. Instead, we speculate that

the visual system is sensitive to the vertical acceleration exhibited by the swing phase fragments. As noted earlier, such variations in velocity along the motion path, or trajectory forms, have been proposed to facilitate the perception of a variety of events (e.g., Bingham et al., 1995).

In order to investigate the possible relationship between acceleration and the local inversion effect, we extended the use of our novel foot displays to a larger number of stimulus samples (foot motions of other animals) in [Experiment 2](#). In this next experiment, we created paired fragment stimuli (as those presented to Group 2 in [Experiment 1](#)) from the foot motions of a human walker, human runner, cat, and pigeon and presented them at both upright and inverted orientations to observers in a direction discrimination task.

If acceleration carries the local motion-based inversion effect in biological motion perception, the size of the effect should vary with different animal foot motions which undoubtedly carry very different motion profiles. In both Chang and Troje (2008) and Troje and Westhoff (2006), there were no significant differences among the inversion effects for the different animals tested. Note however that in those experiments, the foot dots were presented within the context of a full walker. The paired fragment stimuli used in [Experiment 1](#) display solely foot-specific motion information and may be more sensitive to any differences in orientation effects among different stimulus types.

## Experiment 2

### Methods

#### *Participants*

Twenty new naive observers that ranged in age from 17 to 24 years (mean age of 18.8 years; 11 females, 9 males) participated in this experiment. All observers had normal or corrected-to-normal vision.

#### *Stimuli and apparatus*

The stimuli of this experiment were derived from the motion of one foot belonging to a human walker (defined by the ankle point), human runner (defined by the ankle point), cat, and pigeon. The foot motions were shown at their veridical speeds corresponding to gait frequencies of 0.93 Hz, 1.3 Hz, 1.7 Hz, and 1.6 Hz for the human walker, human runner, cat, and pigeon, respectively. The motions were shown in sagittal view from either the right or left side. As in [Experiment 1](#), the full gait cycle for each stimulus type (walker, runner, cat, pigeon) was sampled by specifying 10 start frames, spaced at equal intervals along the cycle, from which the fragment could begin. The

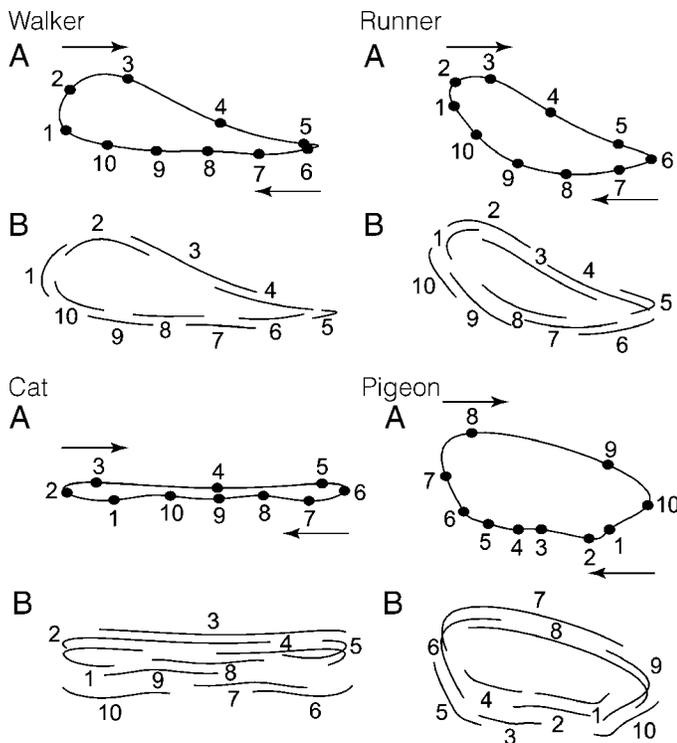


Figure 3. The full gait trajectory with the 10 starting positions (A), and the individual 150 ms trajectories of the 10 fragments (B), for the foot of a human walker, human runner, cat, and pigeon. Trajectories shown here are taken from right-facing sequences.

length that each fragment extended from the start frame was 150 ms. Figure 3 depicts the 10 start frame positions along the full gait trajectory (A), and the individual trajectories of the 10 fragments (B), for each stimulus type. Note that for the human walker, starting positions were slightly different from those defined in Experiment 1.<sup>1</sup>

For each stimulus type, five fragment pairs were created by pairing fragments labeled 1/6, 2/7, 3/8, 4/9, and 5/10. Each display lasted 1000 ms and consisted of 10 sets of a specified fragment pair that were randomly displaced within a  $4.8 \times 4.8$  deg area in the center of the screen. Each set had its own randomly chosen onset time and was visible only during the 150 ms time window. The stimuli were presented at both upright and inverted orientations. Each display subtended a visual angle of  $4.8 \times 4.8$  deg. The apparatus was identical to that of Experiment 1.

### Procedure

Stimuli were viewed binocularly at a distance of 60 cm as maintained by a chin-rest. As in Experiment 1, participants were asked to indicate the facing direction of the perceived entity (left or right).

The practice block comprised of 80 trials that consisted of left and right, and upright and inverted versions of the five fragment pairs for each of the four stimulus types. For

the experiment proper, a total of 640 experimental trials were completed across two identical experimental blocks of 320 trials each. In a single block, all possible combinations of the four stimulus types, five fragment pairs, two orientations, and two directions were repeated four times. Within each repetition, the 80 possible stimuli were presented in random order. All other testing procedures were identical to Experiment 1.

### Results

As in Experiment 1, the data were analyzed both in terms of the proportions of responses consistent with the facing direction of the walker from which the stimuli were derived and in terms of  $d'$  sensitivity measures derived from these rates. Both analyses yielded identical results and the results are presented here in terms of the proportions of responses consistent with walking direction.

A comparison of the mean proportion of responses consistent with the facing direction of the walker for each stimulus type at both orientations, collapsed across fragment pairs is shown in Figure 4. An inspection of the response rates indicated that the rates were higher for the cat (upright = 0.64 proportion of responses; inverted = 0.58 proportion of responses) than for the human walker (upright = 0.61 proportion of responses; inverted = 0.47 proportion of responses), human runner (upright = 0.66 proportion of responses; inverted = 0.42 proportion of responses), and pigeon (upright = 0.55 proportion of responses; inverted = 0.46 proportion of responses) stimuli. Overall, rates for the upright stimuli (0.62

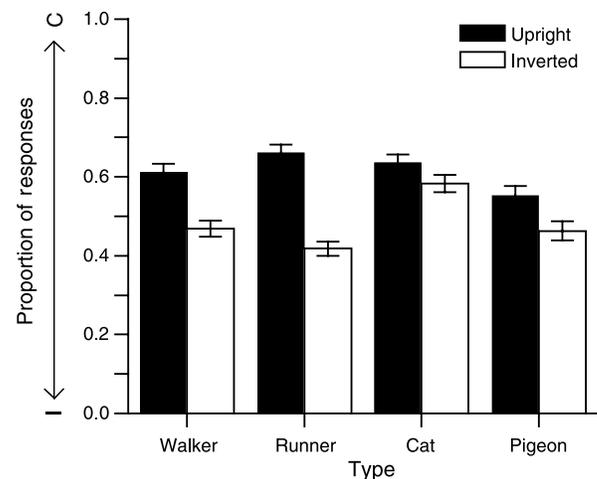


Figure 4. The mean proportion of responses consistent with the facing direction of the walker for each stimulus type at both orientations, collapsed across fragment pairs. Response rates above and below 0.5 indicate larger proportions of responses that were consistent (C) and inconsistent (I) with walking direction, respectively. Error bars represent  $\pm 1$  standard error of the mean.

proportion of responses) were higher than rates for the inverted stimuli (0.48 proportion of responses). As can be seen in Figure 4 however, the difference in rates between upright and inverted orientations varied with stimulus type: the difference was largest for the runner stimuli and smallest for the cat stimuli.

Figure 5 shows the mean proportion of responses consistent with walking direction of five fragment pairs at the two orientations separately for each stimulus type. From this figure, it is evident that for certain stimulus types, the difference in rates between upright and inverted orientations also depended on the particular fragment pair.

The above observations are supported by statistical analyses. The data were first entered in a 2 (block)  $\times$  4 (type)  $\times$  2 (orientation) ANOVA. The analysis showed significant main effects of stimulus type,  $F(3, 57) = 12.60$ ,  $p < 0.001$ , orientation,  $F(1, 19) = 143.95$ ,  $p < 0.001$ , and a significant type  $\times$  orientation interaction,  $F(3, 57) = 21.00$ ,  $p < 0.001$ . As the performance between the two test blocks did not differ,  $F(1, 19) = 0.04$ ,  $p = 0.851$ , data from the two blocks were pooled for further analyses.

Tukey's post-hoc comparisons of the different stimulus types showed that overall, the proportions of responses consistent with walking direction were higher for the cat stimuli than for all other stimulus types ( $p < 0.001$  for all). Average rates for the walker, runner, and pigeon did not differ ( $p > 0.200$  for all).

Individual comparisons of the two orientations for each stimulus type indicated that the rates for upright stimuli were higher than for inverted stimuli for all stimulus types (Bonferroni-corrected  $t$ -tests,  $p < 0.002$  for all). The type  $\times$  orientation interaction was subsequently analyzed with a one-way ANOVA on difference scores, obtained for each participant by subtracting rates for the inverted stimuli from those of the upright stimuli. The analysis showed a significant main effect of stimulus type,  $F(3, 57) = 21.00$ ,  $p < 0.001$ . Tukey's post-hoc comparisons indicated that the inversion effect, measured in terms of the difference between rates for the upright and inverted stimuli, was larger for the runner stimuli than all other types ( $p < 0.001$  for all). The inversion effects for the walker and pigeon stimuli did not differ ( $p = 0.188$ ) but the inversion effect for the walker was significantly larger than the one for the cat ( $p = 0.006$ ). The comparison between the inversion effects for the pigeon and cat was not significant ( $p = 0.507$ ).

Individual two-way ANOVAs were used to analyze the different fragment pairs between the two orientations for each of the four stimulus types. The analysis for the human walker revealed significant main effects of orientation,  $F(1, 19) = 73.00$ ,  $p < 0.001$ , and pair,  $F(4, 76) = 113.07$ ,  $p < 0.001$ , and a significant orientation  $\times$  pair interaction,  $F(4, 76)$ ,  $p = 0.029$ . Tukey's comparisons of the different pairs indicated that while response rates for pairs 1/6 and 5/10 did not differ ( $p = 0.798$ ), they were

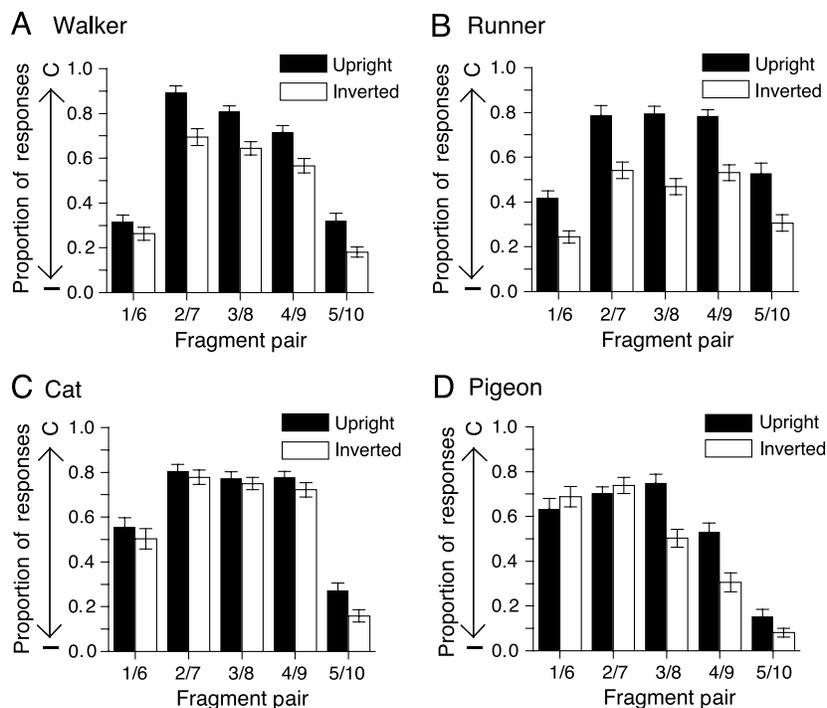


Figure 5. The mean proportion of responses consistent with the facing direction of the walker for five fragment pairs at the two orientations for the human walker (A), human runner (B), cat (C), and pigeon (D). Response rates above and below 0.5 indicate larger proportions of responses that were consistent (C) and inconsistent (I) with walking direction, respectively. Error bars represent  $\pm 1$  standard error of the mean.

significantly lower than the rates for all other pairs ( $p < 0.001$  for all comparisons). The response rate for pair 2/7 was not different from the rate for pair 3/8 ( $p = 0.277$ ), but was significantly higher than the rate for pair 4/9 ( $p < 0.001$ ). The comparison between pairs 3/8 and 4/9 was not significant ( $p = 0.089$ ). The orientation  $\times$  pair interaction was analyzed with Tukey’s comparisons of upright and inverted orientations for each pair. The analyses revealed that the rates for upright stimuli were higher than those for inverted stimuli for pairs 2/7, 3/8, 4/9, and 5/10 ( $p < 0.001$  for all), but not pair 1/6 for which the two orientations did not differ ( $p = 0.113$ ).

A comparable ANOVA for the runner showed significant main effects of orientation,  $F(1,19) = 75.37$ ,  $p < 0.001$ , and pair,  $F(4,76) = 35.51$ ,  $p < 0.001$ , but no interaction. Tukey’s comparisons of the different fragment pairs showed that while the rates for pairs 2/7, 3/8, and 4/9 did not differ ( $p > 0.800$  for all), they were significantly higher than the rates for pairs 1/6 and 5/10 ( $p < 0.001$  for all), which did not differ ( $p = 0.146$ ).

Similarly, the ANOVA for the cat revealed significant main effects of orientation,  $F(1,19) = 13.81$ ,  $p = 0.002$ , and fragment pair,  $F(4,76) = 120.79$ ,  $p < 0.001$ , and no interaction. Here, Tukey’s comparisons of the different fragment pairs revealed that the rates for pairs 2/7, 3/8, and 4/9 did not differ ( $p > 0.600$  for all comparisons), but were significantly higher than the rates of pairs 1/6 and

5/10 ( $p < 0.001$  for all). The rate for pair 1/5 was also significantly higher than the rate for pair 5/10 ( $p < 0.001$ ).

The ANOVA for the pigeon showed significant main effects of orientation,  $F(1,19) = 48.89$ ,  $p < 0.001$ , and fragment pair,  $F(4,76) = 61.25$ ,  $p < 0.001$ , and a significant orientation  $\times$  pair interaction,  $F(4,76) = 19.68$ ,  $p < 0.001$ . Tukey’s comparisons of the different fragment pairs indicated that while the rates for pairs 1/6, 2/7, and 3/8 did not differ ( $p > 0.200$  for all), they were significantly higher than the rates of pairs 4/9 and 5/10 ( $p < 0.001$  for all). In addition, the rate for pair 4/9 was significantly higher than the rate for pair 5/10 ( $p < 0.001$ ). The interaction was analyzed with Tukey’s tests of upright versus inverted orientations per each fragment pair. The analyses revealed that the rates were higher for upright versions than for inverted versions of pairs 3/8, 4/9, and 5/10 ( $p < 0.030$  for all). The two orientations did not differ for pairs 1/6 ( $p = 0.092$ ) and 2/7 ( $p = 0.274$ ).

Finally, in Table 1, we calculated the average vertical accelerations both in real world coordinates and screen coordinates, and a measure of the inversion effect for each of the fragment pairs that comprised the stimuli in this experiment. Here, the inversion effect is quantified by a difference score, computed by subtracting the proportion of responses consistent with walking direction for the inverted stimulus from the proportion of responses consistent with walking direction for the upright stimulus.

Type	Fragment pair	Real world vertical acceleration (m/s <sup>2</sup> )	Screen vertical acceleration (deg/s <sup>2</sup> )	Inversion score
Human walker	1 / 6	0.03 $\uparrow$ / -1.35 $\downarrow$	0.10 $\uparrow$ / -4.01 $\downarrow$	0.05
	2 / 7	9.45 $\downarrow$ / 0.21 $\uparrow$	27.95 $\downarrow$ / 0.63 $\uparrow$	0.20
	3 / 8	0.06 $\downarrow$ / -0.47 $\uparrow$	0.19 $\downarrow$ / -1.39 $\uparrow$	0.17
	4 / 9	-4.16 $\downarrow$ / -1.06 $\uparrow$	-12.30 $\downarrow$ / -3.13 $\uparrow$	0.15
	5 / 10	0.24 $\downarrow$ / -3.45 $\uparrow$	0.71 $\downarrow$ / -10.20 $\uparrow$	0.14
Human runner	1 / 6	4.66 $\uparrow$ / -1.67 $\downarrow$	13.79 $\uparrow$ / -4.95 $\downarrow$	0.18
	2 / 7	8.56 $\downarrow$ / -3.79 $\uparrow$	25.32 $\downarrow$ / -11.21 $\uparrow$	0.25
	3 / 8	2.05 $\downarrow$ / -4.17 $\uparrow$	6.06 $\downarrow$ / -12.33 $\uparrow$	0.33
	4 / 9	-4.54 $\downarrow$ / -1.32 $\uparrow$	-13.43 $\downarrow$ / -3.92 $\uparrow$	0.25
	5 / 10	-1.59 $\downarrow$ / 1.82 $\uparrow$	-4.72 $\downarrow$ / 5.39 $\uparrow$	0.22
Cat	1 / 6	0.77 $\uparrow$ / -2.65 $\downarrow$	2.28 $\uparrow$ / -7.85 $\downarrow$	0.05
	2 / 7	2.34 $\uparrow$ / -0.16 $\uparrow$	6.94 $\uparrow$ / -0.48 $\uparrow$	0.03
	3 / 8	1.09 $\downarrow$ / 0.53 $\uparrow$	3.23 $\downarrow$ / 1.58 $\uparrow$	0.02
	4 / 9	2.26 $\downarrow$ / 0.02 $\downarrow$	6.68 $\downarrow$ / 0.05 $\downarrow$	0.06
	5 / 10	-1.24 $\downarrow$ / -2.66 $\uparrow$	-3.68 $\downarrow$ / -7.88 $\uparrow$	0.11
Pigeon	1 / 6	-4.13 $\downarrow$ / 6.33 $\uparrow$	-12.22 $\downarrow$ / 18.73 $\uparrow$	-0.05
	2 / 7	0.65 $\uparrow$ / 20.41 $\uparrow$	1.92 $\uparrow$ / 60.41 $\uparrow$	-0.04
	3 / 8	-0.95 $\uparrow$ / 5.87 $\downarrow$	-2.81 $\uparrow$ / 17.36 $\downarrow$	0.25
	4 / 9	-4.54 $\uparrow$ / -6.99 $\downarrow$	-13.43 $\uparrow$ / -20.69 $\downarrow$	0.23
	5 / 10	-8.74 $\uparrow$ / -6.98 $\downarrow$	-25.86 $\uparrow$ / -20.65 $\downarrow$	0.07

Table 1. Average vertical accelerations and inversion score for each fragment pair. Sign of acceleration value indicates direction of acceleration. Positive and negative acceleration values indicate downward and upward accelerations, respectively. Arrows indicate vertical direction of the motion. Inversion score was computed by subtracting the proportion of responses consistent with the facing direction of the walker from which the stimulus was derived for the inverted orientation from that for the upright orientation.

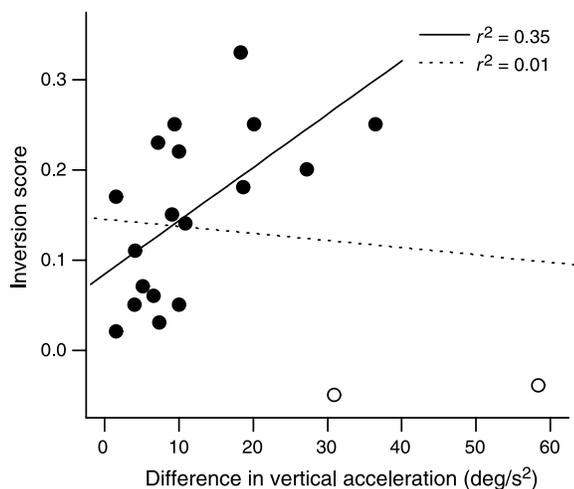


Figure 6. A comparison of the inversion score and the absolute difference in vertical acceleration between the two constituent fragments of each stimulus. The dotted and solid lines represent separate linear regression fits for the full data set and the data set with two outliers (open circles) omitted, respectively.

We subsequently compared the inversion score for each stimulus to the absolute difference in vertical acceleration between its two constituent fragments by means of a linear regression analysis. Figure 6 shows the regression analyses for the full stimulus set and for the stimulus set with two outliers (open circles) removed. Although no relationship is evident when the full set is considered ( $r^2 = .01$ ;  $p = 0.659$ ), a significant positive correlation between the inversion score and absolute difference in vertical acceleration becomes evident once the outliers are removed ( $r^2 = 0.35$ ;  $p = 0.009$ ).

## Discussion

The overall response rates for the walker stimuli in this experiment are very similar to the response rates obtained for the 150 ms fragment pairs in Experiment 1. The results here extend upon the findings of Experiment 1 by showing that direction can also be retrieved from fragments of foot motions of a human runner and other animals. For all stimulus types, this ability depends on the orientation of the stimulus.

Interestingly, although the cat stimuli appear to be the most informative for direction retrieval overall, they carry the smallest inversion effect in comparison to all other stimulus types. As can be seen from Table 1, the cat's foot motion carries the smallest vertical accelerations as compared to all stimulus types.

The inversion effect for the cat stimuli is generally quite small (score of  $\sim 0.05$  for pairs 1/6, 2/7, 3/8, and 4/9). In contrast, the runner's foot motion carries very pronounced vertical accelerations, particularly fragments 2 and 3 of pairs 2/7 (score = 0.25) and 3/8 (score = 0.33),

respectively. Correspondingly, we found here that the runner stimuli carried the largest inversion effect overall as compared to all other stimulus types. Additionally, as shown in Figure 6, a positive relationship is evident between the inversion effect and the absolute difference in vertical acceleration between the two constituent fragments of each stimulus. These findings are consistent with our hypothesis that the local-motion based inversion effect in biological motion perception is carried by the vertical acceleration contained in foot motions.

The finding that different stimulus types are differentially effective for direction retrieval and have differentially sized inversion effects is not consistent with results reported for full-walker scrambled displays (Chang & Troje, 2008; Troje & Westhoff, 2006). In these studies, direction discrimination ability did not differ among the various animal types. As noted earlier however, this apparent discrepancy may be due to the fact that the stimuli in the current study display only foot-specific motion information and are thus more sensitive measures that allow the differences between the various animals to be teased out.

Considered together, the results of this experiment suggest strongly a relationship between acceleration and the local-motion based inversion effect and are congruent with previous suggestions that variations in velocity are evaluated in the perception of both animate and inanimate events (Bingham et al., 1995). In Experiment 3, we tested the importance of acceleration for the local inversion effect by manipulating the velocity profile of the foot motion. Specifically, we presented observers with the natural human walker stimuli of the present experiment, and with stimuli that were matched spatiotemporally to the natural stimuli, but moved with constant speeds along the trajectory paths. If in fact, acceleration carries the local inversion effect in biological motion perception, there should be no difference in performances between the upright and inverted versions of the constant speed stimuli which contain no acceleration along the specified paths.

## Experiment 3

### Methods

#### Participants

A new group of 20 naive observers that ranged in age from 17 to 23 years (mean age = 18.3 years; 12 females, 8 males) participated in this experiment. All observers had normal or corrected-to-normal vision.

#### Stimuli and apparatus

Two sets of stimuli were employed in this experiment. The first set comprised of the paired fragments derived

from the natural foot motion of the human walker in [Experiment 2](#) ([Figure 3](#), human walker). The second set comprised of stimuli derived from fragments that were identical to the natural walker stimuli, but had accelerations removed; that is, each individual dot moved along a path identical to that defined previously but with a constant speed equal to the average speed of the dot with the specified fragment. Note that this manipulation renders only the speed along the path to be constant and does not preclude the possibility that there may be a change in velocity between the beginning and the end of the motion path. That is, in order to achieve the same trajectory paths of the natural stimulus, some acceleration must still be present in the constant speed stimulus due to changes in the direction of the velocity vector. Importantly, this manipulation disrupts the natural velocity profile of the foot motion and in particular, eliminates the vertical asymmetries caused by gravitational acceleration. For each fragment pair then (i.e., 1/6, 2/7, 3/8, 4/9, 5/10), two versions served as the basis for the stimuli in this experiment: one that contained natural acceleration and one that contained no acceleration along the specified paths.

As in [Experiments 1](#) and [2](#), each display lasted 1000 ms in duration and consisted of 10 sets of a specified fragment pair that were randomly positioned within a  $4.8 \times 4.8$  deg area in the center of the screen. Each set had its own randomly chosen onset time and was visible only during the 150 ms time window. The stimuli were presented at both upright and inverted orientations. Each display subtended a visual angle of  $4.8 \times 4.8$  deg. The apparatus was identical to that of [Experiments 1](#) and [2](#).

## Procedure

As in [Experiments 1](#) and [2](#), participants were asked to indicate the facing direction of the perceived entity (left or right). The practice block comprised of 40 trials that consisted of left and right, and upright and inverted versions of the five fragment pairs belonging to each of the two stimulus types (natural and constant).

The experiment proper consisted of 400 trials. In the experimental block, all possible combinations of the two stimulus types, five fragment pairs, two orientations, and two directions were repeated 10 times. Within each repetition, the 40 possible stimuli were presented in random order. All other testing procedures were identical to [Experiment 2](#).

## Results

As in [Experiments 1](#) and [2](#), the data were analyzed both in terms of the proportions of responses consistent with the facing direction of the walker from which the stimuli were derived and in terms of  $d'$  sensitivity measures

derived from these rates. Again, both analyses yielded identical results. As in [Experiments 1](#) and [2](#), the results are presented in terms of proportions of responses consistent with walking direction.

The mean proportion of responses consistent with walking direction of the two stimulus types for the five fragment pairs at upright and inverted orientations are presented in [Figure 7](#). An examination of the mean response rates for upright versus inverted orientations collapsed across stimulus type and fragment pair revealed that in general, the rates for upright stimuli (0.56 proportion of responses) were higher than the rates for inverted stimuli (0.52 proportion of responses). However, a closer inspection of the means separately for the two stimulus types reveals that the rates for upright displays were higher than the rates for the inverted displays for the natural stimuli only.

Response rates were analyzed with a 2 (type)  $\times$  2 (orientation)  $\times$  5 (fragment pair) repeated-measures ANOVA that showed a significant main effect of orientation,  $F(1, 19) = 7.15$ ,  $p = 0.015$ , a significant main effect of fragment pair,  $F(4, 76) = 28.33$ ,  $p < 0.001$ , and a significant type  $\times$  orientation interaction,  $F(1, 19) = 13.11$ ,  $p = 0.002$ . The main effect of type and other interactions were not significant.

Tukey's post-hoc comparisons of the different fragment pairs, collapsed over the two stimulus types and two orientations showed that while the rates for pairs 2/7, 3/8, and 4/9 did not differ ( $p > 0.500$  for all comparisons), they were significantly higher than the rates for pairs 1/6 and 5/10 ( $p < 0.001$  for all), which did not differ ( $p = 0.219$ ).

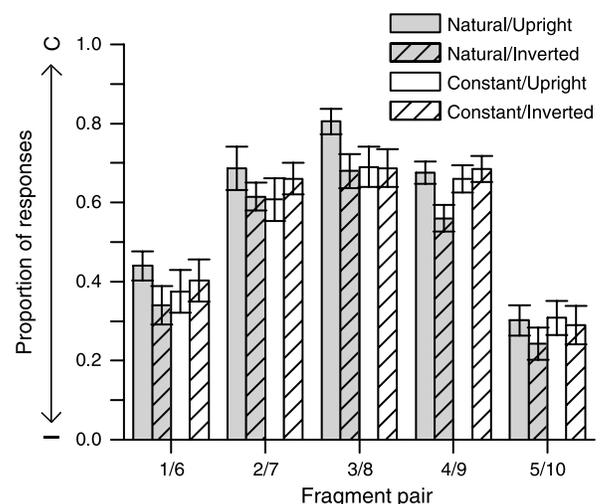


Figure 7. The mean proportion of responses consistent with the facing direction of the walker for the natural walker and constant speed stimuli across the five fragment pairs and two orientations. Response rates above and below 0.5 indicate larger proportions of responses that were consistent (C) and inconsistent (I) with walking direction, respectively. Error bars represent  $\pm 1$  standard error of the mean.

The type  $\times$  orientation interaction was analyzed with Bonferroni-corrected, two-tailed *t*-tests comparing upright and inverted orientations for each stimulus type. The analyses revealed that the rates were higher for upright displays than for inverted displays for the natural stimuli only ( $p < 0.001$ ; upright = 0.58 proportion of responses; inverted = 0.49 proportion of responses). Upright and inverted versions of the constant speed stimuli did not differ ( $p = 0.335$ ; upright = 0.53 proportion of responses; inverted = 0.55 proportion of responses).

## Discussion

The pattern of results for the natural human walker stimuli in this experiment is similar to that obtained for the same set of stimuli in [Experiment 2](#). Importantly, the results obtained here for constant speed stimuli that are otherwise matched to the natural stimuli reveal a complete absence of an inversion effect. This contrast is critical as the two sets of stimuli are identical in all respects (e.g., identical average speeds), and differ only in terms of the presence (natural stimuli) or absence (constant stimuli) of acceleration along the motion path. This finding suggests that the inversion effect associated with the local foot dot motions is carried by the acceleration contained in these motions.

Consistent with the results of [Experiment 2](#), the fragment pairs that were most informative for the natural stimuli were pairs 2/7, 3/8, and 4/9. Interestingly, an inspection of the proportions of responses of the same fragment pairs (2/7, 3/8, and 4/9) for the constant speed stimuli reveals that observers were still able to derive the direction that was consistent with the facing direction of the walker from which the stimuli were derived. In fact, the mean response rates for these pairs are very similar to the mean rates for the corresponding pairs of the natural walker stimuli when collapsed across the two orientations. One possibility is that this pattern may be a result of simple speed effects. That is, for both sets of stimuli, perceived direction may be determined by the higher-speed fragments within each pair. Indeed, in pairs 2/7, 3/8, and 4/9, the facing direction of the display is signaled by the higher-speed fragments. Importantly however, the results show an inversion effect for the natural walker stimuli only. As the two sets of stimuli differ only in terms of the presence or absence of acceleration along the motion path, we conjecture that acceleration accounts for the difference in orientation-specificity observed for the data of the natural and constant speed stimuli.

The results of this experiment show clearly that the visual system exploits the accelerations contained in the natural walker stimuli. Moreover, these accelerations must be assessed in accordance to some framework that renders them anisotropic. These findings suggest that the responsible mechanisms are impressively sensitive to the acceleration—able to retrieve it from our very limited 150 ms trajectories.

## General discussion

Using novel biological motion stimuli that display solely foot-specific information, we showed that the cues that carry the local inversion effect in biological motion perception cannot be retrieved independently from a single local motion of the foot but can be exploited from displays derived from two foot dots that trace counter-phase positions of the gait cycle ([Experiment 1](#)). Extending our findings from human walker stimuli, we showed that displays derived from other foot types also provide information about facing direction and carry an inversion effect. Importantly, the inversion effect was largest for the runner stimuli which exhibit large vertical accelerations and smallest for the cat stimuli, which carry comparatively minor vertical accelerations ([Experiment 2](#)). We showed further a linear correlation between the inversion effect and the absolute difference in vertical acceleration between the two constituent fragments of each stimulus. Finally, we showed that if acceleration is removed from stimuli that are otherwise identical to the natural walker stimuli, the inversion effect disappears ([Experiment 3](#)). Together, these results suggest that the local inversion effect in biological motion perception relies on accelerations contained in the foot motions. These findings are congruent with previous demonstrations of the important role of velocity profiles for the perception of animate and inanimate events (Bingham et al., 1995).

Although we have provided evidence to suggest that the inversion effect is carried by the velocity profile of the foot motion, it remains unclear as to the specific role of such cues for achieving the facing direction of a display. We conjecture that horizontal (left–right) and vertical (up–down) asymmetries of the trajectories of the foot motion play very different roles in the manner in which they contribute to the results of the present experiments, and in general, to the perception of biological motion. While information regarding the facing direction of the walker must be encoded somehow in horizontal asymmetries, the inversion effect must be carried by vertical asymmetries in the stimulus. As noted earlier, these asymmetries could in principle be due to a number of different attributes, including trajectory shape, the direction of the motion along the trajectory, and many other parameters inherent to the velocity profile of the dot moving along the trajectory. Trajectory shape is likely not a valid cue for the inversion effect as we employed a variety of different shapes in [Experiment 2](#). Furthermore, we noted earlier that the present data is also able to discount the polarity of vertical velocity as a cue for the inversion effect (see discussion to [Experiment 1](#)). Thus, although there are still even higher-order motion derivatives that could be considered, the next most parsimonious cue for the inversion effect lies with the polarity of the vertical acceleration carried by the trajectory. How do vertical asymmetries such as those carried by accelerations

then contribute to the observers' ability to retrieve facing direction from stimuli in the present experiments?

Note that only horizontal asymmetries can contain information about the facing direction of the walker. The amount of such information remains the same if the stimulus is inverted (i.e., flipped about the horizontal axis). However, the visual system's ability to make use of this information seems to depend on the orientation of the stimulus and is thus affected by the inversion of the display.

We suggest that the presence of vertical motion that is consistent with a mass being propelled away from the ground and then subsequently pulled back by gravity first flags an event as being animate. Only once the event is deemed to be animate does our visual system attribute a facing direction to it. Recall that there is no net translation in our stimuli. The intended locomotion in one direction is always countered by the inverse motion of the invisible belt of a treadmill or the panning motion of a camera. Overall the stimulus remains stationary. The remaining intrinsic motion can only reveal the intention to move into a certain direction; that is, the facing direction. We conjecture that the visual system attributes such intentionality only to something that indicates a degree of animacy, and uses the vertical motion profile to validate a trajectory as being animate. Thus, the vertical asymmetries may determine the validity of a trajectory for further analysis as an animate being while the horizontal asymmetries may determine the facing direction of valid trajectories.

In order to appreciate the significance of current findings that demonstrate visual sensitivity to velocity profiles (i.e., accelerations) contained in biological motion, it is worth considering findings in the literature for the perception of acceleration with non-biological stimuli. Human observers seem to be remarkably inept at assessing accelerated motion (e.g., Babler & Dannemiller, 1993; Calderone & Kaiser, 1989; Schmerler, 1976). For example, observers have a tendency to perceive uniform acceleration despite sudden changes in the velocity of the stimulus (Burke, 1952). In one direct investigation of the perception of accelerated motion, Schmerler (1976) measured observers' ability to detect accelerating and decelerating motion as a function of the rate of acceleration/deceleration and the ratio of terminal to initial velocity. On each trial, the observers' task was to classify the motion of the stimulus (a horizontal-moving ball) as accelerating, decelerating, or moving with constant velocity. Judgement accuracies varied only slightly for the varying acceleration/deceleration rates, and at all rates, dropped below chance when the ratio of terminal to initial velocity was less than approximately 3. From his data, Schmerler concluded that in order for motion change to be detected 50% of the time, 230%–320% increases or decreases in velocity are necessary. In consideration of our results reported here, it is intriguing that despite human observers' seeming ineptness at judging accelerated motion explicitly, accelerations are in fact processed by the visual system, as evidenced by the results of Experiment 3.

Recall that in Experiment 3, the natural walker stimuli resulted in an inversion effect but the constant speed stimuli did not. The only difference between the two sets of stimuli was the presence (natural stimuli) or absence (constant speed stimuli) of accelerations suggesting that the accelerations contained in the natural stimuli must be exploited by the visual system. According to Table 1, accelerations for the walker stimuli are most pronounced during the swing phase fragments 2 and 3. A closer examination of the motions of fragments 2 and 3 however revealed that their respective ratios of terminal to initial velocities are  $-1.05$  (negative denotes change in direction) and  $1.02$ , respectively. That is, the final and initial velocities for these two fragments are almost identical. Although we cannot conclude if observers explicitly detected acceleration/deceleration from these fragments, these findings raise the possibility that accelerations contained in the swing phase fragments are interpreted by the visual system independently of whether they can be explicitly detected by the observer psychophysically. Still, in reviewing the apparent conflict between observer sensitivity to visual acceleration and sensitivity to trajectory form, Muchisky and Bingham (2002) noted that the ability to detect variation in velocity along a trajectory does not require sensitivity to acceleration. They argued that changes in velocity over space, rather than time, could be exploited by the observer instead.

In another study of acceleration perception with non-biological stimuli, Calderone and Kaiser (1989) presented a stimulus of a single square that moved either up, down, left, or right while accelerating or decelerating. The observers' task was to decide if the square did or did not accelerate/decelerate. Interestingly, for horizontal motions, decelerations were easier to detect while for vertical motions, accelerations were easier to detect. Of particular relevance, thresholds did not differ within the principle axes (upward versus downward or leftward versus rightward). As noted by Calderone and Kaiser, this last finding is surprising given the abundance of objects in the visual environment that often accelerate while moving downward and decelerate while moving upward.

The results presented in our current study suggest that the visual system is sensitive to the orientation (direction) of accelerating biological motions. That is, the vertical accelerations exhibited by the local foot motions must be interpreted according to some framework that renders them anisotropic. The leg muscles are almost inactive during the swing phase of the gait cycle (e.g., Crowninshield & Brand, 1981), and it has been suggested that the foot moves entirely under the influence of gravity during this phase (Mochon & McMahon, 1980). We conjecture that the visual system is sensitive to the accelerations that result as the foot interacts with gravitational force. Specifically, we proposed earlier that the visual system evaluates accelerations according to a gravitational framework in order to validate trajectories as being animate.

The use of gravitational heuristics for visual perception has been reported in the past both for inanimate dynamic events (e.g., McConnell, Muchisky, & Bingham, 1998; Pittenger, 1985; Stappers & Waller, 1993) and for the perception of biological motion (e.g., Jokisch & Troje, 2003; Runeson & Frykholm, 1981; Shipley, 2003). For example, Pittenger (1985) showed that observers could retrieve the length of a swinging pendulum if informed about its period. In another study, Stappers and Waller (1993) presented observers with animations of a fountain on a video background and asked observers to adjust the magnitude of gravity to make the display appear natural. They found that observers were well able to match gravitational acceleration with apparent depth. Gravity-based interpretations have also been found for the perception of biological motion. Runeson and Frykholm (1981) found that observers were able to judge a box's mass from a point-light sequence of an actor lifting a box. They reasoned that observers exploited the relationship between postural changes and the acceleration of the box using dynamic principles. Jokisch and Troje (2003) provided further evidence to suggest that the visual system exploits a fixed relationship between spatial and temporal parameters that exists in a gravity-based environment by showing that observers, when presented with point-light displays of dogs walking with varying frequencies, judged the size of the dog to be smaller at high stride frequencies than at low frequencies. In another study, Shipley (2003) presented a point-light figure walking on his hands in upright and inverted orientations and found that walker detection was better for the upright display which contained familiar dynamic relations.

Although the studies summarized above clearly implicate the use of assumptions about gravity, they do not reveal the reference systems in which these assumptions are employed. Conceivably, orientation effects for biological motion perception could be described according to either observer-centered (e.g., retinal) or allocentric (e.g., gravitational) coordinates. To this end, Bingham et al. (1995) found that the recognition of point-light events was stronger for upright displays than for inverted displays regardless of whether observers were oriented upright or rotated by 180 degrees. The authors therefore concluded that point-light events are perceived in relation to the gravitational field rather than the relative orientation of the observer and the stimulus. These results however appear to contrast those reported by Troje (2003) which showed no advantage for detecting a walker in displays that were oriented upright and presented to rotated observers than in displays that were rotated and presented to upright observers. Instead, performance only depended on whether the display was aligned with the observer regardless of their orientation in space suggesting that orientation constraints are in fact egocentric. As such, the exact coordinates according to which orientation effects for biological motion perception should be described (whether based upon global or local cues) requires further clarification.

Finally, the individual fragments that comprised both sets of displays in [Experiment 3](#) extended only 150 ms in length, suggesting that the accelerations can be exploited by the visual system with very limited information. Indeed, we showed in [Experiment 1](#) (paired fragments) that the inversion effect was still present (although comparatively smaller) for displays comprised of fragments extending just 100 ms in length. Interestingly it has been shown that accurate acceleration detection requires integration times of approximately 100 ms (Werkhoven, Snippe, & Toet, 1992). What is the threshold temporal window for retrieving acceleration cues contained in local biological motions? An answer to this question requires further empirical work.

In sum, it has become evident that at least two inversion effects need to be considered in biological motion perception. While the well-demonstrated inversion-related impairment in perceiving coherently organized displays may be attributable to impaired global processing (e.g., Bertenthal & Pinto, 1994; Pavlova, 1989), there is another inversion effect which relies on the local foot motions (Troje & Westhoff, 2006). Here, we have provided evidence to suggest that this latter inversion effect is carried by vertical accelerations exhibited by foot motions.

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## Footnote

<sup>1</sup>In [Experiment 1](#), a cumulative rounding error that became apparent only after data collection resulted in a slightly shorter distance between starting points of fragments 1 and 2 as compared to the distance between the starting points of all other adjacent fragments. The error was corrected in [Experiment 2](#).

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