Perception of animacy and direction from local biological motion signals

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We present three experiments that investigated the perception of animacy and direction from local biological motion cues. Coherent and scrambled point-light displays of humans, cats, and pigeons that were upright or inverted were embedded in a random dot mask and presented to naive observers. Observers assessed the animacy of the walker on a six-point Likert scale in Experiment 1, discriminated the direction of walking in Experiment 2, and completed both the animacy rating and the direction discrimination tasks in Experiment 3. We show that like the ability to discriminate direction, the perception of animacy from scrambled displays that contain solely local cues is orientation specific and can be well-elicited within exposure times as short as 200 ms. We show further that animacy ratings attributed to our stimuli are linearly correlated with the ability to discriminate their direction of walking. We conclude that the mechanisms responsible for processing local biological motion signals not only retrieve locomotive direction but also aid in assessing the presence of animate agents in the visual environment.

Introduction

The visual mechanisms that underlie the perception of movement patterns characteristic of living animals, collectively termed *biological motion* (Johansson, 1973), are of particular interest given the social implications that accompany identifying and interpreting such patterns. It has been shown that from simple displays of point-lights depicting typically the motions of the joints of an agent, characteristics such as gender (e.g., Barclay, Cutting, & Kozlowski, 1978; Kozlowski & Cutting, 1977), emotion (e.g., Dittrich, Troscianko, Lea, & Morgan, 1996; Pollick, Paterson, Bruderlin, & Sanford, 2001), and identity (Cutting & Kozlowski, 1977) can be extracted reliably. In addition, this perceptual ability is not restricted to human patterns as it has been extended to point-light animations depicting the motions of other legged animals (Mather & West, 1993).

The exact nature of the mechanisms that allow the retrieval of such a wide range of information from biological motion, however, is not well agreed upon. While some believe that information processing relies foremost on local motion signals (e.g., Mather, Radford, & West, 1992), others emphasize the importance of global processes, relating to the spatiotemporal organization of the display (e.g., Beintema & Lappe, 2002; Bertenthal & Pinto, 1994; Chatterjee, Freyd, & Shiffrar, 1996; Shiffrar, Lichtey, & Heptulla Chatterjee, 1997).

A role for local processes has been demonstrated empirically. Consistent with the restricted temporal and spatial properties of local motion detecting processes (e.g., Baker & Braddick, 1985), Mather et al. (1992) found that performances on coherence and direction discrimination tasks were reliable only when the inter-frame interval and frame increments of the point-light stimulus were short (for evidence that mechanisms supporting biological motion perception can operate over extended temporal intervals, however, see Thornton, Pinto, & Shiffrar, 1998).

Still, others have demonstrated the relevance of global analyses for biological motion perception. Beintema and Lappe (2002) tested the perception of a moving human figure in the absence of local image motion by re-allocating each point to another randomly selected position on the limb in successive frames and showed that under these conditions, observers still spontaneously reported seeing walking persons. Correspondingly, Bertenthal and Pinto (1994) embedded a target in a mask of additional, randomly positioned walker point-lights and found that observers could still detect a walking figure. These studies suggest that the perception of structure from a point-light display does not in fact require prior processing of local motions. In addition, the orientation dependency of biological motion perception, a well-documented characteristic describing an impairment in perceiving inverted point-light displays that otherwise maintain the local relations of their upright versions (i.e.,

the "inversion effect"), has been often interpreted in favor of global or configural processing (e.g., Bertenthal & Pinto, 1994).

Although proponents for local or global processing argue for very different mechanisms, they share in common the assumption that biological motion perception is a unitary phenomenon. It has recently become apparent, however, that this approach should be abandoned in favor of a multi-level view that could well accommodate the contributions of both local and global information (Troje, 2008). In addition to the inversion-related impairment in biological motion perception that may well be attributable to global form processing, Troje and Westhoff (2006) demonstrated an inversion effect that is associated solely with local motion cues. In their study, coherent and spatially scrambled point-light displays were presented to observers performing a direction discrimination task. While coherent displays contain structural information that can be exploited, scrambled displays in which individual dots are randomly displaced from their veridical positions contain only local information. Significantly, they showed that even in the absence of structural cues, observers could reliably extract directional information from the scrambled displays. However, the ability to discriminate direction from these displays was significantly impaired when the scrambled walkers were shown inverted rather than upright. This effect was independent of the temporal relationships among the individual dots. Further examination by inverting specific parts of the display revealed that the cues for direction of motion were carried by the ankle dots of the walker.

The importance of the ankle motion for biological motion perception has been reported previously by Mather et al. (1992). In their study, point-light walkers with certain dots omitted (shoulder and hip, elbow and knee, or wrist and ankle) were presented to observers. They showed that performances on coherence and direction discrimination tasks were most affected by the omission of wrist and ankle dots. The findings by Troje and Westhoff (2006) that the ankle dots retain their cues to direction even in scrambled displays and that they carry an orientation-specific effect contribute important extensions to the findings by Mather et al. Particularly, their findings suggest that the inversion effect observed for coherent walkers has two entirely distinct causes. While there seems to be an inversion effect which is due to the configuration or global shape of the walker, there is also a second one, which operates on the local motion of the ankles. Troje and Westhoff suggested that this second inversion effect reflects a visual mechanism that constitutes a general detection system that signals the presence of terrestrial, articulated animals in the visual environment.

If the visual invariants that signal direction in upright, scrambled biological motion displays are also used to signal the presence of an animal in the visual field, then the presence or absence of these invariants should influence the perceived animacy of the display. Here, we

tested this hypothesis by exploiting the orientation-specific characteristic of perceiving scrambled point-light displays in three experiments that investigated the perception of both animacy and direction from the same set of point-light stimuli. In Experiment 1, we investigated if scrambled displays that are oriented upright are perceived as more animate than scrambled displays that are inverted, as our hypothesis predicts. As we show that animacy can be perceived within exposure times as short as 200 ms, we replicated the experiment conducted by Troje and Westhoff (2006) with short exposure times and asked if the ability to discriminate walking direction from our stimuli is similarly robust in Experiment 2. Finally, in Experiment 3, we investigated if the animacy percept induced from our stimuli is related to the ability to discriminate their direction of walking.

Experiment 1

The ability to discriminate direction from spatially scrambled point-light displays is orientation specific (Troje & Westhoff, 2006). In this first experiment, we asked if the perception of animacy from spatially scrambled displays is similarly orientation specific.

Methods

Participants

Twelve naive observers that ranged in age from 17 to 23 years (mean age of 19.25 years; 5 males, 7 females) participated in this experiment. All observers had normal or corrected-to-normal vision.

Stimuli and apparatus

Sample frames of the stimuli are presented in Figure 1. The stimuli were derived from point-light sequences of a walking human, cat, and pigeon. The human walker, computed as the average walker from motion-captured data of 50 men and 50 women (Troje, 2002), was depicted by a set of 11 markers used to represent the motions of the head, one shoulder, one hip, two elbows, two wrists, two knees, and two ankles. The cat sequence was constructed by sampling 14 points from single frames of a video sequence showing a cat walking on a treadmill. Finally, the point-light pigeon sequence was created from motion-captured data of a pigeon fitted with 11 markers. For all sequences, the translating component of the walk was removed such that the animals displayed stationary walking. All walkers were presented in sagittal view (i.e., facing rightward or leftward) and were shown at their veridical speeds with gait frequencies of 0.93, 1.7, and 1.6 Hz for the human, cat, and pigeon, respectively. For each presentation, the starting position of the walker within
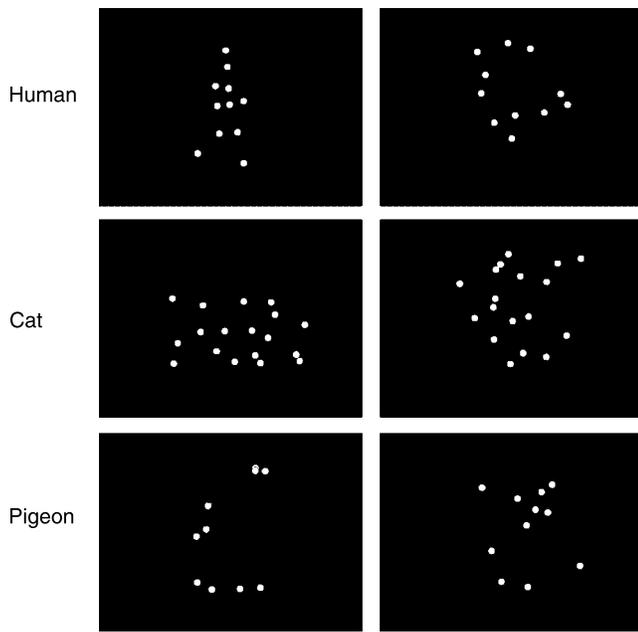
Figure 1. Static frames from right-walking sequences of a coherent human, cat, and pigeon (left panel) and their corresponding scrambled versions (right panel). In the scrambled displays, the local trajectories are intact but spatially displaced.

the gait cycle was selected randomly. The point-light displays were presented upright or inverted about the horizontal axis and were coherent (all points maintained original organization) or spatially scrambled (local trajectory of each point remained intact but was displaced randomly within areas matched to those occupied by the corresponding coherent versions).

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-in. ViewSonic P220f CRT color monitor with 0.25-mm dot pitch, 1280 × 1024 pixels spatial resolution, and 100-Hz frame rate. All stimuli appeared as white dots on a black background and the full point-light figures subtended visual angles of 2.1 × 4.6 deg, 4.6 × 2.4 deg, and 3.6 × 3.6 deg for the human, cat, and pigeon, respectively. In addition, all walkers were embedded in a 6.4 × 6.4 deg mask that consisted of 125 randomly positioned stationary dots with a limited lifetime of 125 ms.

Procedure

Stimuli were viewed binocularly at a distance of 80 cm as maintained by a chin-rest. A six-point Likert-type scale was used to measure animacy judgments. On each trial, the observer's task was to make a confidence indication of whether the stimulus displayed was a "living being" by selecting one of six boxes presented on the computer screen with a mouse click. The six boxes were labeled

from 0 to 5, where 0 represented "definitely not a living being" and 5 represented "definitely a living being."

Participants were first instructed on the task both verbally and by printed instructions on the computer screen. These instructions revealed only that a set of moving dots would be displayed on each trial, upon which a response decision is to be based. A practice block of trials was then presented during which participants familiarized themselves with the task. Here, a total of 48 trials were presented: 24 unmasked walkers consisting of all possible combinations of the three animal types (human, cat, and pigeon), two organizations (coherent and scrambled), two display orientations (upright and inverted) and two walking directions (left and right), and 24 masked walkers of these same combinations. For each trial in the practice block, the stimulus was displayed for 1000 ms, after which the six response boxes were presented across the screen until a response was given.

After the practice block, participants completed the experiment proper which consisted of three experimental blocks that differed only with respect to stimulus duration (200, 500, and 1000 ms). The order in which the blocks were tested was counterbalanced among the participants. Within each experimental block, the 24 possible masked stimuli, consisting of all combinations of animal type, organization, orientation, and walking direction were repeated five times. Therefore, 120 trials were presented in each block (the order of which was counterbalanced for the 24 possible stimuli and randomized), resulting in a total of 360 trials for the experiment proper. The resulting design was a within-subject test of factors animal type, organization, orientation, and stimulus duration.

Results

Mean ratings were evaluated with a 3 (animal type) × 2 (organization) × 2 (orientation) × 3 (stimulus duration) repeated-measures analysis of variance (ANOVA) that revealed a significant main effect of organization, $F(1, 11) = 83.82$, $p < 0.001$, a significant main effect of orientation, $F(1, 11) = 97.04$, $p < 0.001$, a significant organization × orientation interaction, $F(1, 11) = 10.81$, $p = 0.007$, but no effect of animal type, $F(2, 22) = 1.51$, $p = 0.243$, or stimulus duration, $F(2, 22) = 0.97$, $p = 0.394$. All other interactions were not significant.

An examination of group means indicated that coherent stimuli (mean = 4.03) were rated more animate than scrambled stimuli (mean = 1.98), and upright stimuli (mean = 3.49) were rated more animate than inverted stimuli (mean = 2.51). Figure 2 shows the mean ratings for coherent and scrambled stimuli in both upright and inverted conditions. Specifically, mean ratings were 4.69, 3.36, 2.29, and 1.67 for the coherent/upright, coherent/inverted, scrambled/upright, and scrambled/inverted conditions, respectively. Initial Tukey's post hoc comparisons
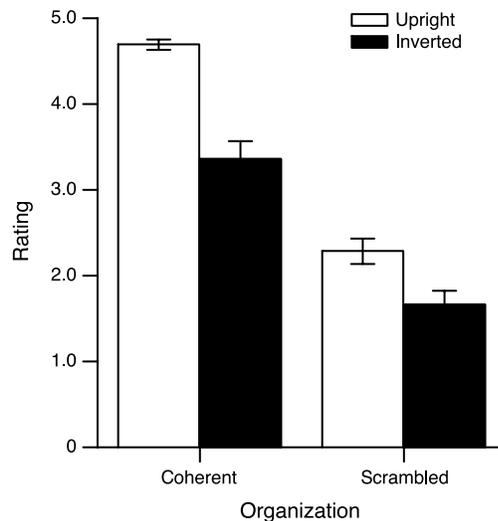
Figure 2. A comparison of mean animacy ratings for coherent and scrambled displays between the upright and the inverted orientations. Error bars represent ±1 standard error of the mean.

crossing the two organizations, and the two orientations failed to reveal the source of the interaction. That is, upright stimuli were rated more animate than inverted stimuli in both coherent and scrambled conditions, and coherent stimuli were rated more animate than scrambled stimuli in both upright and inverted conditions ($p < 0.001$ for all). A subsequent analysis was performed on difference scores obtained for each individual by subtracting the mean ratings of inverted stimuli from those of upright stimuli for the coherent and scrambled conditions while collapsing across all other conditions. Thus, for each individual, a measure of the changes in animacy ratings associated with inversion was obtained for both coherent and scrambled conditions. The scores were entered in a paired t test that showed that the mean difference between upright and inverted stimuli was larger for coherent than for scrambled stimuli ($p = 0.007$). Specifically, the mean differences were 1.33 and 0.62 for coherent and scrambled stimuli, respectively.

Discussion

The higher animacy ratings attributed to coherent stimuli as opposed to scrambled stimuli is not surprising as the perception of animate entities surely depends on information beyond just kinematics, including the ability to detect recognizable form. In addition, the decrease in animacy ratings at the inverted orientation is consistent with previous studies that have reported degraded recognition or perceived quality of biological motion patterns upon inverting stimulus displays (Pavlova, 1989; Pavlova & Sokolov, 2000; Sumi, 1984). Significantly, we show here that the perception of animacy decreases upon inversion not only for coherent displays, but also for

scrambled displays that contain solely local cues. The inversion effect associated with scrambled stimuli cannot be attributed to impaired global, configural information processing. In this respect, the orientation specificity of animacy perception from scrambled displays is congruent with the orientation dependency for discerning direction of motion from scrambled displays documented by Troje and Westhoff (2006).

The lack of effect of animal type suggests that the responsible mechanisms are tuned to some invariant characteristic(s) present in the locomotion patterns of all three animals used in this experiment, and possibly in all terrestrial, legged animals. The lack of effect of stimulus duration suggests further that these mechanisms are remarkably robust and are able to convey information about animacy efficiently at very limited exposure times. Is the retrieval of directional information from scrambled displays similarly robust? In Experiment 2, we maintained the design and the parameters of this first experiment but replaced the animacy rating task with a direction discrimination task in order to assess discrimination performance under identical conditions. It is important to note that the stationary walking stimuli do not contain any *extrinsic* motion (that is, a translatory component referred to as "common motion" by Johansson, 1973). The cues that imply a particular direction are in contrast entirely object centered and therefore *intrinsic*. Indeed, this paradigm has been used in numerous studies of biological motion perception in the past (e.g., Beintema & Lappe, 2002; Neri, Morrone, & Burr, 1998; Thornton, Rensink, & Shiffrar, 2002).

Experiment 2

Methods
Participants

Twelve observers that ranged in age from 18 to 27 years (mean age of 19.83 years; 6 males, 6 females) participated in this experiment. All observers had normal or corrected-to-normal vision. In addition, all observers were naive to the task and had not previously participated in Experiment 1.

Stimuli and apparatus

The stimuli and apparatus were identical to those described for Experiment 1.

Procedure

Here, a two-alternative, forced-choice direction discrimination paradigm was used whereby the observer's task was to indicate whether the stimulus appeared to be

moving leftward or rightward by pressing one of two arrow keys on the keyboard. Feedback was not given for correct/incorrect responses. All other design parameters and the testing procedures were identical to those described for Experiment 1.

Results

Direction discrimination accuracies, measured in terms of proportions of correct responses, were analyzed with a 3 (animal type) $\times$ 2 (organization) $\times$ 2 (orientation) $\times$ 3 (stimulus duration) repeated-measures ANOVA that showed a significant main effect of organization, $F(1, 11) = 143.29$, $p < 0.001$, a significant main effect of orientation, $F(1, 11) = 126.72$, $p < 0.001$, and a significant organization $\times$ orientation interaction, $F(1, 11) = 13.53$, $p = 0.004$. There was no effect of animal type, $F(2, 22) = 1.22$, $p = 0.314$, or stimulus duration, $F(2, 22) = 1.20$, $p = 0.319$, and all other interactions were not significant.

A comparison of means for the main effects revealed that performance was higher for coherent (mean = 0.79) versus scrambled (mean = 0.58) stimuli and for upright (mean = 0.75) versus inverted (mean = 0.61) stimuli. The mean discrimination accuracies for coherent and scrambled stimuli in both upright and inverted conditions are displayed in Figure 3. The proportions of correct responses were 0.87, 0.70, 0.64, and 0.52 for the coherent/upright, coherent/inverted, scrambled/upright, and scrambled/inverted conditions, respectively. As for Experiment 1, the organization $\times$ orientation interaction was first analyzed with Tukey's post hoc comparisons. These comparisons failed to reveal the source of the interaction, indicating that discrimination accuracies were higher for
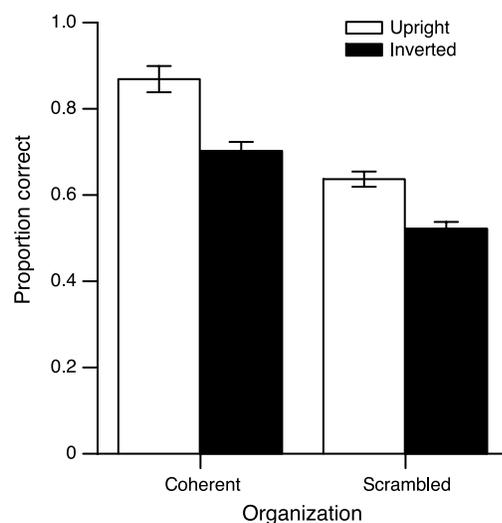

Figure 3. Mean direction discrimination accuracies, expressed as the proportions of correct responses for coherent and scrambled displays at upright and inverted orientations. Error bars represent ±1 standard error of the mean.

coherent than for scrambled stimuli in both upright and inverted conditions and higher for upright than for inverted stimuli in both coherent and scrambled conditions ($p < 0.001$ for all). As a result, difference scores were obtained for each individual by subtracting accuracies of inverted stimuli from those of upright stimuli in coherent and scrambled conditions while collapsing across all other factors. The mean difference was 0.17 for coherent stimuli and 0.12 for scrambled stimuli. A paired t test used to analyze these scores indicated that the reduction in discrimination accuracies due to inversion was higher for coherent than for scrambled stimuli ($p = 0.004$).

Discussion

The results indicate that under identical conditions to Experiment 1, the ability to discriminate direction from scrambled displays, as from coherent displays, is orientation specific. The present results are consistent with those reported by Troje and Westhoff (2006) but more importantly show further that direction retrieval is highly robust, as demonstrated by the stable performance across the stimulus durations tested—including one duration (200 ms) that corresponds to only a small fraction of the full gait cycle duration of all three animals.

The pattern of results obtained in this experiment for the perception of direction is strikingly similar to the pattern of results obtained in Experiment 1 where we obtained instead measurements of perceived animacy. For example, animacy ratings and direction discrimination accuracies decreased upon inversion both more substantially for coherent displays than for scrambled displays. In addition, both measurements were stable across different animal types and changing stimulus durations. It is worth asking then if the two paradigms can be used interchangeably in experiments investigating the cues contained in local biological motions. That is, is the ability to retrieve walking direction from the present stimuli related to the animacy percept induced by these same stimuli? In Experiment 3, we probed this possibility by testing a new group of naive observers on both the animacy rating and the direction discrimination paradigms in order to permit within-subject comparisons. It should be noted that while this approach exploits inter-individual variability, it allows observers to carry strategies from one task to the other. Such carry-over effects were controlled for in Experiments 1 and 2.

Experiment 3

Methods

Participants

A new group of 16 naive observers that ranged in age from 18 to 24 years (mean age of 19.24 years; 7 males,

9 females) were tested in this experiment. All observers had normal or corrected-to-normal vision.

Stimuli and apparatus

The stimuli and the apparatus were identical to those described for Experiments 1 and 2.

Procedure

In this experiment, all participants completed both the Likert-type animacy rating task (see Experiment 1) and the 2AFC direction discrimination task (see Experiment 2). The order of testing was fixed such that the rating task always preceded the discrimination task.

For both tasks, all stimuli were presented with a stimulus duration of 500 ms. Participants completed two blocks of experimental trials (one block per task) and each block comprised of 360 trials, consisting of 15 replications of the 24 possible stimuli that were counterbalanced and randomized. All other design parameters and procedures were identical to those described for Experiments 1 and 2.

Results

Animacy rating

Animacy ratings were analyzed with a 3 (animal type) $\times$ 2 (organization) $\times$ 2 (orientation) repeated-measures ANOVA. The analysis showed significant main effects of organization, $F(1, 15) = 106.65$, $p < 0.001$, and orientation, $F(1, 15) = 65.42$, $p < 0.001$, and a significant organization $\times$ orientation interaction, $F(1, 15) = 6.30$, $p = 0.024$. There was no effect of animal type, $F(2, 30) = 0.20$, $p = 0.980$.

An examination of group means indicated that coherent stimuli (mean = 3.38) were rated more animate than scrambled stimuli (mean = 1.83), and upright stimuli (mean = 2.98) were rated more animate than inverted stimuli (mean = 2.22). The mean ratings for coherent and scrambled stimuli in both upright and inverted orientations are conveyed by the asterisks in Figure 4. Specifically, mean ratings were 3.87, 2.89, 2.10, and 1.55 for the coherent/upright, coherent/inverted, scrambled/upright, and scrambled/inverted conditions, respectively. Tukey's post hoc comparisons indicated that upright stimuli were rated more animate than inverted stimuli in both coherent and scrambled conditions, and coherent stimuli were rated more animate than scrambled stimuli in both upright and inverted conditions ($p < 0.001$ for all). Difference scores obtained for each individual by subtracting the mean ratings of inverted stimuli from those of upright stimuli for the coherent and the scrambled conditions were entered in a paired t test that showed that the mean difference between upright and inverted stimuli was larger for coherent than for scrambled stimuli ($p = 0.024$). Here,
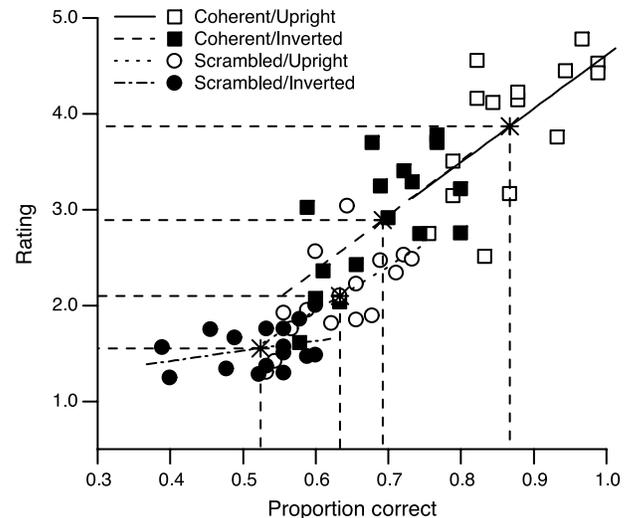

Figure 4. Correlation between animacy rating and discrimination accuracy (expressed as the proportion of correct responses) across individual participants for four conditions that result from crossing the two stimulus organizations and two orientations. Individual data points are overlaid with their respective linear regression lines. Asterisks superimposed on the regression lines convey the corresponding mean ratings and mean accuracies.

the mean differences were 0.98 and 0.55 for coherent and scrambled stimuli, respectively.

Direction discrimination

A comparable analysis of discrimination accuracies showed significant main effects of organization, $F(1, 15) = 185.03$, $p < 0.001$, and orientation, $F(1, 15) = 43.61$, $p < 0.001$, a significant organization $\times$ orientation interaction, $F(1, 15) = 5.54$, $p = 0.033$, but no effect of animal type, $F(2, 30) = 1.50$, $p = 0.240$.

A comparison of means indicated that performance was higher for coherent (mean = 0.78) versus scrambled (mean = 0.58) stimuli and for upright (mean = 0.75) versus inverted (mean = 0.61) stimuli. The mean discrimination accuracies for coherent and scrambled stimuli in both upright and inverted conditions are also conveyed by the asterisks in Figure 4. Specifically, the proportions of correct responses were 0.87, 0.69, 0.63, and 0.52 for the coherent/upright, coherent/inverted, scrambled/upright, and scrambled/inverted conditions, respectively. Tukey's post hoc comparisons indicated that discrimination accuracies were higher for coherent than for scrambled stimuli in both upright and inverted conditions and higher for upright than for inverted stimuli in both coherent and scrambled conditions ($p < 0.001$ for all). A subsequent paired t test based upon difference scores obtained for each subject by subtracting accuracies of inverted stimuli from those of upright stimuli within coherent and scrambled conditions indicated that inversion impaired

performance more substantially for coherent than for scrambled stimuli ($p = 0.033$). Specifically, the mean difference was 0.18 for coherent stimuli and 0.11 for scrambled stimuli.

Cross-task analyses

Data from this experiment were analyzed further by comparing animacy ratings with respect to discrimination accuracies by means of simple linear regressions. Overall, a significant correlation was found between animacy ratings and discrimination accuracies in the positive direction ($r^2 = .84$; $p < 0.001$). According to a 2 (organization) × 2 (orientation) factorial model, four separate linear fits were imposed on the data (Figure 4, overlaid). The analyses indicated that the positive correlation between animacy rating and discrimination accuracy was significant for conditions of coherent/upright ($r^2 = .40$; $p = 0.008$), coherent/inverted ($r^2 = .43$; $p = 0.006$), and scrambled/upright ($r^2 = .43$; $p = 0.006$) but not scrambled/inverted ($r^2 = .09$; $p = 0.25$). Further comparisons of these linear fits with a two-way ANOVA on the regression slopes showed no effects of organization and orientation and no interaction ($p > 0.069$ for all). Similarly, a comparable analysis for regression intercepts revealed no effects of organization and orientation and no interaction ($p > 0.329$ for all).

Finally, a linear model fitted to the current data that describes animacy rating as predicted from discrimination performance within the factorial arrangement is represented by the following equation:

$$r = 4.56d + 0.32a + 0.06b - 0.49. \tag{1}$$

Here, animacy rating, *r,* can be predicted from discrimination performance, *d,* conditional upon stimulus organization and orientation as represented by binary variables *a* and *b,* respectively. The model indicates that animacy rating can be almost entirely predicted by direction discrimination performance. The small size of the coefficients *a* and *b* show that the independent effects of stimulus organization and orientation are comparatively minor.

Discussion

The results of this experiment replicated those of Experiments 1 and 2, suggesting that the observers' strategies for the second task were independent of prior experience with the first task. Importantly, we found here a strong linear relationship between the ability to discriminate direction and the animacy percept induced by our stimuli that was stable across conditions. That is, it appears that those observers who attributed a strong percept of

animacy to a particular stimulus were well able to discern the apparent direction of motion of this same stimulus. Conversely, those observers who attributed a weak percept of animacy to a given stimulus were less able to discern the direction of that stimulus. We therefore conjecture that within our context, the two paradigms elucidate similar perceptual strategies and thus address similar visual mechanisms. It is possible that the correlation in our data can be explained if the two tasks are not perceptually independent; that is, observers may have been able to discriminate walking direction only if an animate agent was first recognized (or more unlikely, vice versa). Nonetheless, it is clear that the manner in which both tasks were solved depended on the orientation of the relevant cues. In consideration of the findings of Troje and Westhoff (2006), we propose that the relevant local cues exploited for scrambled stimuli in the two tasks were contained in the motion of the limbs. However, as we did not isolate specifically the limb motion in the three experiments, we must also acknowledge the possibility that observers at least when asked to attribute animacy did not rely on the ankle trajectories but used instead other arbitrary local cues. This explanation is unlikely, however, given the similarity in the pattern of results obtained from the two paradigms.

General discussion

We showed that despite lacking coherent form information, scrambled point-light displays still elicit a significant degree of perceived animacy. However, the perception of animacy from scrambled displays is orientation specific (Experiment 1). The decrease in the perceived animacy of inverted scrambled stimuli is analogous to the impaired ability to discriminate walking direction from these same displays (Experiment 2). By exploiting inter-individual variability, we showed also a substantial correlation between measures of perceived animacy and direction from our stimuli (Experiment 3). Together, these results provide novel insights into the properties of the perceptual mechanisms responsible for processing local biological motion signals.

Of particular interest is the orientation-specific nature of our data for scrambled stimuli. As these stimuli do not carry coherent structural information, the associated inversion effect cannot be explained by global mechanisms (e.g., template-matching) and rather must be attributed to the processing of local motions. Significantly, the local ankle motions have been shown to be particularly important in the perception of biological motion (Mather et al., 1992; Troje & Westhoff, 2006). Electromyographic data have indicated that leg muscles are almost inactive during the swing phase (e.g., Crowninshield & Brand, 1981). As such, it has been proposed that the foot,

after being set into motion by muscles during the stance phase, moves entirely under the influence of gravity (Mochon & McMahon, 1980)—a locomotive strategy that minimizes energetic cost (Nakamura, Mori, & Nishii, 2004). The visual system may be particularly sensitive to the motion that results as the foot interacts with gravitational force—a unique cue that may signal the presence of other terrestrial, legged animals. Indeed, an examination of the ankle dot's motion during the swing phase reveals that it exhibits large changes in velocity along the vertical axis, presumably due to gravitational influence. The orientation of the ankle dot dictates the manner of velocity change. We speculate that the visual system interprets velocity changes with respect to gravitational acceleration. Inverted displays exhibit the same velocity changes as their upright versions, but in a manner that is not congruent with the direction of gravity. As such, the inverted displays may be less salient for information retrieval than the upright displays, which contain motions that are deemed plausible (i.e., gravitationally consistent).

A role for gravity for the interpretation of biological motion is supported by Runeson and Frykholm (1981), who showed that from point-light sequences of an actor lifting and carrying a box, observers were readily able to judge the box's mass. They concluded that the mass of the box was cued by the relationship between postural changes and the motion of the box—a relationship that can be exploited only with an understanding of gravitational force. In another study, Jokisch and Troje (2003) presented point-light displays of dogs walking with varying frequencies and showed that observers judged the size of the dog to be smaller at high stride frequencies than at low frequencies. They suggested that the visual system uses implicit knowledge of a fixed relation between spatial and temporal parameters that exists in a gravity-based environment in order to retrieve size information from the point-light gait patterns. The use of gravitation-based heuristics for interpreting biological motion is further corroborated by Shipley (2003) who presented a point-light figure walking on his hands in both upright and inverted orientations and found that walker detection was better for the upright display which contained familiar dynamic relations.

Nonetheless, orientation effects are interesting to consider in light of a recent finding that newly hatched chicks possess an orientation bias (Vallortigara & Regolin, 2006). In their study, the authors showed that visually naive chicks presented with point-light sequences of a walking hen aligned their bodies with the apparent direction of movement of upright walking hens but oriented randomly with inverted hens. The apparently innate orientation bias in chicks raises an intriguing possibility that other vertebrates, such as humans, may also have a similar predisposition. Developmental studies have shown that 3-month-old infants can discriminate an upright walker from an inverted walker (Bertenthal, Proffitt, & Cutting, 1984; Fox & McDaniel, 1982), but little is known about sensitivity to biological motion patterns in younger infants. An orientation bias associated with local biological motion signals that may be innate to humans requires further empirical work with human newborns (Johnson, 2006).

The apparent difference in saliency between upright and inverted versions of local signals contained in biological motion sets forth a contrast that should be investigated when exploring possible neural concomitants. Neurophysiological and neuroimaging accounts have often implicated the posterior superior temporal sulcus (STS) in the perception of coherent biological motion (e.g., Bonda, Petrides, Ostry, & Evans, 1996; Grossman et al., 2000; Oram & Perrett, 1994; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Interestingly, this region has also been shown to be activated by simple moving objects whose interactions appear causal or intentional, thereby inducing a percept of animacy (Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005). Consistent with psychophysical impairments in interpreting coherent biological motion displays that are inverted rather than upright, Grossman and Blake (2001) have shown relatively smaller STS activity in response to inverted displays as compared to upright displays. This reported difference in STS activation, however, may reflect only the inversion effect proposed to be associated with global form processing. The neural structures that underlie orientation dependency in response to local biological motion signals remain to be teased out, although recent findings have shown that the extrastriate areas V3 and V3A are differentially responsive to upright and inverted versions of scrambled biological motion displays (Jiang & He, 2007).

Finally, a better understanding of the substrates relevant to interpreting local biological motion signals may well have implications that extend to autistic individuals who are characterized by social deficits (Kanner, 1943). The abilities to detect and to interpret animate activity are fundamental to social interactions. As such, it is appealing to ask if deficits in social function may be attributed at least in part, to impairments in the neural mechanisms that subserve these perceptual skills. Indeed, it has been shown that autistic individuals are impaired in the recognition of point-light animations depicting human activity (Blake, Turner, Smoski, Pozdol, & Stone, 2003). Blake et al. (2003) interpreted their results in terms of an impaired ability to integrate local motion signals into coherent form. However, we have shown here that information about animacy can also be retrieved from local biological motion signals that cannot be integrated into meaningful form. It is worth considering then if the mechanisms underlying the perception of local biological cues may be too implicated in such disorders of social function.

Acknowledgments

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