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Physical and Biological Constraints Govern Perceived Animacy of Scrambled Human Forms

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Abstract

Point-light animations of biological motion are perceived quickly and spontaneously, giving rise to an irresistible sensation of animacy. However, the mechanisms that support judgments of animacy based on biological motion remain unclear. The current study demonstrates that animacy ratings increase when a spatially scrambled animation of human walking maintains consistency with two fundamental constraints: the direction of gravity and congruency between the directions of intrinsic and extrinsic motion. Furthermore, using a reverse-correlation method, we show that observers employ structural templates, or form-based "priors," reflecting the prototypical mammalian body plan when attributing animacy to scrambled human forms. These findings reveal that perception of animacy in scrambled biological motion involves not only analysis of local intrinsic motion, but also its congruency with global extrinsic motion and global spatial structure. Thus, they suggest a strong influence of prior knowledge about characteristic features of creatures in the natural environment.

Keywords

animacy, biological motion, reverse correlation, visual perception, social perception, causality

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In the natural environment, dynamic visual signals can come from either living or nonliving entities. Whereas inanimate objects move only when external forces act upon them, animate objects (e.g., mammals, insects) manifest complex motion patterns through body movements. There is evidence that basic perception of both physical causality and animacy arises very early in human cognitive development (Csibra, Gergely, Bíró, Koós, & Brockbank, 1999; Leslie & Keeble, 1987; Premack, 1990; Rochat, Morgan, & Carpenter, 1997; Schlottmann & Ray, 2010). The seminal works of Michotte (1946/1963) and Heider and Simmel (1944) showed that a strong sense of causality and of animacy could each arise spontaneously from basic perceptual cues. Contemporary studies and theories have further highlighted the immediacy and irresistibility of causal interpretations of simple dynamic displays (Dittrich & Lea, 1994; Schlottmann & Shanks, 1992; White, 1988), leading to the intriguing suggestion that animacy and causality are driven by specialized low-level perceptual processes (Scholl & Tremoulet, 2000).

To eliminate contextual influences on observers' inferences regarding the causal and social structure of the world, most studies of animacy perception have focused on visual displays consisting of rigidly moving shapes (e.g., circles or squares in motion). Such displays solely depict the extrinsic movements of agents, excluding the complex intrinsic motions (e.g., limb movements) that typically take place when creatures move in the natural environment. Because intrinsic movements are generally the cause of extrinsic translation of the body, they provide a strong and reliable cue for predicting directionality, which may help in inferring the intentional goals and other social characteristics of moving creatures. The lack of intrinsic motion in the stimuli used in most studies of animacy perception raises the question of whether

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previous laboratory findings can be generalized to perception of animacy in more complex and naturalistic biological-motion patterns.

At the same time, intrinsic motion of body parts is central to a related research area that focuses on perception of biological motion (Blake & Shiffrar, 2007). The direction and character of biological motion, typically conveyed by points of light on the joints of an animal or human actor, are perceived just as spontaneously and irresistibly as is animacy (Johansson, 1973), and such perception is believed to involve specialized mechanisms (Giese & Poggio, 2003; Kourtzi, Krekelberg, & van Wezel, 2008). Typical studies of biological motion have used treadmill movement, which retains the intrinsic limb movements, but eliminates extrinsic body motion (Bertenthal & Pinto, 1994; Mather, Radford, & West, 1992; Neri, Morrone, & Burr, 1998; Pinto & Shiffrar, 1999; Thurman & Grossman, 2008; Troje & Westhoff, 2006). Although focusing on intrinsic motion of body parts has allowed researchers to isolate and study many interesting aspects of the perception of action in body movements, the exclusion of extrinsic motion limits investigation of how observers infer intentional action (e.g., perception of meaningful interactions between actors, such as chasing vs. following). More generally, the focus on extrinsic motion in studies of animacy perception, together with the distinct focus on intrinsic motion in studies of biological-motion perception, has contributed to a disconnect between these two research areas.

A study by Chang and Troje (2008) found that spatially scrambled point-light creatures were perceived as animate despite disruption to the canonical biological form, particularly when the local trajectories represented upright, rather than inverted, movements. Furthermore, animacy ratings correlated significantly with the ability to subsequently discriminate the walking direction of the scrambled animations. This finding suggests that animacy may be associated with basic perceptual mechanisms, such as the proposed "life detector" (Troje & Westhoff, 2006), which enable detection of vital intrinsic motion information signaling directionality. However, it remains unclear what role global cues such as extrinsic motion and global structure might also play in perception of animacy based on scrambled biological motion.

In the present study, we examined the possibility that animacy perception may involve prior knowledge based on the physical constraints (specifically, consistency between intrinsic and extrinsic motion as well as gravity) and biological constraints (specifically, body structure) imposed on moving creatures in the natural environment. First, we investigated whether observers base animacy judgments on the expected causal relationship between intrinsic limb movements and the extrinsic motion of body translation. If observers utilize this constraint, perceived animacy should increase when extrinsic motion is consistent with the directionality implied by the intrinsic local signals. Also, animations based on scrambled biological motion were inverted with respect to the observer in some experimental conditions so that we could investigate the impact of the gravity constraint on perceived animacy. Next, we examined the possibility that scrambled displays may in fact preserve some configural information that facilitates perception of animacy. By applying reverse-correlation analyses to animacy ratings aggregated across many trials, we aimed to reconstruct structural templates that correlate with high animacy ratings, and thereby to reveal prototypical form-based "priors" for biological creatures. Success in this effort would support the hypothesis that prior knowledge of abstract configural properties governed by biological constraints plays an important role in the perception of animacy in biological motion.

Experiment 1

Experiment 1 was designed to determine the influence of extrinsic, translational motion on animacy ratings of scrambled point-light walkers. We included a condition with spatially intact (normal) walkers to help anchor the upper range of animacy responses and to estimate the main effect of spatial scrambling. We also included phase-scrambled walkers to measure animacy ratings for spatiotemporally incoherent walkers that nonetheless retained the general structure and orientation of the human body form (e.g., head point on top and feet points on bottom).

Method

Participants. Participants were 20 undergraduate students (ages 18–29 years, M = 22.1; 8 male, 12 female) recruited from the Psychology Department's research participation pool at the University of California, Los Angeles (UCLA). All participants were naive to the purpose of the experiment and were compensated with course credit. All experimental procedures were in accordance with the protocol of the university's institutional review board.

Stimulus materials and apparatus. A sample of human walking was obtained from the CMU Graphics Lab Motion Capture Database (n.d.; funded by Grant EIA-0196217 from the National Science Foundation). We projected the three-dimensional human motion data into profile view and converted it into point-light format, with 11 points representing the head, midshoulders, midpelvis, elbows, wrists, knees, and feet. The walking animation (1 cycle) was down-sampled to 60 frames per cycle and was presented at 60 Hz, consistent with a normal gait speed. A chin rest was used to maintain a constant viewing distance (44 cm).

Spatially scrambled walkers were created by randomizing the starting locations of all point lights within a square area subtending 4° × 4°, which was the same size as the height of an intact walker. This manipulation destroyed the global spatial relations between the points, but maintained the local biological kinematics. Phase-scrambled animations were created by randomizing the starting frame of each point light independently within a walking cycle. The starting frame of the phase-intact walkers was the same on each trial, and corresponded to the middle of the swing phase of the gait cycle (crossed posture). This posture was chosen as the starting posture because at that time point, the *x,y* positions of the points corresponded roughly to their average positions over the course of the entire gait cycle. Stimuli with spatial scrambling or phase scrambling varied from trial to trial because of the independent randomization of the starting locations and phases of the points. Extrinsic motion was incorporated into the animations by adding a constant rightward horizontal translation (8°/s; see Video S1 in the Supplemental Material available online). Six photographs of various empty rooms served as background images to provide environmental context to the animations (26.6° wide × 17.7° high).

Procedure. Participants were asked to rate, on a 5-point scale (1 for the lowest degree of animacy, 5 for the highest), the animacy of "creatures" composed of black dots. They were asked to imagine that the dots in each animation were connected to parts of the body of a creature, and thus moved as the creature would move. Animacy was described as referring to how "lifelike" or "biologically plausible" the creatures were perceived to be. To reduce biases, we provided no other information about the supposed nature of the creatures. Participants were encouraged to use the entire rating scale across trials.

On each trial, a random photograph was chosen as the background image, and a point-light animation was imposed upon the image (Fig. 1; see Videos S1–S4 in the Supplemental Material for examples of scrambled animations). A within-subjects design was employed to measure the effects of walker type (spatially intact or scrambled), phase (intact or scrambled), and extrinsic motion (with or without) on animacy ratings. When extrinsic motion was absent, the animation moved in place as if on a treadmill in the middle of the background image. When extrinsic motion was present, the intrinsic and extrinsic motion directions were always consistent (i.e., the rightward walker translated rightward). All experimental conditions were presented in a randomized order within a single block of trials.

Participants first viewed 8 example trials before the experimental trials commenced. The experiment consisted of 120 trials (15 trials per condition) in total. Trials were self-paced, and each animation was presented for two walking cycles (2 s). For each trial, participants responded on a keyboard to indicate their animacy rating, and then the next trial began.

Results and discussion

Mean animacy ratings are plotted in Figure 2. Intact walkers were rated as more animate than phase-scrambled and spatially scrambled walkers, as indicated by significant main effects of walker type, $F(1, 19) = 50.35$, $p < .001$, $\eta^2 = .726$, and phase, $F(1, 19) = 49.85$, $p < .001$, $\eta^2 = .724$. Animacy ratings were significantly higher for stimuli containing extrinsic translational motion than for those without such motion, $F(1, 19) = 27.36$, $p < .001$, $\eta^2 = .590$. A significant interaction between walker type and phase was obtained, $F(1, 19) = 10.96$, $p < .001$, $\eta^2 = .595$; phase had a much larger effect for spatially intact walkers, compared with spatially scrambled walkers. Thus, phase information did not play an important role in the perception of animacy when biological forms were disrupted by spatial scrambling. Finally, we found that extrinsic motion had a much greater impact on animacy judgments for spatially scrambled walkers than for spatially intact walkers, as indicated by an interaction between walker type and the

Fig. 1. Illustration of select still frames from an example stimulus in Experiment 1. The point lights are spatially scrambled, and the animation contains rightward extrinsic (translational) motion. Time progression is from left to right. The background image has been cropped, and the dots enlarged, for visualization purposes. See Video S1 in the Supplemental Material for a dynamic example of a spatially scrambled, translating point-light stimulus.

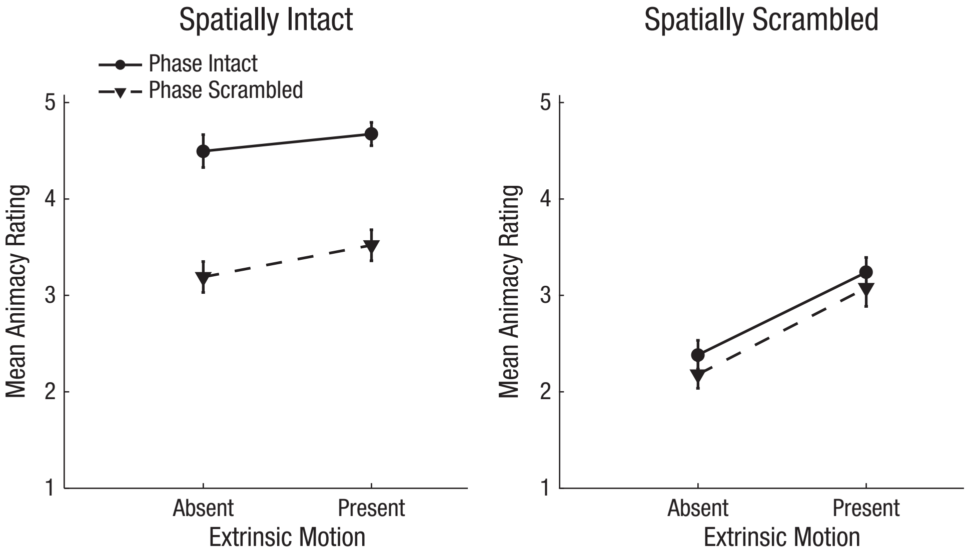

Fig. 2. Results of Experiment 1: mean animacy ratings of point-light walkers as a function of the presence or absence of extrinsic motion and whether or not the walkers were phase scrambled. The graph on the left shows results for walkers that were spatially intact, and the graph on the right shows results for walkers that were spatially scrambled. Error bars represent between-subjects standard errors of the mean.

presence/absence of extrinsic motion, $F(1, 19) = 25.70$, $p < .001$, $\eta^2 = .575$.

The results of Experiment 1 show that introducing extrinsic translational motion congruent with the direction implied by the intrinsic movements increased the perceived animacy of spatially scrambled walkers. This result may have been due to intrinsic movements being interpreted as the cause of extrinsic motion, thereby conveying a clearer impression of directionality and intentional behavior in the moving agents. This possibility was investigated more directly in Experiment 2 by manipulating the congruency between the intrinsic and extrinsic motion directions of spatially scrambled walkers.

Experiment 2

In Experiment 2, we manipulated the ecological validity of the motion signals by varying the congruency between the intrinsic and extrinsic motion directions of the walkers (i.e., both leftward and rightward walkers were translated rightward) and by inverting the animations with respect to the environment. If observers incorporate prior knowledge about the environment and expectations of global translation based on patterns of intrinsic movement, then animacy ratings of point-light walkers should be highest when the intrinsic movements are congruent with respect to both gravity and the direction of extrinsic motion.

Method

Ten unpaid UCLA undergraduate students (ages 19–26 years, $M = 21.9$; 4 male, 6 female) participated in this experiment for course credit. Inverted animations were created by reflecting the walkers about the horizontal axis, and leftward walkers were created by reflecting the rightward walkers used in Experiment 1 across the vertical axis. The experimental setup was the same as in Experiment 1, except that only spatially scrambled walkers were used, and two within-subjects factors were included in the design: orientation of walker (upright or inverted) and congruency between intrinsic and extrinsic motion (congruent or incongruent). All animations exhibited left-to-right global translation, so that scrambled rightward walkers were congruent with the extrinsic motion direction, and leftward walkers were incongruent with the extrinsic motion direction. (See Videos S2 and S3 in the Supplemental Material for examples of the animations in the incongruent and inverted conditions, respectively.)

Results and discussion

Mean animacy ratings are plotted in Figure 3. Post hoc *t* tests revealed that scrambled biological motion generated from an upright walker with congruent extrinsic and intrinsic motion was perceived as more animate than any other scrambled biological motion (all *p*s < .003, Bonferroni corrected); animacy ratings did not differ significantly between the other conditions. A 2 × 2 within-subjects repeated measures analysis of variance revealed a significant interaction between orientation and the congruency of intrinsic and extrinsic motions, $F(1, 9) = 18.04$, $p = .002$, $\eta^2 = .667$. Thus, two fundamental constraints—gravity and the congruency between intrinsic

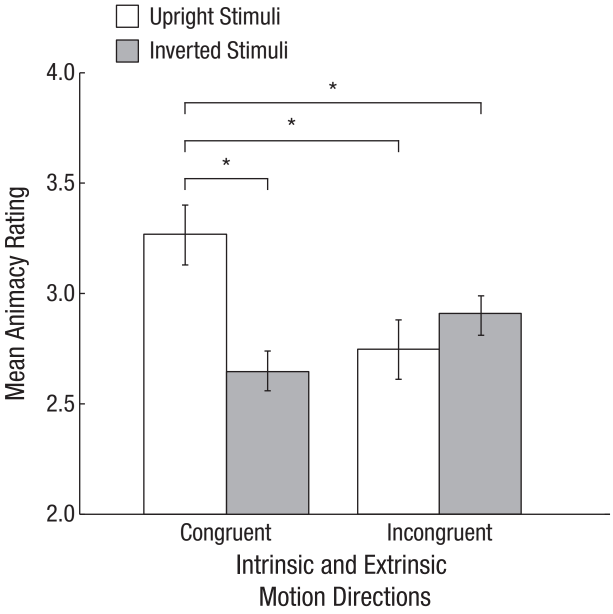

Fig. 3. Results of Experiment 2: mean animacy rating of spatially scrambled point-light walkers as a function of their orientation (upright or inverted) and the congruency between their extrinsic translational motion and their intrinsic motion. Error bars represent standard errors of the mean. Asterisks indicate significant differences between conditions ($p < .005$).

and extrinsic motion—had an interactive influence on animacy judgments. The finding that congruency affected animacy judgments for upright scrambled walkers supports the hypothesis that, as a default, intrinsic motion of a biological agent is assumed to cause the extrinsic movement of its body when point movements satisfy the gravity constraint. By contrast, the relation between intrinsic and extrinsic motion did not affect the animacy ratings for upside-down scrambled walkers. The absence of such an influence may have been due to the ecological invalidity of biological movements that contradict gravity (Chang & Troje, 2008; Hirai, Chang, Saunders, & Troje, 2011).

Experiment 3

Previous work has shown that perceived directionality in scrambled walkers depends on particular high-level motion cues, such as the pattern of acceleration or deceleration and the asymmetrical trajectories of the feet points. These findings suggest that directionality is not derived simply from lower-level differences in motion energy (Chang & Troje, 2009; Troje & Westhoff, 2006). Further investigation by Hirai et al. (2011) found that the location of the feet points relative to other points in scrambled point-light displays interacts with these motion cues to determine the perceived directionality. Configuring points into a coherent form has also been shown to augment direction discrimination (McKay, Simmons, McAleer, & Pollick, 2009). In Experiment 3, we investigated the influence of global spatial cues on animacy ratings. We reasoned that when the original humanlike form is disrupted by spatial scrambling, configural cues consistent with *some* biological form governed by biological constraints may be preserved to some extent. We used a reverse-correlation approach to measure the relative contribution of each point light across space, aiming to discover the spatial structure of form-based templates (priors) involved in animacy judgments.

Method

Two sets of 6 unpaid UCLA undergraduate students (ages 19–33 years, $M = 23.2$; 4 male, 8 female) participated in this experiment for course credit. Participants were assigned to a group that performed the task with either all upright or all inverted scrambled point-light displays. The experimental setup was similar to that of Experiment 1. On each trial, a rightward walker was spatially scrambled (with phase intact) and translated rightward across a randomly selected background image. Hence, intrinsic body motion and extrinsic translational motion were congruent on each trial. The experiment consisted of 480 trials of scrambled walkers, presented in two 240-trial blocks with a short break (a few minutes) between the blocks. Spatially scrambled walkers were generated in the same way as in the previous experiments, by randomizing the starting locations of all point lights within a square area in each trial.

Results and discussion

Using reverse-correlation analysis (a type of multiple linear regression) with animacy rating as the outcome variable and the random spatial locations of points (across trials) as explanatory variables, we constructed spatial maps for each point light to visualize how the starting locations of each point affected subjective ratings of perceived animacy. We first sorted the trials into three bins according to animacy rating: low (1 or 2), intermediate (3), or high (4 or 5). Trials with an intermediate rating (i.e., 3) were excluded from further analysis (22% of trials on average). For each point, we proceeded trial by trial to create an image with zeros in all locations except for a small Gaussian bump (7 × 7 pixels, $SD = 0.4$ pixels) at that point's starting position on that trial. Each image was multiplied by either −1, if the rating was low (i.e., rating of 1 or 2), or +1, if the rating was high (i.e., rating of 4 or 5). For each participant we summed all of these images, essentially creating a single difference image of high versus low animacy ratings for each point light. Next, the difference images were standardized (z-scored) and spatially smoothed with a Gaussian filter ($SD = 8$ pixels) for visualization and statistical analysis. Final group maps were created by averaging across the individual participants' maps. Positive *z* scores signify spatial regions correlating with high animacy ratings, and negative *z* scores indicate regions correlating with low animacy ratings.

Analysis of the group maps (Fig. 4) revealed that the spatial locations of some point lights were a significant factor contributing to animacy judgments across trials. For upright scrambled walkers, animacy was rated significantly higher (as indexed by greater *z* scores) when the extremity joints, particularly the feet, were located in the lower portion of the display. In contrast, animacy ratings were significantly lower when these same joints fell in the upper portion of the display. Horizontal location of these points also mattered: Higher animacy ratings were associated with locations on the left side of the lower portion of the display in the case of the feet and with locations on the right side of the lower portion of the display in the case of the wrists; note that these horizontal locations corresponded with the rightward direction of locomotion. Animacy ratings were also higher when the head point was presented in the upper region, along with the shoulder and hip points, which together were relatively immobile during the animation compared with the extremity points, which had higher-amplitude movements. The midlimb body points (elbows and knees) contributed very little to animacy judgments, which is consistent with previous findings on discrimination of the direction of movement in intact human walkers (Mather et al., 1992; Thurman, Giese, & Grossman, 2010).

We conducted a logistic regression analysis with animacy rating as the outcome variable and the *x* and *y* spatial locations of the 11 point lights as explanatory variables. We first transformed the ratings to binary responses corresponding to high (rating of 4 or 5) or low (1 or 2) animacy, omitting trials with a rating of 3. The beta weights estimated from the logistic regression analysis are plotted in Figure 4. Overall, these results are consistent with the reverse-correlation analysis, also revealing significant contributions of foot and wrist points to animacy ratings in both the horizontal and the vertical directions, although vertical location clearly had a dominant influence.

For the inverted scrambled walkers, we obtained a pattern generally opposite to that obtained for the upright walkers (Fig. 4). Animacy ratings were highest when the extremities were in the upper regions, and when the

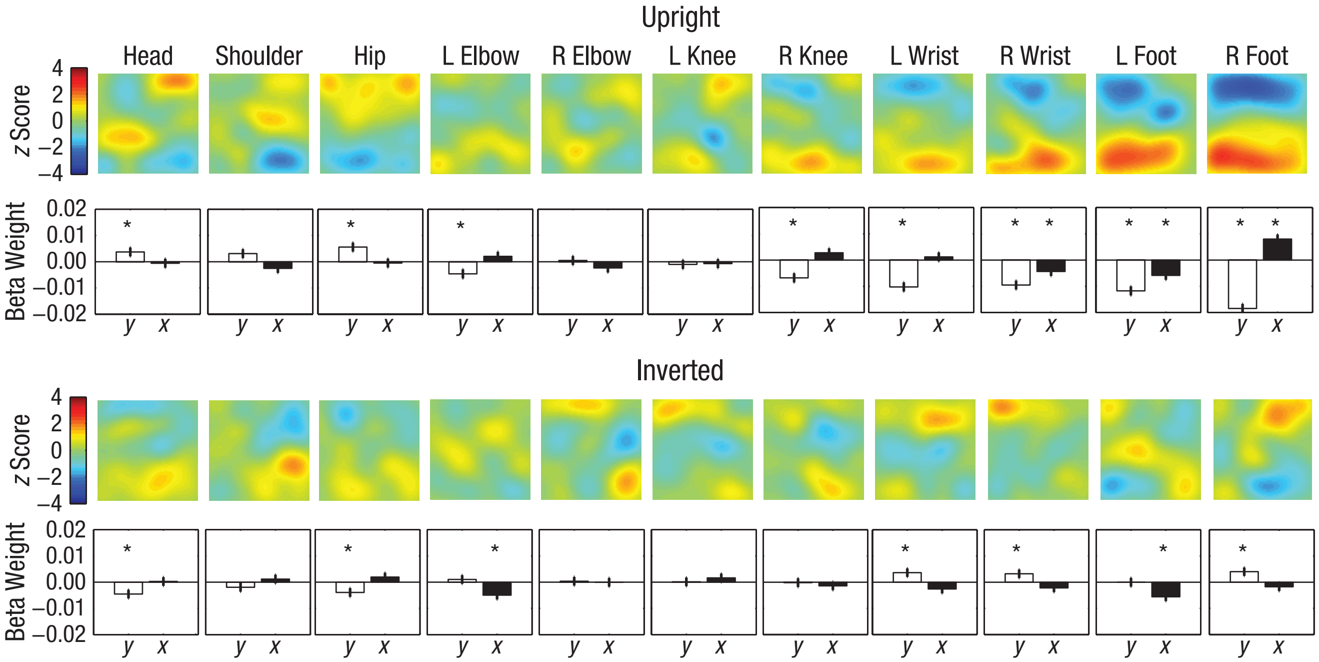

Fig. 4. Results of the reverse-correlation and logistic regression analyses in Experiment 3. The spatial maps are difference maps derived from reverse-correlation analyses. For each point light, they indicate the relative contribution of locations throughout the display to high animacy ratings (positive *z* scores) and low animacy ratings (negative *z* scores), separately for upright and inverted scrambled walkers. The uncorrected threshold for significance ($p < .01$) is a *z* score of ±1.96 (roughly, the deep red and blue regions identify locations significantly associated with high and low animacy ratings, respectively). The bar graphs show the beta weights estimated from logistic regression analyses predicting animacy ratings from vertical (y) and horizontal (x) spatial positions, separately for upright and inverted scrambled walkers. In the y spatial direction, positive beta weights indicate a positive relationship between increasing animacy ratings and increasing height of point locations in the display, and negative beta weights indicate an inverse relationship between animacy ratings and vertical position. In the x spatial direction, positive beta weights indicate increasing animacy ratings from the left to the right of the display, whereas negative beta weights indicate decreasing animacy ratings from left to right. Error bars represent standard errors, and asterisks indicate statistically significant beta weights ($p < .05$). L = left; R = right.

head and torso points were in the lower regions. However, in comparison with the findings for upright scrambled walkers, the results for inverted scrambled walkers showed that fewer extremity points had a significant impact on perceived animacy, and the magnitude of the beta weights was generally reduced for the inverted walkers.

Figure 5a shows the spatial location with the maximal *z* score (all peak *z*s > 2.7, *p*s < .01) for each point in the upright condition (midlimb points are omitted because these points did not yield any locations that reached the peak *z* score of at least 2.7). Figure 5c shows the locations with maximal *z* scores for the same critical points in the inverted condition. Thus, these illustrations depict the inferred structure of the prototypical internal template used for animacy judgments. The structure of the upright template resembles a four-legged animal with its head pointing in the direction of locomotion and its feet and wrist points touching the ground in the lower region of the display (Fig. 5a; see Video S4 in the Supplemental Material for the prototype animation). The feet are both located posterior to the wrist points (with respect to locomotion direction), which is remarkably consistent with the body plan of most land animals (e.g.,

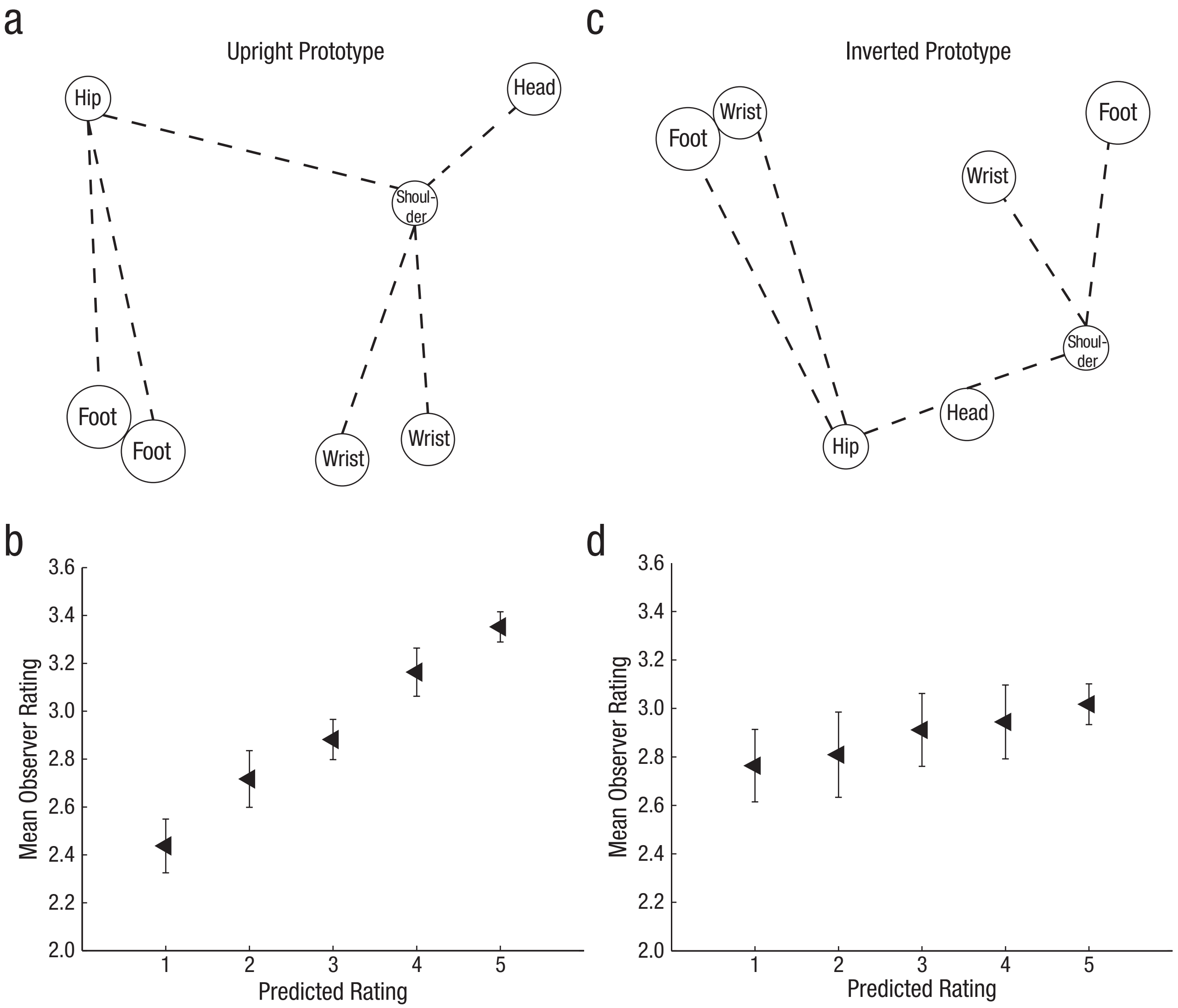

Fig. 5. Creature prototypes and correspondence between observed and predicted animacy ratings in Experiment 3. Results for upright walkers are shown on the left, and results for inverted walkers are shown on the right. The creature prototypes (a, c) were derived from reverse-correlation analyses. The spatial location of each point was determined by the location of the maximum *z* score in the group map. The relative size of the circle representing each point is roughly scaled to reflect the degree to which that point contributed to animacy ratings. The graphs (b, d) show mean observed animacy rating as a function of the rating predicted by the independent template-matching procedure (*n* = 6 for each condition). Error bars represent standard errors of the mean.

dogs, horses, rabbits). The overall structure of the prototype derived from inverted scrambled displays was itself inverted with respect to the upright prototype (Fig. 5c). Although the data were noisier and less consistent across observers in the inverted condition, the prototype generally resembled the structure of an inverted animal.

Finally, using a leave-one-out procedure, we assessed how well the animacy ratings of an observer could be predicted by the spatial prototype derived independently from the data of the remaining 5 observers. For a given observer, we used a straightforward template-matching procedure to compute a similarity score on each trial; specifically, we determined the euclidean distance between each point in the random display and the corresponding point in the template and then summed these values. After computing the similarity of all presented displays to the prototype, we divided the distribution into quintiles and used these quintile rankings as the basis for predicting animacy ratings across trials. For instance, the predicted rating was 5 for a display in the top 20% of displays that were most similar to the template, the predicted rating was 4 for a display in the 60th to 80th percentile of similarity to the template, and so forth. To estimate how well these predicted ratings corresponded to actual ratings, we computed each observer's average actual rating given a particular predicted rating and then averaged these values across observers. Figures 5b and 5d show the results of this analysis. A clear linear trend is apparent for both conditions, and particularly for the upright displays: The actual animacy ratings increased monotonically as the predicted ratings increased. Hence, animacy judgments of a given observer could be reliably predicted from the similarity of the scrambled walker stimulus to the prototypical template derived independently from the other observers. This result also demonstrates the overall consistency of prototype structure across human observers.

General Discussion

In the present study, we examined the influence of global factors (extrinsic motion, body orientation, and spatial structure) on animacy ratings of scrambled human walking patterns. Although the displays we used lacked a consistent or recognizable global shape because of random spatial scrambling, observers still reported a relatively strong sense of animacy due to local motion signals associated with familiar biological movement patterns (Chang & Troje, 2008). In Experiment 1, we found that moving the scrambled walker across a naturalistic background made the animation appear more animate than typical displays that are globally stationary (e.g., treadmill walkers). This result shows that perceived animacy is not entirely due to intrinsic local motion signals, but is also influenced significantly by global factors.

We hypothesize that animacy ratings increased when the displays contained extrinsic motion because these displays invoked prior knowledge about the causal relationship between intrinsic and extrinsic motion in biological creatures in natural settings. That is, extrinsic motion of an animate body is typically and primarily *caused* by intrinsic limb movements that serve the purpose of locomotion. This causal relationship between limb movement and global body movement is a fundamental property of animate bodies, so it is highly plausible that the visual system is particularly sensitive to such cues. Supporting this proposal, Experiment 2 found that animacy ratings increased when scrambled walkers maintained consistency with two fundamental constraints: the direction of gravity and congruency between intrinsic and extrinsic motions. Though the present data do not speak to the exact source of this prior knowledge (i.e., whether it is innate or developed through individual learning), evidence suggests that very early in human development, there exist visual mechanisms to detect invariants of biological motion (Simion, Regolin, & Bulf, 2008; Troje & Westhoff, 2006) and to perceive physical causality and animacy (Csibra et al., 1999; Leslie & Keeble, 1987; Premack, 1990; Rochat et al., 1997; Schlottmann & Ray, 2010). In fact, there is evidence that even 6-month-old infants may be sensitive to the causal relationship between intrinsic and extrinsic motion as a cue for perceiving animacy and goal-directed movements in schematic biological animations (Schlottmann & Ray, 2010).

Using reverse-correlation analyses, we further showed that animacy ratings were strongly associated with structural templates that closely resemble four-legged animals facing in the direction of locomotion—even though these templates were recovered from scrambled, two-legged human walkers. These templates were consistent across observers, and this consistency suggests that the tetrapod body plan, which is extremely similar across the majority of land mammals (Davidson & Erwin, 2006), is represented at an abstract and fundamental level in the human brain. The recovered templates for inverted displays were also inverted with respect to the environment, a finding mirroring recent results on direction discrimination (Hirai et al., 2011) and providing further evidence for a critical link between perceived directionality and perceived animacy in biological motion (Chang & Troje, 2008). As pointed out by Hirai et al. (2011), "observers assign a facing direction to a stimulus only if they determine it to be animate" (p. 1548). Hence, animacy judgments may play an important role in determining whether observers will search for validating cues to assign perceived directionality to a motion display.

Taken together, the current findings reveal that perception of animacy in scrambled biological motion depends not only on analysis of local intrinsic motion, but also on congruency with global extrinsic motion and spatial structure. These global factors are governed by physical and biological constraints of creature movement and appear to be deeply represented in the human brain. Such representations may originate from innate perceptual mechanisms tuned to some critical features of creature movement or to learned expectations acquired through experience. Future developmental studies will be required to establish the source of this pervasive prior knowledge.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

References

Bertenthal, B. I., & Pinto, J. (1994). Global processing of biological motions. *Psychological Science*, *5*, 221–224.

Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, *58*, 47–73.

Chang, D. H. F., & Troje, N. F. (2008). Perception of animacy and direction from local biological motion signals. *Journal of Vision*, *8*(5), Article 3. Retrieved from http://www.journalofvision.org/content/8/5/3

Chang, D. H. F., & Troje, N. F. (2009). Acceleration carries the local inversion effect in biological motion perception. *Journal of Vision*, *9*(1), Article 19. Retrieved from http://www.journalofvision.org/content/9/1/19

CMU Graphics Lab Motion Capture Database. (n.d.). Retrieved from http://mocap.cs.cmu.edu/

Csibra, G., Gergely, G., Bíró, S., Koós, O., & Brockbank, M. (1999). Goal attribution without agency cues: The perception of "pure reason" in infancy. *Cognition*, *72*, 237–267.

Davidson, E. H., & Erwin, D. H. (2006). Gene regulatory networks and the evolution of animal body plans. *Science*, *311*, 796–800.

Dittrich, W. H., & Lea, S. E. G. (1994). Visual perception of intentional motion. *Perception*, *23*, 253–268.

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

Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *The American Journal of Psychology*, *57*, 243–259.

Hirai, M., Chang, D. H. F., Saunders, D. R., & Troje, N. F. (2011). Body configuration modulates the usage of local cues to direction in biological-motion perception. *Psychological Science*, *22*, 1543–1549.

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

Kourtzi, Z., Krekelberg, B., & van Wezel, R. J. A. (2008). Linking form and motion in the primate brain. *Trends in Cognitive Sciences*, *12*, 230–236.

Leslie, A. M., & Keeble, S. (1987). Do six-month-old infants perceive causality? *Cognition*, *25*, 265–288.

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

McKay, L. S., Simmons, D. R., McAleer, P., & Pollick, F. E. (2009). Contribution of configural information in a direction discrimination task: Evidence using a novel masking paradigm. *Vision Research*, *49*, 2503–2508.

Michotte, A. (1963). *The perception of causality* (T. R. Miles & E. Miles, Trans.). London, England: Methuen. (Original work published 1946)

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

Pinto, J., & Shiffrar, M. (1999). Subconfigurations of the human form in the perception of biological motion displays. *Acta Psychologica*, *102*, 293–318.

Premack, D. (1990). The infant's theory of self-propelled objects. *Cognition*, *36*, 1–16.

Rochat, P., Morgan, R., & Carpenter, M. (1997). Young infants' sensitivity to movement information specifying social causality. *Cognitive Development*, *12*, 537–561.

Schlottmann, A., & Ray, E. (2010). Goal attribution to schematic animals: Do 6-month-olds perceive biological motion as animate? *Developmental Science*, *13*, 1–10.

Schlottmann, A., & Shanks, D. R. (1992). Evidence for a distinction between judged and perceived causality. *The Quarterly Journal of Experimental Psychology*, *44*, 321–342.

Scholl, B., & Tremoulet, P. (2000). Perceptual causality and animacy. *Trends in Cognitive Sciences*, *4*, 299–309.

Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences, USA*, *105*, 809–813.

Thurman, S. M., Giese, M. A., & Grossman, E. D. (2010). Perceptual and computational analysis of critical features for biological motion. *Journal of Vision*, *10*(12), Article 15. Retrieved from www.journalofvision.org/content/10/12/15

Thurman, S. M., & Grossman, E. D. (2008). Temporal "Bubbles" reveal key features for point-light biological motion perception. *Journal of Vision*, *8*(3), Article 28. Retrieved from http://www.journalofvision.org/content/8/3/28

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

White, P. A. (1988). Causal processing: Origins and development. *Psychological Bulletin*, *104*, 36–52.