

Do rats (*Rattus norvegicus*) perceive biological motion?

Laura M. MacKinnon · Nikolaus F. Troje ·
Hans C. Dringenberg

Received: 6 April 2010 / Accepted: 22 July 2010 / Published online: 3 August 2010
© Springer-Verlag 2010

Abstract It is unknown whether the rodent visual system can perceive biological motion, an ability present in primates, cats, and several bird species. Using a water-maze visual discrimination task, we find that rats can be trained to distinguish between left- and rightward motion of abstract point-light displays of walking humans. However, rats were unable to generalize to a novel point-light display (a walking cat), or to a display of a backward walking human, where overall body configuration and local, ballistic foot motion provide directly opposing cues regarding movement direction. Together, these experiments provide the first demonstration of the ability of rodents to extract motion direction cues from abstract, point-light displays. However, when isolated, neither the overall body configuration nor the local motion of the feet appears to provide sufficient information for rats to reliably extract movement direction in biological motion displays.

Keywords Biological motion · Vision · Water maze · Rat

Introduction

The study of biological motion perception was initiated by Johansson (1973, 1976), who attached small lights to the major joints of a walking human, dressed entirely in black, and moving against a black background. Observers viewing

films of such a moving human receive a severely impoverished, visual percept (isolated, white dots moving in a completely dark space). Surprisingly, however, the visual system readily decodes this abstract image to produce a vivid perception of a human figure in motion (Johansson 1973, 1976). Consequently, it appears that the primate visual system contains specialized, highly sophisticated circuits that allow the detection, reconstruction, and interpretation of animate motion cues in the environment (Troje 2008).

The perceptual cues and neural mechanisms mediating biological motion perception have received considerable attention. An initial hypothesis suggested that invariant spatial relationships (i.e., overall configuration) among the major joints provide key information for the perception of biological motion (Cutting 1981). Interestingly, however, observers are able to detect movement direction in scrambled point-light displays that do not contain configural cues (Troje and Westhoff 2006). In contrast, presenting inverted point-light displays (scrambled or unscrambled) significantly impairs the ability to extract motion direction cues (Sumi 1984; Troje and Westhoff 2006). Based on these findings, Troje and Westhoff (2006) have proposed that the ballistic, gravity-dependent motion of the feet, which is disrupted by the inversion, provides critical information for the detection of motion direction (see also Chang and Troje 2009). Further, since ballistic foot motion is present in all terrestrial animals with legs, these cues might serve as a general “life detector” for the recognition of animate conspecific and heterospecific organisms (Johnson 2006; Troje and Westhoff 2006).

The ability of the visual system to perceive the direction of motion and label it as animate clearly offers benefits to the fitness and survival of many, if not all, animal species. Consequently, biological motion perception might be a

L. M. MacKinnon · N. F. Troje · H. C. Dringenberg (✉)
Department of Psychology, Queen’s University,
Kingston, ON K7L 3N6, Canada
e-mail: dringenb@queensu.ca

N. F. Troje · H. C. Dringenberg
Centre for Neuroscience Studies,
Queen’s University, Kingston, ON K7L 3N6, Canada

rather general phenomenon throughout the animal kingdom. Consistent with this assumption, biological motion perception has been demonstrated in several non-human species, including non-human primates, cats, pigeons, and chicks (Blake 1993; Dittrich and Lea 1993; Oram and Perrett 1994b; Regolin et al. 2000; Vallortigara et al. 2005; Vallortigara and Regolin 2006; also see Brown et al. 2010 for a discussion of possible sex differences in biological motion perception). Surprisingly, the ability of rodents to perceive biological motion has not been tested. We therefore presented point-light displays of a human, walking to the left or right, to rats and examined whether they can extract movement direction from these abstract, visual stimuli. Additional tests with altered (backward walking human) or novel point-light displays (cat) were conducted to assess the relative importance of configurational information as opposed to ballistic foot motion cues for the ability of rats to detect and discriminate movement direction.

Methods

Subjects

All experimental procedures were carried out in accordance with published guidelines of the Canadian Council on Animal Care and were approved by the Queen's University Animal Care Committee. Six adult, male Long-Evans rats (300–450 g) were used. Rats were housed in pairs in a colony room under a 12/12 h reversed light cycle with free access to food and water.

Procedure

The experiment consisted of an initial training period, which was followed by a test period. During both periods, behavioral assessments were conducted in a modified water maze apparatus (Fig. 1), consisting of a circular pool (160 cm diameter, 60 cm height) and Plexiglas Y-shaped insert (138 cm length, 40 and 80 cm width at the proximal and distal end, respectively). A black Plexiglas divider (50 cm length, 60 cm height) was placed in the distal end of the Y-insert, separating it into two equally sized goal arms. During training, an escape platform constructed of clear Plexiglas (47 cm height, 37 cm length, 12.5 cm width) was located in one of these goal arms. The pool was filled with water ($21 \pm 1^\circ\text{C}$) to a depth of ~ 50 cm (i.e., 2–3 above the escape platform), and white, non-toxic paint was mixed into the water to ensure that the platform was not visible to the rats. A clear Plexiglas sheet was placed across the distal end of the goal arms to allow placement of a computer screen (Acer AL1716, 17" viewable TFT-LCD screen, $1,280 \times 1,024$ pixels) for visual stimulus presentation

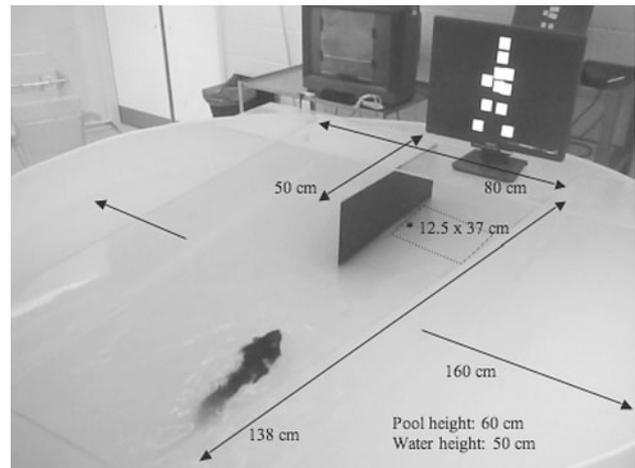


Fig. 1 The water maze apparatus used for visual discrimination training. On the trial shown, the rat completed a biological motion discrimination trial using a human point-light display walking to the left, indicating that the escape platform was located in the right goal arm (Asterisk note that the edges of the escape platform are enhanced for the purpose of this figure)

(Fig. 1). Pilot experiments confirmed that rats could easily see the screen and images projected onto it to reliably discriminate the two goal arms.

Rats were gently placed into the water facing the pool wall at the proximal end of the Y-maze insert and required to swim toward the goal arms, one of which contained the hidden escape platform. For different training phases, various visual cues were presented on the computer screen, which served as cues to indicate the platform location on any given trial. A trial ended when a rat mounted the escape platform or after 60 s had elapsed, in which case the rat was removed from the water and given a 30-s break in a holding cage prior to commencement of the next trial. For each training session, rats received a total of 20 trials, administered as two blocks of 10 trials, with a 3-min rest period under a heat lamp between the two blocks. For each trial, an experimenter recorded the first goal arm entered (i.e., left or right), with an entry defined as a rat placing more than half of its body in the goal arm. Following completion of the 20 trials, rats were placed under a heat lamp before being returned to the colony room. Behavioral training was divided into four phases, and rats received 5 days of training/week.

Training Phase 1

During Phase 1, rats learned to use the computer monitor as a visual cue indicating platform location. During this phase, the location of the monitor on the Plexiglas sheet (left or right) coincided with the platform location in one of the two goal arms. Screen and platform location changed in a semi-random fashion from trial to trial, with the restriction that each of the two locations was used for 5 of the 10 trials

comprising a trial block. For each rat, daily training continued until a pre-set performance criterion was achieved ($\geq 70\%$ correct trials for three consecutive training days), at which point a rat proceeded to the next training phase.

Training Phase 2

For this and all subsequent training phases, the computer monitor always remained stationary above the right goal of the maze. During Phase 2, illumination of the monitor screen (black vs. white) served as a cue indicating platform location. For half of the rats, back and white screens indicated platform location in the right and left goal arms, respectively, while the other half of the rats received training using the opposite screen/goal arm association. The same performance criterion outlined above was applied to proceed to the next training phase.

Training Phase 3

For this phase, the screen was either black or showed a point-light display of a human walker, derived by averaging motion-captured data from 100 different walkers (see Troje 2002). Stimuli were composed of 11 individual light points (white, square dots, 4 inch²) against a black background. The human walker was shown in the sagittal view, walking either left- and rightwards (0.93 Hz gait frequency), as if positioned on a moving treadmill (Fig. 1). Half of the rats were exposed to a leftward walker, while the remaining rats saw a rightward walker. For all rats, the black screen and point-light display indicated platform location in the right and left goal arm, respectively.

Training Phase 4

During the final training phase, for each trial, rats were presented with one of two human point-light displays, walking either left or right. For half of the animals, the platform was situated in the left and right goal arm for left- and rightward walking displays, respectively; the remaining rats were trained with the opposite association between platform location and movement direction.

After rats had achieved the performance criterion for Phase 4, two further tests were carried out to assess which visual information is used by rats to distinguish different movement directions. For these experiments, testing was carried out every second day for a total of five test days (20 trials/day) for both Test 1 and Test 2.

Test 1: Human backwards walker

The same procedure as described for Training Phase 4 was used (i.e., left- and rightward human walker discrimina-

tion). However, 4 of the total 20 trials were catch trials, consisting of point-light displays of a human walking backwards (2 trials per trial block, one each for left- and rightward movement). In these displays, overall motion-mediated body configuration and the local motion of the individual dots (e.g., the feet) provide conflicting, opposing cues regarding movement direction. Catch trials were randomly inserted into regular trials, with the restriction that the first and last trials were always regular trials, and two catch trials never occurred consecutively. Further, for all catch trials, the platform was removed from the pool to eliminate reinforcement and prevent learning. Instead, a rat was manually removed from the water after it had entered one of the goal arms. If rats were using either only motion-mediated configuration information, or only information contained in the local motion (e.g., feet), it should become apparent from these tests which one it is.

Test 2: Cat walker

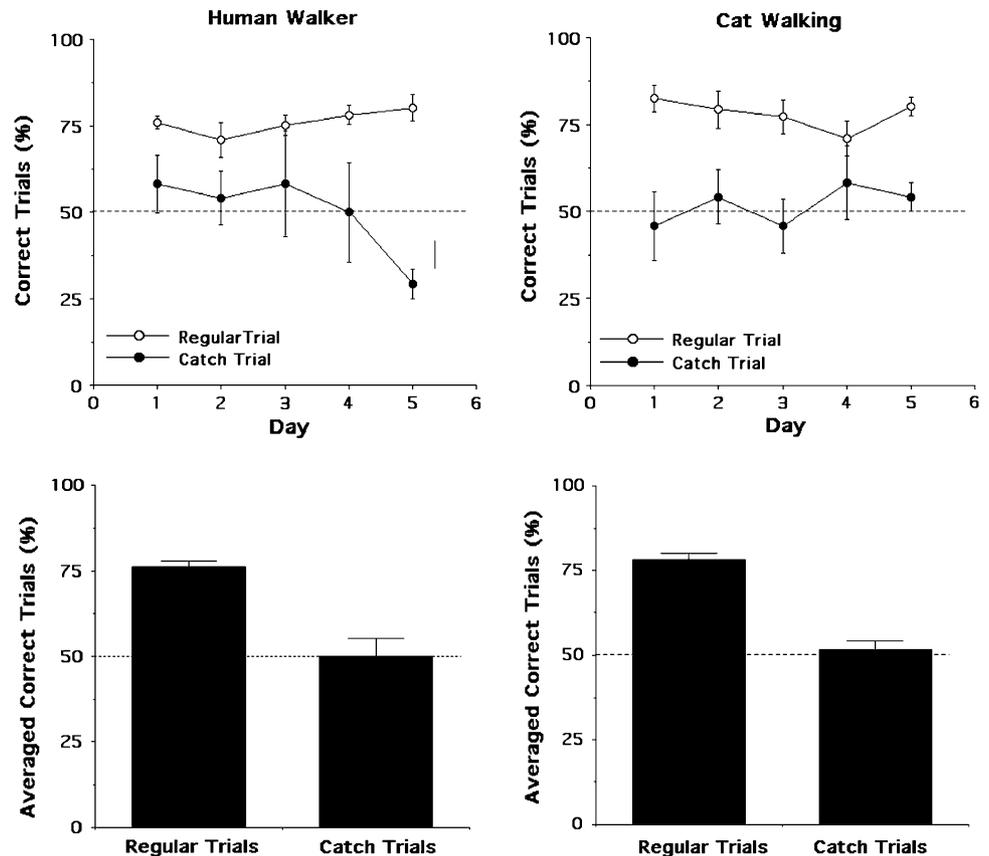
The same procedure as described for Test 1 was used, with the exception that catch trials consisted of point-light displays (14 light points) depicting a left- or rightward walking cat (created by sampling single frames of a video sequence of a cat walking on a treadmill; gait frequency of 1.7 Hz; see Troje and Westhoff 2006). Sensitivity to ballistic limb motion is thought to trigger an evolutionary old mechanism, present in various species (Johnson 2006). Thus, we hypothesized that rats are able to generalize from a human to cat walker for accurate detection or movement direction. Conversely, if overall body configuration is important, substituting a novel point-light display for a familiar one might lower the accuracy of direction discrimination on catch trials.

All data are expressed as mean \pm SEM. For all training and test sessions, behavioral performance was scored as number of correct trials of total trials, and these values were then converted to a percent correct score. Data were subjected to a repeated measure analysis of variance (ANOVA) using the software package CLR Anova (v. 1.1, Clear Lake Research Inc., Houston, Texas). The level of statistical significance was set at $P < 0.05$.

Results

All rats ($n = 6$) successfully acquired the visual discriminations during the four initial training phases. However, for each successive training phase, animals required more training sessions to reach the performance criterion ($\geq 70\%$ correct trials on three consecutive training sessions), on to the next training phase: Phase 1 (left vs. right screen), 3.3 ± 0.8 sessions; Phase 2 (black vs. white screen),

Fig. 2 Visual discrimination performance of rats for point-light displays depicting a left- or rightward walking human (regular trials), backward (*left and right*) walking human (catch trials in *left column*), or walking (*left and right*) cat (catch trials in *right column*). *Top and bottom panels* show performance (% correct trials) for each test day/session and averaged over all days, respectively. Rats readily discriminated movement direction on regular trials. However, discrimination performance was impaired when a display of a backward walking human or a walking cat was presented (catch trials)



4.7 ± 1.2 sessions; Phase 3 (black screen vs. point-light display of walking human), 6.2 ± 1.4 sessions; Phase 4 (left- vs. rightward walking human point-light display), 10.3 ± 1.7 sessions. Consequently, although more training was required to master the increasingly complex visual discriminations, all animals were able to use motion information contained in the point-light displays to successfully discriminate movement direction of human walkers (Phase 4).

For Test 1, catch trials (4 trials in every session of 20 trials, five test sessions, administered every second day) of a backward walking human were inserted into regular trials. “Correct” responses were defined in terms of the direction indicated by the foot motion (rather than whole body configuration) as a cue to indicate platform location. For the 16 regular trials, rats showed reliable discrimination of left- and rightward walking point-light displays (Fig. 2, left; average of 76 ± 1.6% correct across all test sessions). In contrast, for catch trials, performance fell to chance levels (average of 50 ± 5.4% correct trials across all sessions). A repeated-measures ANOVA revealed a significant effect of trial type ($F(1,5) = 46.2$, $P < 0.01$), but no effect of session/day ($F(4,20) = 0.8$, $P = 0.6$), and no trial × session interaction ($F(4,20) = 1.6$, $P = 0.2$). Thus, rats failed to make direction discriminations when foot and configural information provided conflicting

information regarding the direction of the human point-light display.

For Test 2, catch trials (4 trials in every session of 20 trials, five test sessions, administered every second day) of a cat walking to the left and right were inserted into regular trials. Again, rats showed reliable direction discrimination for regular trials (Fig. 2, right; average of 78 ± 2.0% correct across all test sessions). However, for catch trials, performance declined to chance levels (average of 52 ± 2.5% correct trials). A repeated-measures ANOVA showed a significant main effect of trial ($F(1,5) = 25.5$, $P < 0.01$), but no effect of session/day ($F(4,20) = 0.3$, $P = 0.9$), and no trial × session interaction ($F(4,20) = 1.2$, $P = 0.3$). Thus, rats were not able to generalize from point-light displays showing a walking human to those depicting a walking cat.

Discussion

With the present set of experiments, we examined whether rats are able to extract invariant direction cues from highly abstract, point-light displays of right- and leftward walking humans. Surprisingly, all rats tested learned to reliably discriminate movement direction, even though relatively extensive training (~10 days) was required for the animals to achieve high levels of discrimination performance.

Previous work demonstrated that newly hatched, visually naïve chicks exhibit a strong preference for biological motion point-light displays over displays of dots that moved in non-biological ways (Vallortigara et al. 2005), indicative of a seemingly innate attraction to some kind of invariant specific to biological motion. Further, when presented with an upright point-light display of a walking hen, visually inexperienced chicks align themselves with the apparent movement direction of the display, an effect that is lost by inverting the point-light display (Vallortigara and Regolin 2006). These data indicate that the visual system is exquisitely sensitive to the detection of direction cues contained in biological motion displays, an ability that, at least in some species, appears to exist without prior visual experience. The fact that extensive training was required for rats to discriminate left- and rightward walking displays indicates a much reduced sensitivity to direction cues contained in the displays. Nevertheless, the fact that reliable discrimination could be acquired shows that rodents can process biological motion stimuli to an extent that allows them to derive the apparent “movement” direction of a stationary walker.

To date, neurons responsive to complex, biological motion have not been described in the rat visual system, even though they have been characterized in the superior temporal sulcus of the primate brain (Oram and Perrett 1994a, b). The detection of transient and moving stimuli in rodents relies heavily on projections from the optic tectum/superior colliculus to secondary and/or high visual cortex areas, which function largely independent of the primary visual cortex (Dean 1990). However, the relative contributions of cortical and subcortical systems to the detection and discrimination of motion direction in rodents remain to be determined.

A recent hypothesis suggests that the ballistic motion of the feet provides a critical cue for the detection of biological motion, a hypothesis based on findings that scrambled point-light displays of walking humans or non-human animals (which lack all structural, configurational cues) still contain information regarding movement direction. However, direction cues are lost when these scrambled point-light displays are inverted, that is, when the normal, gravity-dependent foot motion no longer is available to the visual system (Troje and Westhoff 2006; Troje 2008). In order to address the question of whether rats use foot motion to extract movement direction, we inserted catch trials of either a backward human walker (pitting foot motion against whole body configuration) or a walking cat with a configuration entirely different from the human figure the rats had learned. We hypothesized that, in both cases, rats would use local foot motion in order to judge movement direction and, therefore, the location of the escape platform in the water maze. In contrast, we found that, for both types

of probe trials, discrimination performance declined to chance levels, despite good performance (~76–78% correct) on regular trials showing left- and rightward walking humans. The most parsimonious interpretation of these results is that foot motion alone is not sufficient for rats to extract motion direction cues from point-light displays. Consequently, it is possible that both foot motion and configural cues are required for rats to successfully perform direction discriminations. As an alternative explanation, it is possible that the relative novelty of the catch trial stimuli might have resulted in poor performance. We consider this an unlikely possibility, given that catch trial performance did not improve over the five consecutive test days, during which stimuli become more familiar to the animals. Future work employing a modified training/testing procedure to reduce novelty effects (e.g., initial training with a greater number of stimuli, or more extensive catch trial testing) could be useful to address this issue.

In summary, the present experiments demonstrate that rats can learn to detect movement direction contained in biological motion point-light displays. It appears that this ability, once acquired, does not generalize to novel point-light displays and that ballistic foot motion alone does not provide sufficient information for rats to extract direction cues. Future work should be directed at characterizing the specific perceptual and neural mechanisms mediating the perception of motion direction in rodents.

Acknowledgments This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants to H.C.D. and N.T. Further, L.M.M. was the recipient of an NSERC Undergraduate Student Research Award. We thank Jason Hermanutz, Jonathan Hui, and Stephen Scovil for assistance with these experiments.

References

- Blake R (1993) Cats perceive biological motion. *Psychol Sci* 4:54–57
- Brown J, Kaplan G, Rogers LJ, Vallortigara G (2010) Perception of biological motion in common marmosets (*Callithrix jacchus*): by females only. *Anim Cogn* (2010) 13:555–564
- Chang DHF, Troje NF (2009) Acceleration carries the local inversion effect in biological motion perception. *J Vis* 9:1–17
- Cutting JE (1981) Coding theory adapted to gait perception. *J Exp Psychol Hum Percept Perform* 7:71–87
- Dean P (1990) Sensory cortex: visual perceptual functions. In: Kolb B, Tees RC (eds) *The cerebral cortex of the rat*. MIT Press, Cambridge, pp 275–307
- Dittrich WH, Lea SEG (1993) Motion as a natural cue for pigeons: generalization and a feature-positive effect. *J Exp Anal Behav* 59:115–129
- Johansson G (1973) Visual perception of biological motion and a model for its analysis. *Percept Psychophys* 14:201–211
- Johansson G (1976) Spatio-temporal differentiation and integration in visual motion perception. *Psychol Res* 38:379–393
- Johnson MH (2006) Biological motion: a perceptual life detector? *Curr Biol* 16:R376–R377

- Oram NW, Perrett DI (1994a) Responses of anterior superior temporal polysensory (STPa) neurons to “biological motion” stimuli. *J Cogn Neurosci* 6:99–116
- Oram MW, Perrett DI (1994b) Neural processing of biological motion in the macaque temporal cortex. *Proc SPIE* 2054:155–166
- Regolin L, Tommasi L, Vallortigara G (2000) Visual perception of biological motion in newly hatched chicks as revealed by an imprinting procedure. *Anim Cogn* 3:53–60
- Sumi S (1984) Upside-down presentation of the Johansson moving light-spot pattern. *Perception* 13:282–286
- Troje NF (2002) Decomposing biological motion: a framework for analysis and synthesis of human gait patterns. *J Vision* 2:371–387
- Troje NF (2008) Biological motion perception. In: Basbaum AI, Kaneko A, Shepherd GM, Westheimer G, Albright TD, Masland RH, Dallos P, Oertel D, Firestein S, Beauchamp GK, Bushnell MC, Kaas JH, Gardner E (eds) *The senses: a comprehensive reference*, vol 2. Elsevier, Oxford, pp 231–238
- Troje N, Westhoff C (2006) The inversion effect in biological motion perception: evidence for a “Life Detector”? *Curr Biol* 16:821–824
- Vallortigara G, Regolin L (2006) Gravity bias in the interpretation of biological motion by inexperienced chicks. *Curr Biol* 16:R279–R280
- Vallortigara G, Regolin L, Marconato F (2005) Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLoS Biol* 3:e208