



Original Articles

Visually-naïve chicks prefer agents that move as if constrained by a bilateral body-plan

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ABSTRACT

From the first hours of life, the prompt detection of animate agents allows identification of biologically relevant entities. The motion of most animate agents is constrained by their bilaterally-symmetrical body-plan, and consequently tends to be aligned with the main body-axis. Thus parallelism between the main axis of a moving object and its motion trajectory can signal the presence of animate agents. Here we demonstrated that visually-naïve newborn chicks (*Gallus gallus domesticus*) are attracted to objects displaying such parallelism, and thus show preference for the same type of motion patterns that elicit perception of animacy in humans. This is the first demonstration of a newborn non-human animal's social preference for a visual cue related to the constraints imposed on behaviour by bilaterian morphology. Chicks also showed preference for rotational movements – a potential manifestation of self-propulsion. Results are discussed in relation to the mechanisms of animacy and agency detection in newborn organisms.

1. Introduction

From the first hours of life, the detection of animate agents allows identification of biologically relevant entities: prey, predators and social companions. Responses appropriate for these fundamental categories may be innately guided by key stimuli features. For instance, for domestic chicks, the presence of concentric eye structure (Jones, 1980), object size (Schulman, Hale, & Graves, 1970) and relative speed of motion (Schleidt, Shalter, & Moura-Neto, 2011) contribute to the activation of either feeding, anti-predatory or social responses (review in Versace and Vallortigara (2015)). However, animate objects in general tend to attract attention. Newborns of species as distant as primates and birds preferentially attend to visual features typical of animate agents (Di Giorgio et al., 2017; Rosa-Salva, Mayer, & Vallortigara, 2015). These predispositions appear early in development, prior to visual experience with other agents (see also Reid et al., 2017) and are triggered by features that may be diagnostic of living things in general, rather than just of the members of own species. For example, newly-hatched chicks, face-naïve monkeys and human newborns spontaneously attend to face-like stimuli (Morton & Johnson, 1991; Rosa-Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011; Rosa-Salva, Regolin, & Vallortigara, 2010, 2012; Sugita, 2008; Versace, Fracasso, Baldan, Dalle Zotte, & Vallortigara, 2017) and to schematic point-light displays of biological motion (Simion, Regolin, & Bulf, 2008; Vallortigara, Regolin,

& Marconato, 2005).

The general tendency to pay attention to animate creatures has important implications for the development of social behaviour. One function of these spontaneous preferences might be to constrain the input for the developing circuits that will specialize in the processing of visual information from animate agents (Di Giorgio et al., 2016; Johnson, 2005; Vallortigara, 2012). In the species-typical environment of chicks and human newborns, a spontaneous preference for animate creatures will result in increased visual exposure and/or filial imprinting towards the appropriate social stimuli (e.g., the parent's face, the mother hen). Thus, innate social predispositions towards animate agents in general do not need to support recognition of own species: subsequent learning mechanisms may lead to restricting social behaviour to conspecifics and to the caregiver (Bateson, 1966; Bolhuis, 1991; McCabe, 2013; Vallortigara, 2012; Vidal, 1980).

Broadly speaking, animate agents behave in ways in which inanimate objects do not. The mechanisms behind the innate social predispositions are attuned to detecting elementary motion patterns, which are highly diagnostic of animate agency. For example, chicks are attracted by self-propelled objects whose motion thus reveals an internal energy source (a defining feature of animacy). A simple two-dimensional shape, that starts to move by itself is preferred for imprinting over the one, which is set in motion by another object (Mascalzoni, Regolin, & Vallortigara, 2010). By a similar token, chicks are attracted

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by moving objects that can accelerate and decelerate by themselves (Rosa-Salva, Grassi, Lorenzi, Regolin, & Vallortigara, 2016).

Furthermore, the self-propelled motions of animate agents tend to be constrained by the structure of their bodies. Thus, certain constrained motion patterns may also signal the presence of animate agency. For instance, chicks are attracted by the semi-rigid motion-pattern displayed in the gait of the legged vertebrates as a consequence of their skeletal structure (Vallortigara et al., 2005).

Perhaps the most universal and evolutionary ancient constraints on animal motion are those imposed on the behaviour of *bilateria* by their body plan (i.e. *bilateral symmetry*). *Bilateria* tend to maintain a single preferred orientation of their bodies with respect to the motion direction: translational motion tends to be aligned with the body's axis of symmetry and it tends to transport the animal forward. Crucially, most modern animal species and their prehistoric ancestors, including the common ancestor of all vertebrates (Knoll & Carroll, 1999), are *bilateria*. Thus, stable orientation with respect to motion direction, parallelism between the main axis and the motion path as well as forward-facing movement constitute patterns of constrained motion that reliably signal the presence of animate agents. Indeed, parallelism between the main axis and the path elicits higher animacy attribution in human observers (Tremoulet & Feldman, 2000). The human adult perceptual system may operate with an implicit expectation of such parallelism for any elongated symmetrical moving object (Dolgov, Birchfield, et al., 2009; Dolgov, McBeath, et al., 2009; Jardine & Seiffert, 2011; Morikawa, 1999) as well as with an expectation that agents typically move forwards (McBeath, Morikawa, & Kaiser, 1992; Pavlova, Krägeloh-Mann, Birbaumer, & Sokolov, 2002). It has also been shown that 6-months-old infants spontaneously encode body direction of a novel agent locomoting across a computer screen and use this information when anticipating its future behaviour (Hernik, Fearon, & Csibra, 2014).

In the context of feeding behaviour several predator species, including lizards (Cooper, 1981), birds (Smith, 1973) and ferrets (Apfelbach & Wester, 1977) have been shown to rely on their prey's propensity for forward-facing motion when directing head-first attacks. Moreover, toads and frogs are sensitive to axis-path parallelism, which directs their feeding responses by signaling that a visual object belongs to the "prey" category, whereas an object moving perpendicularly to its main axis does not (Ewert, 1987). Notably, an opposite preying pattern was found in chicks, and attributed to the fact that the atypical perpendicular axis-path orientation may signal that the potential insect-prey is injured and easier to catch (Clara, Regolin, Vallortigara, & Rogers, 2009).

However, social responses to visual cues of animate agency related to bilaterian morphology have never been investigated in non-human animals. The aim of this study was thus to fill this gap, by testing whether visually naïve chicks' social responses are facilitated by the patterns of constrained motion typical of animate bilaterian agents. This is part of our larger effort to describe the minimal, elementary motion features that direct early social behaviour in our animal model, which have often been found to have a similar function also in human infants (Di Giorgio et al., 2017); but see (Versace, Schill, Nencini, & Vallortigara, 2016).

2. General materials and methods

2.1. Ethical statement

All applicable European and Italian guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards of the University of Trento, where the study was conducted. The study has been approved by the research ethics committee of the University of Trento and by the Italian Ministry of Health (permit number 117/2016).

2.2. Subjects

Subjects were domestic chicks (*Gallus gallus domesticus*) of the Aviagen Ross 308 strain. Fertilized eggs were obtained from a commercial hatchery (Agricola Berica, Montegalda, VI, Italy). During incubation and hatching eggs and chicks were kept in complete darkness, preventing any visual experience prior to testing. Each chick was tested only once and a new set of naïve chicks was obtained for each experiment. After testing chicks were immediately caged in groups with food and water available ad libitum, at constant temperature (32 °C) and variable light conditions following the natural sequence of day and night. Soon afterwards chicks were donated to local farmers.

2.3. Apparatus

The test apparatus was a white corridor (85 × 30 × 30 cm) closed at two ends by two computer monitors (LCD Monitor BenQ XL2410T) displaying the experimental stimuli. At each end a 30 × 30 cm portion of the monitor (henceforth: the scene) was visible to the chicks. The corridor was divided in three sectors: a central sector (45 × 30 cm), equidistant from the two monitors, and two identical lateral sectors (20 × 30 cm each), adjacent to the two monitors and elevated by 1.5 cm above the central sector. Consequently the animals had to climb up when entering any of the two lateral sectors. A video-camera recorded the testing from above the apparatus while feeding the image to a screen located in the same room, on which the experimenter observed the chicks' behaviour and coded it on-line. The apparatus was illuminated only by the two stimulus-monitors (Rosa-Salva et al., 2016). The testing apparatus was located in a silent room, where only the experimenter was present. The apparatus was not soundproofed, so an occasional external noise could have been heard by the chicks. However, in order to rule out systematic effect of potential external noise-sources or other environmental gradients, the position of the target-stimulus in the apparatus was counterbalanced across chicks in each experiment.

2.4. Test stimuli

Stimuli were animations created with Adobe Aftereffects (CC 2015) software. In all experiments, stimuli showed the same red rectangular object with rounded corners (6.3 × 3.7 cm) moving over a uniform black background delineated by two grey digitally-inserted vertical edges (0.75 cm wide) on each side of the scene. The red object always entered and exited the scene in motion, emerging from behind the edge on one side and slipping behind one on the opposite side. In all the stimuli the red object moved on the same V-shaped path. Each motion cycle begun with the red object starting from the upper-left side of the scene and moving towards the mid-point at the bottom of the scene (the "dip" of the V-shaped path). From there the object took a symmetrical path towards the upper-right side of the scene (Fig. 1). Soon after disappearing from view (0.09 s) the object re-emerged from where it had exited on the right side and took the same V-shaped path leftwards. The cycle ended with the object exiting at the upper-left side. The next cycle started 0.09 s after the end of the previous one. Each cycle lasted 12 s. Each test trial lasted for 6 min, during which the cycles were looped.

In each experiment a pair of different stimuli was presented simultaneously. For each experiment, we defined one *target stimulus* and one *distractor stimulus*. The target stimulus was the one that we expected to be preferred by the chicks' because of the characteristics of the presented motion. These differed along two dimensions: orientation of the object with respect to the motion-path and the amount of object's rotation at the time of direction change. By manipulating these two features of the visual stimuli we generated versions of the two stimuli, which differed with respect to four potential motion-cues to animate agency: axis-path parallelism, re-alignment, front-back consistency and rotation. We discuss these four factors further in the description of the stimulus-pair for Experiment 1 (see also Fig. 1).

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