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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).

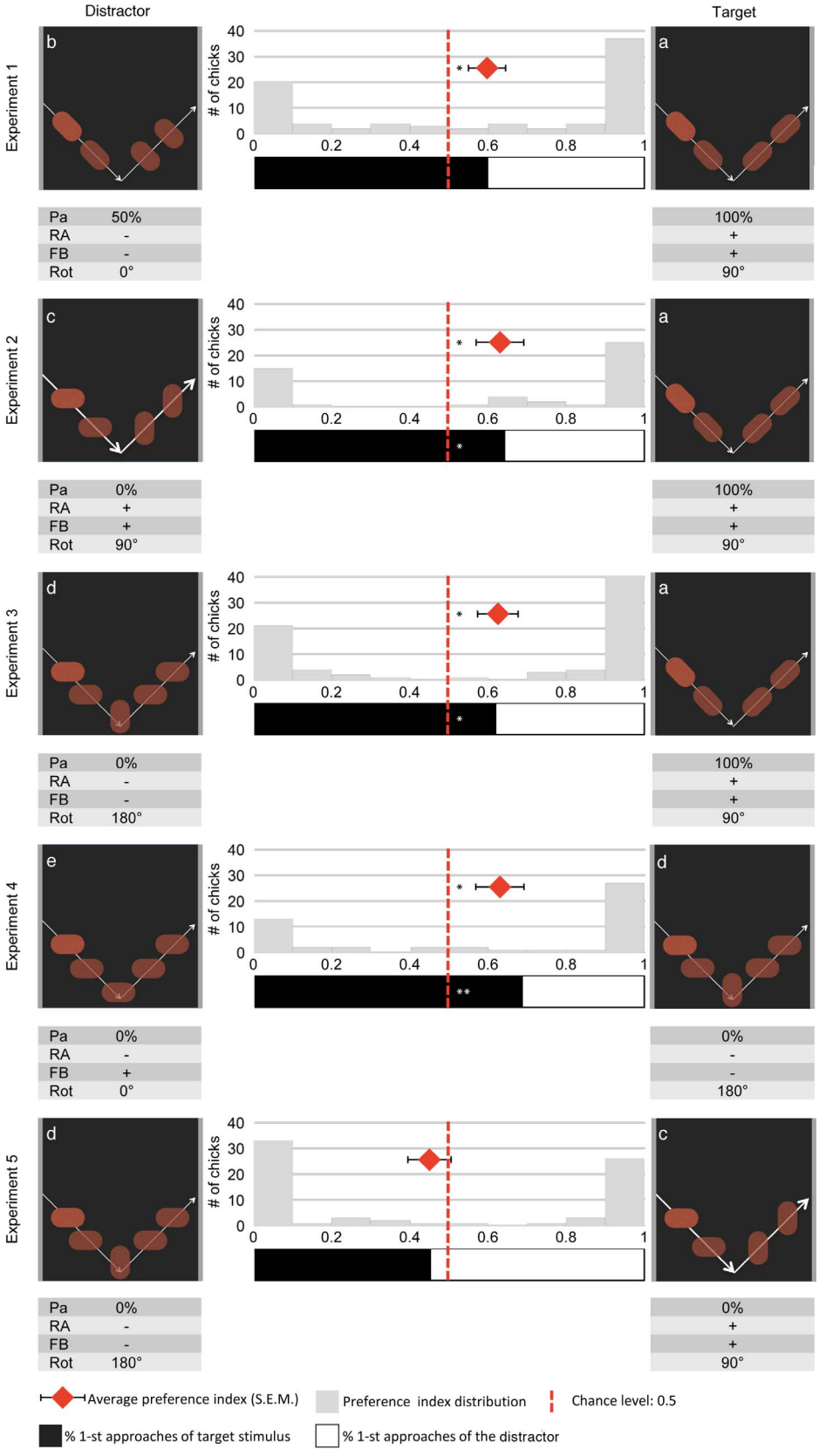

Fig. 1. Schematic representations of the motion features in the distractor (left column) and target stimuli (right column) of each experiment, together with summaries of the key factors for each stimulus: Pa = parallelism, RA = re-alignment, FB = front-back consistency, Rot = rotation. For each experiment graphs show distribution of preference-scores across chicks (gray bars), mean preference-score (red diamond) with its standard error (whiskers), as well as percentage of chicks who first approach the target (black bar) and the distractor stimulus (white bar). $^{*}p < .05$, $^{**}p < .01$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.5. Procedure

The test was run on the first day after hatching. Each subject was taken from the incubator in complete darkness and carried in a closed opaque container to the experimental room. At the beginning of the test the chick was placed in the central sector of the experimental apparatus, facing one of the two long walls (the initial orientation of the chicks towards one or the other long wall was counterbalanced between

subjects). Each subject's behaviour was recorded for 6 min. If the chick remained in the central sector, this indicated no choice, whereas entering one of the two lateral sectors was coded as a preference for the stimulus at that side of the apparatus. Chicks' behaviour was coded online using a purpose-built software, which calculated the time (in seconds) spent by the chick in each of the three sectors during the overall test period, according the experimenter's button-presses indicating entering any of the three sectors. Behavioural measures considered were the first stimulus approached by each subject (i.e. the first lateral sector entered during the test) and the ratio of time spent near the target stimulus over the total choice time (i.e. a preference index representing the ratio of time spent by the subject in the lateral sector near the target stimulus, during the whole test duration, with respect to the time spent in both lateral sectors) calculated with the formula:

Time spent near the target stimulus/(time spent near the target stimulus + time spent near the distractor stimulus).

Values of this ratio could range from 0 (full preference for the distractor stimulus), to 1 (full preference for the target stimulus), whereas 0.5 represented the absence of preference.

All measures were scored online, but a 10% of all subjects were scored again offline by a second experimenter unaware of the position of the two stimuli in the apparatus. Overall we recoded videos of 25 animals randomly chosen from all the experiments, obtaining a Pearson's correlation of 0.999, $p < .001$ between the ratio calculated based on the original and on the offline coding, with an average absolute difference of 0.010 (SEM 0.025). Thus, the online scores were confirmed when re-coded blind to the position of the stimuli.

2.6. Data analysis

The number of chicks that first approached the target or the distractor stimulus was compared using chi-square test of independence. The ratio of time spent near the target stimulus over the total test time was compared to chance-level of 0.5 using a one-sample two-tailed *t*-test. This analysis was then confirmed using the non-parametric Wilcoxon signed rank test. All databases have been uploaded as supplementary electronic materials (see data of Exp. 1–5, in supplementary materials (Rosa-Salva, Hernik, Broseghini, & Vallortigara, 2018).

3. Experiment 1

In the first experiment we tested chicks' preference between two stimuli modeled on those used earlier to study the impact of the relationship between object orientation and its motion path on the perception of animacy in human observers (Tremoulet & Feldman, 2000).

The test stimuli used in this work can be characterised by different properties related to animacy and agency perception. In the present experiment, as well as in the corresponding condition in Tremoulet and Feldman (2000), the target stimulus presents all of these relevant properties, such as keeping a constant, parallel alignment between its main body-axis and the motion direction as well as performing rotational movements, while the distractor stimulus lacks these features or presents them to a lesser extent. The simultaneous manipulation of all the relevant factors in favour of the target stimulus should be particularly effective in uncovering any preference chicks' might have for the perceptual properties under investigation.

3.1. Subjects

Eighty-two domestic chicks (46 males) were used for this experiment.

3.2. Stimuli

For both stimuli the object started each cycle with its main axis aligned with the motion direction (i.e., parallel to it, with an angle of 0°). However, only in the target stimulus (stimulus a, see Fig. 1 and suppl. mat.) the object rotated by 90° at the time of the 90° direction-change, thus maintaining its axis parallel to the path. Whereas, in the distractor stimulus (stimulus b, see Fig. 1 and suppl. mat.) the object did not rotate at all and simply kept translating along the V-shaped trajectory. Thus the object always maintained its original absolute orientation, without re-aligning itself with the new trajectory. For the upward slope of the "V" path, the object in the distractor display had its main symmetry axis at a 90° angle to the motion path.

The stimuli can be described using the following factors:

(i) Axis-path Parallelism (Pa): Translational motion with 0° angle between the object's main axis and its motion trajectory. For each stimulus Pa can be quantified as the percentage of motion duration, during which the angle between the object's main axis and the motion-path equals 0°.
(ii) Re-Alignment (RA): Maintaining a stable spatial relationship between the object's main axis and its trajectory after a motion-direction change. RA requires that the angle between the axis and the trajectory is the same before and after the change of direction. In our stimuli-set RA is a binary variable: re-alignment is either present or absent in a given stimulus.
(iii) Front-Back consistency (FB): Maintaining the same extremity towards the direction of translational motion after a motion-direction change. Note that this property could be detected even when the two extremities of the object are visually identical (as in the present study), by constant tracking of the object's orientation in motion. In our stimuli-set RA is a binary variable: front-back consistency is either present or absent in a given stimulus.
(iv) Rotation (Rot): Rotational motion, which is a cue to self-propulsion. Rotation during a change of direction requires an additional energy cost in addition to the cost of direction-change. For each stimulus Rot can be quantified as the size of the angle between the object's main axis before and after change of motion-direction.

In this experiment, the target stimulus differed from the distractor stimulus in the amount of Pa (the objects' axis was parallel to it motion-path 100% of the time in the target stimulus and only 50% of the time in the distractor stimulus) and Rot (90° rotation in the target stimulus and 0° rotation in the distractor stimulus). Moreover, only the target stimulus presented RA and FB. The relevant properties of the pairs of stimuli used in each experiment are summarized in Fig. 1.

3.3. Results

Chicks showed a significant preference for the target stimulus, as revealed by the ratio of time spent near the target stimulus (mean 0.6, S.E.M. 0.05, $t_{81} = 2.192$, $p = .031$, $d = 0.241$, $Z = 2.227$, $p = .026$, Fig. 1). A similar, but not significant, trend was observed also for the other dependent variable, with 49 out of 82 chicks approaching the target stimulus first ($X^2_1 = 3.112$, $p = .077$, Fig. 1).

3.4. Discussion

We found a preference for the stimulus displaying the same characteristics as the one eliciting higher animacy ratings in human observers (Tremoulet & Feldman, 2000). This adds to the growing evidence that visually naïve chicks are guided by innate predispositions directing their initial social responses towards objects with specific perceptual features. These features seem to correspond to those that elicit animacy perception in adult humans and, in some case, also preferential attention in newborns (Di Giorgio, Lunghi, Simion, &

Vallortigara, 2017; Mascalzoni et al., 2010; Morton & Johnson, 1991; Rosa-Salva et al., 2010, 2011, 2016; Simion et al., 2008; Vallortigara et al., 2005).

As discussed, chicks' preference for the target stimulus (and humans' animacy perception in Tremoulet and Feldman (2000)) could be due to four factors: the different amount of Pa displayed in the two stimuli, the presence of RA, FB or Rot > 0 only in the target stimulus. Rot > 0 may elicit social preference in virtue of being a cue of self-propulsion. Pa, RA and FB reflect the constraints imposed by a bilateral body plan on animal behaviour. Given their common origins and co-variation in the environment we can expect the three latter factors to be interdependent and potentially independent from Rot, which in principle could signal self-propulsion even when Pa, RA and FB cannot be computed. In the rest of the paper we will investigate the role of these two separate groups of factors, focusing on Rot among the cues of self-propulsion and on Pa among the body-plan-constraints factors. In the latter group Pa stands out in several ways. Sensitivity to Pa has been suggested in human observers, who give higher animacy ratings to elongated objects moving along the main axis than to a disk lacking a main symmetry axis (Tremoulet & Feldman, 2000). Among non-human animals, some anuran species demonstrated sensitivity to the presence or absence of Pa, albeit in the domain of predation responses (Ewert, 1987). The choice to focus on Pa is also supported by the high saliency of this property in our stimuli: the presence or absence of Pa can be assessed independently multiple times, at almost any single time-point of the stimulus. This is not true for RA and FB, which require a comparison of the orientation of the object in motion before and after the direction change.

4. Experiment 2

The aim of this experiment was to study the effect of Pa in isolation from other factors. We thus tested chicks' preference between two stimuli, which were equated for the presence of RA, FB and Rot. The only difference between the two displays was that in the target stimulus the object's main axis was always parallel to the motion path, whereas in the distractor stimulus the object was always oriented at an angle with respect to its path.

4.1. Subjects

Fifty-three domestic chicks (26 males) were used for this experiment.

4.2. Stimuli

In Experiment 2 the target stimulus was identical to that of Experiment 1 (stimulus a). In the distractor stimulus (stimulus c, see Fig. 1 and suppl. mat.) the moving object had its main axis oriented at an angle of about 45° to the motion direction. The object was always oriented horizontally (in absolute terms), when travelling the first half of its trajectory, and vertically during the second half. In both stimuli the object rotated by 90° when changing direction, thus maintaining a stable angle with respect to its motion-path (RA+) and keeping the same extremity towards its motion direction (FB+).

4.3. Results

Chicks showed a significant preference for the target stimulus (mean ratio of time spent near the target stimulus: 0.63, S.E.M. 0.06, $t_{52} = 2.167$, p = .035, d = 0.296, Z = 1.979, p = .048; 34 out of 53 chicks approaching the target stimulus first $X^2_1 = 4.245$, p = .039, Fig. 1).

4.4. Discussion

In Experiment 2, chicks clearly preferred to approach an object whose main axis was parallel to the motion path, over one oriented at an angle to its trajectory. The test stimuli were matched for all other factors at play (Rot, RA and FB). To the best of our knowledge, this is the first clear-cut demonstration of a preference for *parallelism* between main body-axis and motion-trajectory in any model of social preferences.

5. Experiment 3

Having established the effect of Pa, in the current experiment we went on to investigate the effect of Rot. We wanted to test whether the presence of a higher amount of rotation could drive chicks' preference against the effect of the three factors of the body-plan-constraints group. We thus confronted a display characterised by the presence of Pa, RA and FB with another one lacking all these three properties, but presenting a rotation twice as wide.

5.1. Subjects

Seventy-six domestic chicks (27 males) were used for this experiment.

5.2. Stimuli

In Experiment 3 the target stimulus was identical to the previous experiments (stimulus a). In the distractor stimulus (stimulus d, see Fig. 1 and suppl. mat.) the red object entered the scene with its main axis at a 45°angle above the motion path (like in the distractor stimulus c in Experiment 2). At the moment of motion-path change, it rotated by 180°. The angle between the object's axis and the motion-path was thus different in the first (45°) and second half (125°) of the travel. The distractor stimulus did not present neither Pa, RA nor FB: the object was never parallel to its trajectory, did not maintain its axis at a consistent angle with respect to it and the leading end of the object in the first half of the path, became the trailing and in the second half. In this experiment we decided to consider stimulus a the target and stimulus d the distractor stimulus, based on the results of the previous two studies, which indicated preference for stimulus a.

5.3. Results

Chicks showed a significant preference for the target stimulus (mean ratio of time spent near the target stimulus 0.63, S.E.M. 0.051, $t_{75} = 2.438$, p = .017, d = 0.278, Z = 2.360, p = .018; 47 out of 76 chicks approaching the target stimulus first, $X^2_1 = 4.263$, p = .039, Fig. 1).

5.4. Discussion

Experiment 3 demonstrated a preference for the stimulus characterised by the factors reflecting constraints from the bilateral body-plan (Pa, RA and FB) over a stimulus that involved twice as wide rotation. This is the third consecutive result showing a preference for this set of factors, indicating a robust phenomenon. In this case the body-plan-constraints factors were even able to drive chicks' preference against the putative effect of Rot, which is a cue to self-propulsion and thus a potential facilitator of animacy perception. This result also allows us to rule out one alternative explanation for the results of Experiment 1, namely that in Experiment 1 the preference for the target stimulus might have been driven solely by the amount of rotation (90° *vs* 0°). In Experiment 3 the stimuli pair involved exactly the same amount of difference in Rot (90°) in favour of the distractor stimulus, but we still observed a preference for the target stimulus.

Even though this result confirms those of Experiments 1 and 2, it might appear surprising that the body-plan-constraints factors can drive chicks' preferences more reliably than a clear manifestation of self-propulsion. In fact, other cues of self-propulsion have been proven to elicit robust social preferences in chicks (Mascalzoni et al., 2010; Rosa-Salva et al., 2016), even when in conflict with a factor such as FB (Rosa-Salva et al., 2016). However, while chicks' predispositions for other self-propulsion cues have already been shown (Mascalzoni et al., 2010; Rosa-Salva et al., 2016), their social attraction to rotational movement has never been directly investigated.

6. Experiment 4

The aim of this experiment was to test chicks' hypothetical preference for stimuli characterised by Rot, under conditions that may allow for this preference to be better expressed than those in Experiment 3. Specifically, we tested chicks' preference among two stimuli, both of which were lacking most cues related to the constraints from bilaterian morphology. The target stimulus involved a very wide rotation, while the distractor stimulus involved no rotation at all.

6.1. Subjects

Fifty-one domestic chicks (33 males) were used for this experiment.

6.2. Stimuli

In Experiment 4, the target stimulus (for which we expected a preference) was the same display that was used as distractor stimulus in Experiment 3 (stimulus d). In the distractor stimulus (stimulus e, see Fig. 1 and suppl. mat.) the red object was also oriented at a 45° angle to the motion-path (horizontally in absolute terms). However, no rotation was performed at the time of direction change, and the object simply kept on translating in the new direction while maintain its absolute horizontal orientation. Thus, in the distractor stimulus the object did not preserve its original orientation with respect to its trajectory: it first moved with its leading extremity raised at 45° above the trajectory, and continued pointing 45° below the path after the change of direction.

To sum up, both stimuli lacked Pa and RA, while Rot was present only in the target stimulus (the difference in the amount of Rot between the two stimuli was of 180°, twice as big as in Experiments 2 and 3). On the other hand, only the distractor stimulus was characterised by FB. However, we assume that this factor should play a minor role, if any, in the absence of Pa, which – in the context of our stimuli – is easier to detect. Indeed, a previous study already demonstrated that any potential effect FB might have can be reversed by self-propulsion cues (Rosa-Salva et al., 2016).

6.3. Results

Chicks showed a significant preference for the target stimulus (mean ratio of time spent near the target stimulus 0.63, S.E.M. 0.061%, $t_{50} = 2.133$, $p = .038$, $d = 0.298$, $Z = 2.135$, $p = .033$; 35 out of 51 chicks approaching the target stimulus first $X^2_1 = 7.078$, $p = .008$, Fig. 1).

6.4. Discussion

To the best of our knowledge, Experiment 4 provided the first demonstration of preferential attention to rotational over translational movements, either in chicks or in any other animal including humans. These results add to the growing literature showing social predispositions for kinematic features associated with self-propulsion in visually naive chicks (Mascalzoni et al., 2010; Rosa-Salva et al., 2016). In fact, even against any putative contrasting effect of the factor FB, chicks showed a strong preference for the self-propelled stimulus performing a wide rotation over the one that did not show this cue of self-propulsion. However, it remains unclear why, in Experiment 3, chicks preferred the stimulus characterised by the three factors of the body-plan-constraints group over the one showing the wider rotation. In the last experiment and in the General discussion we will address some possible explanations for that.

7. Experiment 5

So far we were able to isolate the role of the effects of the factors Pa and Rot in chicks' preferences. Here we wanted to further investigate the potential interactions between Rot and the body-plan-constraints factors. Specifically, in Experiment 5 we wanted to test whether, in the absence of Pa, the other factors from the body-plan-constraints cluster will still determine chicks' preferences or if chicks will respond preferentially to the stimulus presenting the wider amount of Rot. Neither of the stimuli used was characterised by Pa (i.e., neither of the objects showed axis-path parallelism). However, the target stimulus was characterised by Re-Alignment of the axis after the trajectory change, Front-Back consistency and a smaller Rotation, whereas the distractor stimulus presented a wider Rotation, but lacked RA and FB.

7.1. Subjects

Seventy-one domestic chicks (33 males) were used for this experiment.

7.2. Stimuli

The target stimulus was the animation used as distractor stimulus in Experiment 2 (stimulus c). The distractor stimulus was formerly used as target stimulus in Experiment 4 (stimulus d).

7.3. Results

No significant preference for any of the two stimuli emerged in the present experiment for either of the dependent variables (mean preference score 0.45, S.E.M. 0.05, $t_{70} = -0.889$, $p = .377$, $d = 0.107$, $Z = 0.767$, $p = .443$; 32 out of 71 chicks approaching the target stimulus first $X^2_1 = 0.690$, $p = .406$, Fig. 1).

7.4. Discussion

The absence of significant preference observed in Experiment 5 cannot be interpreted univocally, since we were not able to reject the null hypothesis. However, we would like to propose some tentative hypotheses, to be tested in future studies. The first issue raised by these results is the absence of significant preference for the properties RA and FB. None of the previous experiments provided us with direct evidence that chicks respond to these two properties, thus we can hypothesize that these features simply do not elicit any social preference in chicks. Alternatively, chicks might be sensitive to RA and/or FB only for objects oriented with their axis parallel to the motion path. The presence of Pa might be a prerequisite for detecting RA or FB, suggesting an internal hierarchy of the factors within the body-plan-constraints cluster.

Another issue concerns the absence of preference for the stimulus displaying the wider rotation. From the results of Experiment 4, we know that chicks are sensitive to this property. However, in the current experiment both stimuli presented some degree of Rot, with a difference of 90° in the amount of Rot between the two. On the contrary, in Experiment 4 the target stimulus involved a 180° rotation, while the distractor stimulus featured no rotation at all. Thus chicks in Experiment 4 might have distinguished the stimuli only in terms of presence *vs.* absence of Rot, without encoding difference in the amount of Rot. Alternatively, chicks may respond to differences in the scope of

the rotational movement only above a certain threshold (e.g., responding only to a minimal difference of 180° or more). Both these scenarios are consistent with the results of Experiments 4 and 5. Finally, the null effect of Experiment 5 may reflect the fact that chicks' preference is driven just as strongly by all the relevant factors in the stimuli: RA, FB on the one hand and degree of Rot on the other. In this case, the opposite effects from the two groups of factors may cancel each other out, resulting in a lack of preference between the stimuli.

8. General discussion

This series of studies tested the role of several behavioural cues to animate agency in eliciting spontaneous social preference among visually naïve newly-hatched chicks. Crucially we focused on cues that had never been tested before in the social domain in animals, but had been found to drive animacy perception in human observers (Tremoulet & Feldman, 2000): three cues reflecting the bilateral body plan's constraints on behaviour (parallelism, re-alignment and front-back consistency), as well as one manifestation of self-propulsion (self-initiated rotational motion). Specifically, we found evidence for the role of parallelism and rotational motion. These results add to the evidence of an innate mechanism for detection of animate agents, shared between phylogenetically distant species (Di Giorgio et al., 2017; Mascalzoni et al., 2010; Reid et al., 2017; Rosa-Salva et al., 2010, 2016; Simion et al., 2008; Sugita, 2008; Vallortigara et al., 2005).

Chicks showed social preference for the object moving along its main body axis. This type of stimulus had been shown to elicit predatory behaviours in anurans (Ewert, 1987), while in chicks preferential pecking responses had been found towards small prey-like objects oriented orthogonally to motion direction (Clara et al., 2009). Our results strongly suggest that the latter finding does not reflect a domain-general preference for orthogonal movement in domestic chicks and it may be specific to the context of chicks feeding on insect-size objects.

Behavioural characteristics associated with the bilateral body plan drive several phenomena in human perception, including animacy attribution (Dolgov, Birchfield, et al., 2009) axis-aligned-motion bias (Dolgov, McBeath, et al., 2009; Jardine & Seiffert, 2011; Morikawa, 1999), forward-facing bias (McBeath et al., 1992; Pavlova et al., 2002) and spontaneous encoding of the front-back orientation of moving agents in human infants (Hernik et al., 2014). Future studies with chicks could investigate if they are also sensitive to other kinematic factors from the body-plan-constraints cluster besides parallelism: front-back consistency and re-alignment. In particular, studies targeting sensitivity to front-back consistency could use stimuli in which the front end of the object is marked by local features that distinguish it from the rest of the object's "body". This may allow the front-back consistency to have greater impact on chicks' behaviour.

This study also offers the first demonstration of a preference for rotational movements, a cue of self-propulsion never investigated before in humans or other animals, even though other conceptually related cues of self-propulsion, such as speed-changes, have been found to affect both (Rosa-Salva et al., 2016; Tremoulet & Feldman, 2000). Together with our previous results (Mascalzoni et al., 2010; Rosa-Salva et al., 2016), chicks' sensitivity to rotation suggests that their mechanisms for animacy recognition might respond to a variety of kinematic patterns associated with self-propulsion. To test whether a single unified general mechanism is involved in the response to the different cues of self-propulsion, or whether different mechanisms are in place for each cue, future studies could map brain activity in groups of chicks exposed to different self-propulsion cues (Lorenzi, Mayer, Rosa-Salva, & Vallortigara, 2017).

Future studies may also address the relationship between self-propulsion cues, such as rotational movements, and motion features associated with the bilateral body plan, such as parallelism. Are their effects independent and additive or interdependent in chicks? How do they affect chick's preferences when pitted against each other and what is their hierarchy, if there is any? In human infants, encoding of the front-back orientation in motion depends on self-propulsion (Hernik et al., 2014). By a similar token, parallelism may affect chicks' preference only for clearly self-propelled objects, as those in the current studies.

Our experiments consistently revealed sensitivity to the motion cues under investigation, indicating the presence of reliable phenomena. Moreover, the degree of preference observed for the target stimuli is remarkably consistent across experiments, suggesting that similar underlying mechanisms are at play. However, it should be noted that the observed measures of effect size are moderate (in the range of $d = 0.24–0.3$, conventionally considered as "small") and the average preference score is around 0.6–0.63 (corresponding to spending on average 60–63% of the time near the target stimulus). These values are consistent with previous studies on spontaneous social predisposition of domestic chicks. While social predispositions can occasionally generate relatively large effect sizes (e.g., Exp. 2 of Rosa-Salva et al. (2016)), moderate effect sizes ($d \simeq 0.19–0.35$), associated with preference ratios ranging from 0.55 to 0.63, are far more common (Mascalzoni et al., 2010; Rosa-Salva et al., 2010, 2016; Vallortigara & Regolin, 2006; Vallortigara et al., 2005).

There are several reasons why moderate effects in the current series of experiments should not be surprising. Our procedure measured spontaneous behaviour and was designed to allow studying effects of individual aspects of the stimuli in isolation. In the natural environment, a multitude of static and dynamic cues of animacy co-occur in the visual information provided by animate social stimuli (mother hen, siblings etc). It is conceivable that the level of attraction of each single property, in isolation, would elicit only a moderate effect on the chicks, since the reliable presence of an adaptive response would be ensured by the summation of the responses to multiple redundant cues provided by natural stimuli. Furthermore, in each of our experiments, *both* the target and the distractor stimulus involved some of the visual properties that are socially preferred by chicks. The objects were always red, had curved outline and size appropriate for eliciting social approach in chicks (all three features favoured by chicks when imprinting on objects, see Rosa-Salva et al., 2015 for a review). Moreover, in each experiments, both stimuli presented some dynamic properties associated with animate agency: spontaneous changes of trajectory (Rosa-Salva et al., 2016; Tremoulet & Feldman, 2000) and motion against gravity (Szego & Rutherford, 2008). The presence of these attractive properties in both stimuli could have masked at least in part the effect of the visual cues under investigation.

Finally, we would like to discuss our results in relation to the conceptual distinction between agency and animacy. Even though in the natural environment animacy and agency are strongly associated, several authors make a conceptual distinction between the two and hypothesize distinct systems for dealing with them (Leslie, 1994). Animacy (also known as 'mechanical agency') manifests itself by self-propulsion (Frankenhuis & Barrett, 2013; Leslie, 1994, 1995; Stewart, 1982 but see Baron-Cohen, 1994; Premack, 1990), whereas agency is characterised by goal directed, efficient behaviour, revealing an agent's volitional control over its own actions (Biro & Leslie, 2007; Csibra, 2008; Frankenhuis & Barrett, 2013; Frankenhuis, House, Barrett, & Johnson, 2013; Johnson, 2003; Johnson, Slaughter, & Carey, 1998; Premack & Premack, 1997; Shimizu & Johnson, 2004).

Intriguingly, infants can attribute goals and intentionality to agents independently from the presence of self-generated movements (Biro, Csibra, & Gergely, 2007; Csibra, 2008; Csibra, Gergely, Bíró, Koós, & Brockbank, 1999; Shimizu & Johnson, 2004, but see Luo & Baillargeon, 2005; Saxe, Tenenbaum, & Carey, 2005). Cues that are directly linked to intentional agency are variability of behaviour, consistent approach of the same goal-object, efficiency (Biro & Leslie, 2007; Csibra, 2008; Premack & Premack, 1997) and contingent reactivity at a distance (Frankenhuis & Barrett, 2013; Frankenhuis et al., 2013; Johnson, 2003;

Johnson et al., 1998; Shimizu & Johnson, 2004, but see Csibra et al., 1999; Gergely, Nádasdy, Csibra, & Bíró, 1995). Chicks of other gallinaceous species show imprinting facilitation for unfamiliar agents displaying contingent reactivity to their calls, suggesting that they are socially attracted by this agentive trait (Harshaw, Tourgeman, & Lickliter, 2008; Ten Cate, 1986).

How do the results of the present study fit in the conceptual landscape created by the animacy-agency distinction? Rot is a cue of self-propulsion and as such can be expected to serve the same functions as other manifestations of self-propulsion, e.g. a spontaneous onset of translational motion. However, it is less clear how the motion properties associated with the constraints of the bilateral body-plan relate to animacy and agency.

On the one hand, behaviours related to bilateral body-plan, are consequences of animal morphology constraining behaviour, as it is also the case for semi-rigid motion. As such they could serve as general visual markers of animacy. They may be neither sufficient nor necessary for processing of the observed behaviour in terms of agency (Biro et al., 2007; Csibra, 2008; Csibra et al., 1999; Gao, McCarthy, & Scholl, 2010; Shimizu & Johnson, 2004; Southgate, Johnson, & Csibra, 2008), but their effects may depend on the presence of other animacy markers, such as self-propulsion (Hernik et al., 2014).

On the other hand, the type of constraints in the two cases (semi-rigid *vs.* bilateral-symmetry-constrained motion) is very different. The jointed skeletal structure of legged vertebrates constraints their movements to semi-rigid motions deterministically, because bones cannot bend during normal course of action. On the contrary, the preferred orientation of the body in motion does not always stem from a mechanical necessity. Many animals can, and occasionally do, choose a non-preferred orientation when moving (e.g. when they walk sideways or backwards). The preferred forward-facing motion along the main body axis minimizes energy expenditure and typically allows for the sensory organs, mouth and prehensile limbs to be directed towards meaningful action targets, such as food. In this sense, parallelism, realignment and front-back consistency can also signal efficiency and choice to maintain a particular orientation during locomotion. Consequently they may be interpreted as behavioural manifestations of agency and volitional control over own behaviour.

However, ultimately the propensity to rely on parallelism and other behaviours related to bilateral body plan as cues to animacy or agency may differ across cognitive systems and depend both on the perceptual and cognitive competencies of the observer and on the prevalent behaviours of agents in the observer's niche. In the present case, we need to be particularly careful in the interpretation of chicks' preferences in terms of animacy or agency attribution. The behavioural tests which have been developed for chicks up till now provide evidence for their preference among different stimuli, typically when they are looking for social companions. We can determine what characteristics chicks find more attractive in a potential imprinting object (Mascalzoni et al., 2010; Rosa-Salva et al., 2016; Ten Cate, 1986; Vallortigara et al., 2005) or a potential snack (Clara et al., 2009). However, we do not know whether sensitivity to such factors plays any role outside these very specific domains, nor in what way the representations behind chicks' responses to such factors may be interrelated. For example, it is unknown if the presence of features revealing self-propulsion in a stimulus causes chicks to expect it to show other animacy-related properties. Upon observing an object start move by itself (Mascalzoni et al., 2010), will chicks expect it to be able to spontaneously change speed or direction (Rosa-Salva et al., 2016)? The same holds true for agency attribution, since it has never been tested whether chicks' form any anticipation about agents' consistency and rationality in pursuing a goal, nor whether this is related to the presence of preferred agentive traits, such as contingent reactivity (Harshaw et al., 2008; Ten Cate, 1986).

Nevertheless, together with earlier findings of social preferences for self-propulsion (Mascalzoni et al., 2010; Rosa-Salva et al., 2016), semi-rigidity (Simion et al., 2008; Vallortigara et al., 2005) and contingent reactivity (Harshaw et al., 2008; Ten Cate, 1986), the current demonstrations of sensitivity to axis-path parallelism and spontaneous rotation suggest a broad preference in naïve newborn chicks for a range of visual features that to human observers are clear manifestations of animacy and agency.

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Authors' contributions

OR-S, MH, and GV designed the study. AB and OR-S created the stimuli. AB run the behavioural experiments. OR-S run the statistical analysis. OR-S and MH wrote the manuscript. GV revised the manuscript. All authors gave final approval for publication.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2018.01.004.

References

Apfelbach, R., & Wester, U. (1977). The quantitative effect of visual and tactile stimuli on the prey-catching behaviour of ferrets (*Putorius furo L.*). *Behavioural Processes, 2*(2), 187–200.

Baron-Cohen, S. (1994). How to build a baby that can read minds: Cognitive mechanisms in mind-reading. *Cahiers de Psychologie Cognitive/Current Psychology of Cognition, 13*, 513–552.

Bateson, P. (1966). The characteristics and context of imprinting. *Biological Reviews, 41*, 177–220.

Biro, S., Csibra, G., & Gergely, G. (2007). The role of behavioral cues in understanding goal-directed actions in infancy. *Progress in Brain Research, 164*, 303–322.

Biro, S., & Leslie, A. M. (2007). Infants' perception of goal-directed actions: Development through cue-based bootstrapping. *Developmental Science, 10*(3), 379–398.

Bolhuis, J. J. (1991). Mechanisms of avian imprinting: A review. *Biological Reviews of the Cambridge Philosophical Society, 66*(4), 303–345.

Clara, E., Regolin, L., Vallortigara, G., & Rogers, L. J. (2009). Chicks prefer to peck at insect-like elongated stimuli moving in a direction orthogonal to their longer axis. *Animal Cognition, 12*(6), 755–765.

Cooper, W. E. (1981). Visual guidance of predatory attack by a scincid lizard, *Eumeces laticeps*. *Animal Behaviour, 29*(4), 1127–1136.

Csibra, G. (2008). Goal attribution to inanimate agents by 6.5-month-old infants. *Cognition, 107*(2), 705–717.

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*(3), 237–267.

Di Giorgio, E., Frasnelli, E., Rosa-Salva, O., Scattoni, M. L., Puopolo, M., Tosoni, D., ... Vallortigara, G. (2016). Difference in visual social predispositions between newborns at low- and high-risk for autism. *Scientific Reports, 6*, 26395.

Di Giorgio, E., Loveland, J. L., Mayer, U., Rosa-Salva, O., Versace, E., & Vallortigara, G. (2017). Filial responses as predisposed and learned preferences: Early attachment in chicks and babies. *Behavioural Brain Research, 325*(Pt B), 90–104.

Di Giorgio, E., Lunghi, M., Simion, F., & Vallortigara, G. (2017). Visual cues of motion that trigger animacy perception at birth: The case of self-propulsion. *Developmental Science, 20*(4), e12394.

Dolgov, I., Birchfield, D. A., McBeath, M. K., Thornburg, H., & Todd, C. G. (2009). Amelioration of axis-aligned motion bias for active versus stationary judgments of bilaterally symmetric moving shapes' final destinations. *Attention, Perception, & Psychophysics, 71*(3), 523–529.

Dolgov, I., McBeath, M. K., & Sugar, T. (2009). Evidence for axis-aligned motion bias: Football axis-trajectory misalignment causes systematic error in projected final destinations of thrown American footballs. *Perception, 38*(3), 399–410.

Ewert, J.-P. (1987). Neuroethology of releasing mechanisms: Prey-catching in toads. *Behavioral and Brain Sciences, 10*(03), 337–368.

Frankenhuis, W. E., & Barrett, H. C. (2013). Design for learning: The case of chasing. In: M. D. Rutherford, & V. A. Kuhlmeier (Eds.), *Social perception: Detection and interpretation of animacy, agency, and intention* (pp. 171–195). Cambridge, Massachusetts: MIT Press.

Frankenhuis, W. E., House, B., Barrett, H. C., & Johnson, S. P. (2013). Infants' perception of chasing. *Cognition, 126*(2), 224–233.

Gao, T., McCarthy, G., & Scholl, B. J. (2010). The wolfpack effect. Perception of animacy irresistibly influences interactive behavior. *Psychological Science, 21*(12), 1845–1853.
Gergely, G., Nádasdy, Z., Csibra, G., & Bíró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition, 56*(2), 165–193.
Harshaw, C., Tourgeman, I. P., & Lickliter, R. (2008). Stimulus contingency and the malleability of species-typical auditory preferences in northern bobwhite (*Colinus virginianus*) hatchlings. *Developmental Psychobiology, 50*(5), 460–472.
Hernik, M., Fearon, P., & Csibra, G. (2014). Action anticipation in human infants reveals assumptions about anteroposterior body-structure and action. *Proceedings Biological Sciences, 281*(1781), 20133205.
Jardine, N. L., & Seiffert, A. E. (2011). Tracking objects that move where they are headed. *Attention, Perception, & Psychophysics, 73*(7), 2168–2179.
Johnson, S. C. (2003). Detecting agents. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358*(1431), 549–559.
Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience, 6*(10), 766–774.
Johnson, S., Slaughter, V., & Carey, S. (1998). Whose gaze will infants follow? The elicitation of gaze-following in 12-month-olds. *Developmental Science, 1*(2), 233–238.
Jones, R. B. (1980). Reactions of male domestic chicks to two-dimensional eye-like shapes. *Animal Behaviour, 28*(1), 212–218.
Knoll, A. H., & Carroll, S. B. (1999). Early animal evolution: Emerging views from comparative biology and geology. *Science, 284*(5423), 2129–2137.
Leslie, A. M. (1994). ToMM, ToBy, and agency: Core architecture and domain specificity. *Mapping the Mind: Domain Specificity in Cognition and Culture*, 119–148.
Leslie, A. M. (1995). A theory of agency. *Causal cognition: A multidisciplinary debate* (pp. 121–141). Oxford, England: Clarendon Press.
Lorenzi, E., Mayer, U., Rosa-Salva, O., & Vallortigara, G. (2017). Dynamic features of animate motion activate septal and preoptic areas in visually naïve chicks (*Gallus gallus*). *Neuroscience, 354*, 54–68.
Luo, Y., & Baillargeon, R. (2005). Can a self-propelled box have a goal? Psychological reasoning in 5-month-old infants. *Psychological Science, 16*(8), 601–608.
Mascalzoni, E., Regolin, L., & Vallortigara, G. (2010). Innate sensitivity for self-propelled causal agency in newly hatched chicks. *Proceedings of the National Academy of Sciences of the United States of America, 107*(9), 4483–4485.
McBeath, M. K., Morikawa, K., & Kaiser, M. K. (1992). Perceptual bias for forward-facing motion. *Psychological Science, 3*(6), 362–367.
McCabe, B. J. (2013). Imprinting. *Wiley Interdisciplinary Reviews: Cognitive Science, 4*(4), 375–390.
Morikawa, K. (1999). Symmetry and elongation of objects influence perceived direction of translational motion. *Perception & Psychophysics, 61*(1), 134–143.
Morton, J., & Johnson, M. H. (1991). CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review, 98*(2), 164.
Pavlova, M., Krägeloh-Mann, I., Birbaumer, N., & Sokolov, A. (2002). Biological motion shown backwards: The apparent-facing effect. *Perception, 31*(4), 435–443.
Premack, D. (1990). The infant's theory of self-propelled objects. *Cognition, 36*(1), 1–16.
Premack, D., & Premack, A. J. (1997). Motor competence as integral to attribution of goal. *Cognition, 63*(2), 235–242.
Reid, V. M., Dunn, K., Young, R. J., Amu, J., Donovan, T., & Reissland, N. (2017). The human fetus preferentially engages with face-like visual stimuli. *Current Biology, 27*(12), 1825–1828 e3.
Rosa-Salva, O., Hernik, M., Broseghini, A., & Vallortigara, G. (2018). Data of Exp. 1–5. Uploaded as supplementary electronic materials in the Journal Cognition.
Rosa-Salva, O., Farroni, T., Regolin, L., Vallortigara, G., & Johnson, M. H. (2011). The evolution of social orienting: Evidence from chicks (*Gallus gallus*) and human newborns. *PLoS ONE, 6*(4), e18802.
Rosa-Salva, O., Grassi, M., Lorenzi, E., Regolin, L., & Vallortigara, G. (2016). Spontaneous preference for visual cues of animacy in naïve domestic chicks: The case of speed changes. *Cognition, 157*, 49–60.
Rosa-Salva, O., Mayer, U., & Vallortigara, G. (2015). Roots of a social brain: Developmental models of emerging animacy-detection mechanisms. *Neuroscience & Biobehavioral Reviews, 50*, 150–168.
Rosa-Salva, O., Regolin, L., & Vallortigara, G. (2010). Faces are special for newly hatched chicks: Evidence for inborn domain-specific mechanisms underlying spontaneous preferences for face-like stimuli. *Developmental Science, 13*(4), 565–577.
Rosa-Salva, O., Regolin, L., & Vallortigara, G. (2012). Inversion of contrast polarity abolishes spontaneous preferences for face-like stimuli in newborn chicks. *Behavioural Brain Research, 228*(1), 133–143.
Saxe, R., Tenenbaum, J. B., & Carey, S. (2005). Secret agents: Inferences about hidden causes by 10- and 12-month-old infants. *Psychological Science, 16*(12), 995–1001.
Schleidt, W., Shalter, M. D., & Moura-Neto, H. (2011). The hawk/goose story: The classical ethological experiments of Lorenz and Tinbergen, revisited. *Journal of Comparative Psychology, 125*(2), 121–133.
Schulman, A. H., Hale, E. B., & Graves, H. B. (1970). Visual stimulus characteristics for initial approach response in chicks (*Gallus domesticus*). *Animal Behaviour, 18*, 461–466.
Shimizu, Y., & Johnson, S. C. (2004). Infants' attribution of a goal to a morphologically unfamiliar agent. *Developmental Science, 7*(4), 425–430.
Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States of America, 105*(2), 809–813.
Smith, S. M. (1973). A study of prey-attack behaviour in young loggerhead shrikes, *Lanius ludovicianus* L. *Behaviour, 44*(1/2), 113–141.
Southgate, V., Johnson, M. H., & Csibra, G. (2008). Infants attribute goals even to biomechanically impossible actions. *Cognition, 107*(3), 1059–1069.
Stewart, J. A. (1982). *Perception of animacy*. Philadelphia, PA: University of Pennsylvania.
Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *Proceedings of the National Academy of Sciences of the United States of America, 105*(1), 394–398.
Szego, P. A., & Rutherford, M. D. (2008). Dissociating the perception of speed and the perception of animacy: A functional approach. *Evolution and Human Behavior, 29*(5), 335–342.
Ten Cate, C. (1986). Does behavior contingent stimulus movement enhance filial imprinting in Japanese quail? *Developmental Psychobiology, 19*(6), 607–614.
Tremoulet, P. D., & Feldman, J. (2000). Perception of animacy from the motion of a single object. *Perception, 29*(8), 943–951.
Vallortigara, G. (2012). Core knowledge of object, number, and geometry: A comparative and neural approach. *Cognitive Neuropsychology, 29*(1–2), 213–236.
Vallortigara, G. (2012). Aristotle and the chicken: Animacy and the origins of beliefs. *The theory of evolution and its impact* (pp. 189–199). Springer.
Vallortigara, G., & Regolin, L. (2006). Gravity bias in the interpretation of biological motion by inexperienced chicks. *Current Biology, 16*(8), R279–R280.
Vallortigara, G., Regolin, L., & Marconato, F. (2005). Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLoS Biology, 3*(7), e208.
Versace, E., Fracasso, I., Baldan, G., Dalle Zotte, A., & Vallortigara, G. (2017). Newborn chicks show inherited variability in early social predispositions for hen-like stimuli. *Scientific Reports, 7*, 40296.
Versace, E., Schill, J., Nencini, A. M., & Vallortigara, G. (2016). Naïve chicks prefer hollow objects. *PLoS ONE, 11*(11), e0166425.
Versace, E., & Vallortigara, G. (2015). Origins of knowledge: Insights from precocial species. *Frontiers in Behavioral Neuroscience, 9*, 338.
Vidal, J.-M. (1980). The relations between filial and sexual imprinting in the domestic fowl: Effects of age and social experience. *Animal Behaviour, 28*(3), 880–891.