

Original Articles

Spontaneous preference for visual cues of animacy in naïve domestic chicks: The case of speed changes

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ABSTRACT

Animacy perception arises in human adults from motion cues implying an internal energy source to the moving object. The internal energy of the object is often represented by a change in speed. The same features cause preferential attention in infants. We investigated whether speed changes affecting adults' animacy ratings elicit spontaneous social preferences in visually-naïve chicks. Human observers evaluated the similarity between the movement of a red blob stimulus and that of a living creature. The stimulus entered the screen and moved along the azimuth; halfway through its trajectory it could either continue to move at a constant speed or linearly increase in speed. The average speed, the distance covered and the overall motion duration were kept constant. Animacy ratings of humans were higher for accelerating stimuli (Exp. 1). Naïve chicks were then tested for their spontaneous preference for approaching the stimulus moving at a constant speed and trajectory or an identical stimulus, which suddenly accelerated and then decelerated again to the original speed. Chicks showed a significant preference for the 'speed-change stimulus' (Exp. 2). Two additional controls (Exp. 3 and 4) showed that matching the variability of the control 'speed-constant' stimulus to that of the 'speed-change stimulus' did not alter chicks' preference for the latter. Chicks' preference was suppressed by adding two occluders on both displays, positioned along the stimulus trajectory in such a way to occlude the moment of the speed change (Exp. 5). This confirms that, for chicks to show a preference, the moments of speed change need to be visible. Finally, chicks' preference extended to stimuli displaying a direction change, another motion cue eliciting animacy perception in human observers, if the speed- and direction-profile were consistent with each other and resembled what expected for biological entities that invert their motion direction (Exp. 6). Overall, this is the first demonstration of social predispositions for speed changes in any naïve model or non-human animal, indicating the presence of an attentional filter tuned toward one of the general properties of animate creatures. The similarity with human data suggests a phylogenetically old mechanism shared between vertebrates. Finally, the paradigm developed here provides ground for future investigations of the neural basis of these phenomena.

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1. Introduction

Since the seminal works of Heider and Simmel (1944) and of Michotte (1963), scholars of cognitive sciences have been fascinated by the perceptual phenomena elicited by simple cartoon animations displaying two-dimensional shapes moving in various ways on a homogeneous background. Observers presented with these stimuli typically report the perception of 'functional relations' that are not present in the actual events (e.g., the red square 'pushes away' the blue one 'causing' its movement; the small circle

is 'escaping' from the big triangle, etc.). Over the decades, a number of studies revealed that some kinematic patterns elicit fast, automatic, stimulus driven and 'irresistible' impressions of causality, animacy, agency and goal directed-behaviour; all concepts typically associated with higher order cognitive functions rather than with perceptual phenomena (Scholl & Tremoulet, 2000). Moreover, human infants and even newborns preferentially attend to some of the patterns that elicit the perception of causality, animacy or agency in adults (Di Giorgio, Lunghi, Simion, & Vallortigara, 2016; Frankenhuis & Barrett, 2013; Frankenhuis, House, Barrett, & Johnson, 2013; Mascalzoni, Regolin, Vallortigara, & Simion, 2013). In other cases, the presence of certain motion cues seems to guide infants' categorisation of visual objects (e.g., as animate creatures

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and as intentional agents) and their expectations on objects' future behaviour (e.g., goal-directed rational behaviour; Csibra, 2008; Luo, 2011; Luo & Baillargeon, 2005; Luo, Kaufman, & Baillargeon, 2009; see also Uller and Nicols, 2000 in chimpanzees). This has been interpreted as reflecting a series of implicit assumptions that are hard-wired into the visual system and that inform its operations, supporting the interpretation of the world in terms of animate and inanimate entities (Scholl & Tremoulet, 2000).

The automatic and irresistible nature of animacy perception raises questions on its domain specificity, level of modularity or encapsulation and, especially, its developmental and phylogenetic origins. In the last years, the comparative study of human newborns' visual attention and of visually naïve animals' spontaneous social preferences was applied to tackle similar questions in the cases of face and semi-rigid biological motion perception (Rosa-Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011; Rosa-Salva, Mayer, & Vallortigara, 2015; Rosa-Salva, Regolin, & Vallortigara, 2010; Simion, Regolin, & Bulf, 2008; Vallortigara & Regolin, 2006; Vallortigara, Regolin, & Marconato, 2005). The use of animal models allows both to uncover the phylogenetic history of a given trait and to assess claims on its innate versus cultural origin (Carey, 2009; Spelke, 2000; Spelke & Kinzler, 2007; Vallortigara, 2012). Moreover, the use of newly hatched offsprings of a precocial bird species (the domestic chicken) has an additional advantage for the questions at hand, namely the possibility to effectively control for previous visual experience, and to do so without creating abnormal developmental trajectories. This is not feasible working on altricial species (such as human and non-human primates), despite the efforts undertaken by researchers working with these models (e.g., Sugita, 2008).

One of the most relevant aspects of animacy perception is that extremely simple stimuli can elicit the impression of animacy. Typically, the earlier researches in this field used relatively complex displays that involved the interaction between multiple moving shapes and environmental elements (obstacles, boundaries). This highlighted the role of the spatiotemporal contingencies in the motion of different visual objects and in relation to the spatial configuration of the environment (e.g., Bassili, 1976; Dittrich & Lea, 1994; Gelman, Durgin, & Kaufman, 1995). Among those earlier researchers, Stewart (1982) hypothesised that animacy would be perceived in response to motions implying an internal energy source to the moving object, such as starts from rest (in which an object starts to move autonomously as opposed to being put in motion by physical contact with another object) (see also Abrams & Christ, 2003). Subsequent works, however, seemed to indicate that animacy perception depended on the interplay between the kinematic pattern of the moving stimulus and the spatial configuration of the surrounding environment (Gelman et al., 1995). A complication in the interpretation of this first wave of studies was that the displays used tended to involve relatively complex trajectories and/or environments. More recently, researches set out to disentangle the specific motion cues that mediate perceptual animacy using simple schematic displays that satisfy the 'visual system's assumptions' in the most minimal possible way. In a seminal study, Tremoulet and Feldman (2000) studied perceived animacy by presenting a single visual object moving on a homogeneous background and found that animacy was associated with changes in speed (specifically, accelerations) and changes in trajectory (in relation also to the orientation of the object's main axis). "Starts from rest" were not tested in this study, because the stimulus "entered the screen" already in motion. Subsequent research replicated and extended these findings: human adults consistently attribute higher animacy to single shapes moving against gravity and changing autonomously speed or direction of motion; for stimuli moving at a constant speed, the higher the speed, the higher the animacy attribution (Abrams

& Christ, 2003; Gyulai, 2004; Szego & Rutherford, 2007, 2008). Frankenhuys et al. (2013) recently attempted to bridge the gap between studies using relatively complex displays with multiple moving objects or obstacles and studies that try to describe the elementary motion properties associated with animacy. Complex displays representing one visual object "chasing" another one, who is fleeing away, have been often used in the study of perceptual animacy (Csibra, Bíró, Koós, & Gergely, 2003; Gao, Newman, & Scholl, 2009; Rochat, Morgan, & Carpenter, 1997). Instances of chasing elicit strong impressions of animacy and agency in adults and are preferentially looked at by infants as young as 3 months of age (for a review see Frankenhuys & Barrett, 2013). However, a number of kinematic parameters characterized chasing scenes (presence of sudden accelerations, frequent changes in trajectories, and a specific relation between the movements of the two visual objects), making it difficult to disentangle the role of the single elementary motion properties. Frankenhuys and colleagues approached this issue by testing preferential looking for displays with the individual constitutive properties of chasing, as well as their combination (chasing), in 4- and 10-month olds. Preferential attention to the complex full-blown chasing display resulted to depend mostly (82–100% of the effect size) on the presence of repeated accelerations, and to a minor degree on the correlation between the trajectories of the two visual objects; on the contrary, high turning rates did not seem to contribute significantly to infants' preferences.

An important distinction that emerges from most recent studies in this field is that between cues that determine the attribution of animacy (characterising entities with an internal energy source for self-propelled motion, which may also allow them to be mechanical/causal agents), from those that determine the attribution of intentional agency (entities capable of goal directed, efficient and rational actions). Attribution of animacy is supposed to be operated by the core-system for physical reasoning, based on the presence of motion features indicating an internal energy source. Independent mechanisms belonging to the core-domain of naïve psychology would be responsible for the attribution of agency, when an object provides evidence that it has autonomous control over its actions, for example by responding contingently to events or environmental constraints (Carey, 2009; Spelke, 2000; Spelke & Kinzler, 2007). In the present paper we specifically concern ourselves with animacy, that is the property of being alive and distinguishes an animate creature endowed with an internal energy source from an inanimate object that can move only when an external force is applied to it. For further discussion on other related constructs (e.g. intentional agency) we refer the reader to the literature illustrating the conceptual distinction between animacy, physical or causal agency, intentionality, etc. (e.g., see Baron-Cohen, 1994; Frankenhuys & Barrett, 2013; Leslie, 1994, 1995; Premack, 1990; in particular, for the discussion on the dissociation between self-propulsion cues and goal attribution see Biro & Leslie, 2007; Csibra, 2008; Csibra, Gergely, Bíró, Koós, & Brockbank, 1999). However, even though animacy and agency are two independent concepts, they should not be considered mutually exclusive or operated by antagonist processes, since the two properties usually co-occur in the same entities in the natural environment and can be disentangled only by careful experimental manipulations.

In the present work we apply the "minimal" approach of Tremoulet and Feldman (2000) to the study of social predisposition in naïve domestic chicks (*Gallus gallus*), by focusing on the role of changes in the speed of motion of a single visual object. Chicks of gallinaceous birds have already demonstrated a set of predispositions that favour approach to, and/or subsequent filial imprinting on, appropriate social partners. In the absence of any visual experience, chicks seem to be attracted by visual stimuli whose features are typical of animate creatures (for a review see Rosa-Salva et al.,

2015). Motion per se is already effective in attracting chicks' attention and in producing imprinting; however not all kinds of motion are equally attractive. As mentioned above, naïve chicks prefer to approach point-light-displays of biological semi-rigid motion over rigid or random motion (Vallortigara et al., 2005). Also, preferential imprintability was demonstrated in quails for objects moving contingently to the calls emitted by the chick, with respect to identical objects whose movement was not related to chicks' calls (Ten Cate, 1986). More recently, dark-hatched chicks revealed preferential imprintability for visual objects displaying self-produced motion (Mascalzoni, Regolin, & Vallortigara, 2010). Chicks were first exposed to a movie of the classical Michotte launching effect, featuring two shapes of different colours, one appearing self-propelled (spontaneously starting to move from a resting state), the other apparently put in motion by the push from the first object. In a subsequent choice test, in which both objects appeared to be moving autonomously back and forth, chicks preferred to approach the formerly self-propelled stimulus, an indication that they imprinted on it rather than on the other during the exposure to the launching scene. However, it is not known whether chicks are sensitive to other elementary motion cues that elicit animacy perception in humans, beside start from rest, and whether this sensitivity might be detected by a direct test of spontaneous preference (without the need to test for differential imprintability). Here, for the first time, we investigated naïve animals' unlearned preferences for an elementary motion cue of animacy, implemented in the motion of a single visual object, without any interaction with other objects. Given the recent evidence that speed-changes determine infants' visual preferences in complex displays (Frankenhuis et al., 2013), it is of particular relevance to study the response to this motion feature in a naïve model system. The investigation of these phenomena in animal models is particularly informative for crucial questions in cognitive sciences; namely the origins of sensitivity to animacy cues and its neural correlates. By employing domestic chicks as an animal model we can disentangle the role of inborn and experience-dependent factors in sensitivity to animacy cues. Moreover, we open the way for future investigations on the neural correlates of this phenomenon, which could take advantage of invasive procedures not available in humans (e.g., immunohistochemical procedures or in situ hybridization procedures for the staining of immediate early genes' products, electrophysiological recording of neural activity, brain lesioning).

2. General materials and methods

2.1. Subjects

Subjects were domestic chicks (*Gallus gallus domesticus*) of the "Hybro" strain (a local strain derived from the White Leghorn breed). Fertilized eggs were obtained from a commercial hatchery (Agricola Berica, Montegalda, VI, Italy). During incubation and hatching eggs and chicks were maintained in complete darkness, preventing any visual experience prior to the test. Each chick was tested only once. After testing chicks were immediately caged in groups with food and water available ad libitum, at constant temperature 32.3 °C and variable light conditions following the natural sequence of day and night. Soon afterwards chicks were donated to local farmers.

2.2. Apparatus

The test apparatus was a white corridor (85 × 30 × 30 cm) open at the two ends to allow the insertion of two video screens (LCD Monitor BenQ XL2410T), which showed the experimental stimuli. The corridor was virtually divided in three sectors: a central sector

(45 cm long), equidistant from the two sides of the corridor, and two identical lateral sectors (each 20 cm long), adjacent to the two screens. The central sector was delimited by two steps 1.5 cm high, which the animals had to climb to enter the lateral sectors. A video-camera was placed above the apparatus, recording the animals' behaviour during the test. The camera was connected to a monitor screen in the same room, enabling the experimenter to score behaviour on-line during the test. The only illumination to the apparatus was given by the two screens playing the video-stimuli.

2.3. Test stimuli

Stimuli were video-animations representing the movement of a simple shape, created using MATLAB R2012b with the Psychtoolbox-3 extensions (Kleiner, Brainard, & Pelli, 2007). Each test trial lasted for 6 min, during which two motion patterns were presented in loop on the two screens. Each motion-loop represented a red round-shaped stimulus moving linearly on a dark background (see Fig. 1). The portion of the screen visible to the animals (30 cm long) was delimited by a grey U-shaped frame, consisting of two lateral walls (each 3 cm wide, but located on the screen so as to occupy only 2.5 cm of visible screen space) and a floor, over which the red stimulus was moving (the visible trajectory of the red stimulus motion was thus 24.6 cm long). The red stimulus always entered the observer's view already in motion, appearing from behind one of the lateral grey walls. Similarly, once completed its motion, the red stimulus disappeared from view while still moving, slipping behind one of the lateral grey walls.

In each experiment two stimuli were presented simultaneously at the two ends of the corridor. One stimulus was always characterized by the presence of visible speed-changes during his trajectory on the screen, whereas the other moved at a constant speed. The side screen of presentation of the two stimuli was randomized between subjects.

2.4. Procedure

The test was run between the first day and the morning of the third day after hatching. Each subject was individually extracted from the incubator in complete darkness and carried, in a closed box, 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. Each subject's behaviour was recorded for six minutes. If the chick remained in the central sector, this indicated no choice, whereas entrance and permanence of the chick in one of the two lateral sectors was regarded as a preference for the stimulus placed at that side of the runway. A computer-driven event recorder allowed the experimenter to score the time (in seconds) spent by the chick in each of the three areas during the overall test period. 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 speed-change stimulus over the total choice time (i.e. an index representing the ratio of time spent by the subject in the lateral sector near the speed-change stimulus, during the whole test duration, with respect to the time spent in both lateral sectors) calculated with the formula:

$$\frac{\text{time spent near the speed-change stimulus}}{\text{time spent near the speed-change stimulus} + \text{time spent near the speed-constant stimulus}}$$

Values of this ratio could range from 0 (full choice for the speed-constant stimulus), to 1 (full choice for the speed-change stimulus), whereas 0.5 represented the absence of preference.

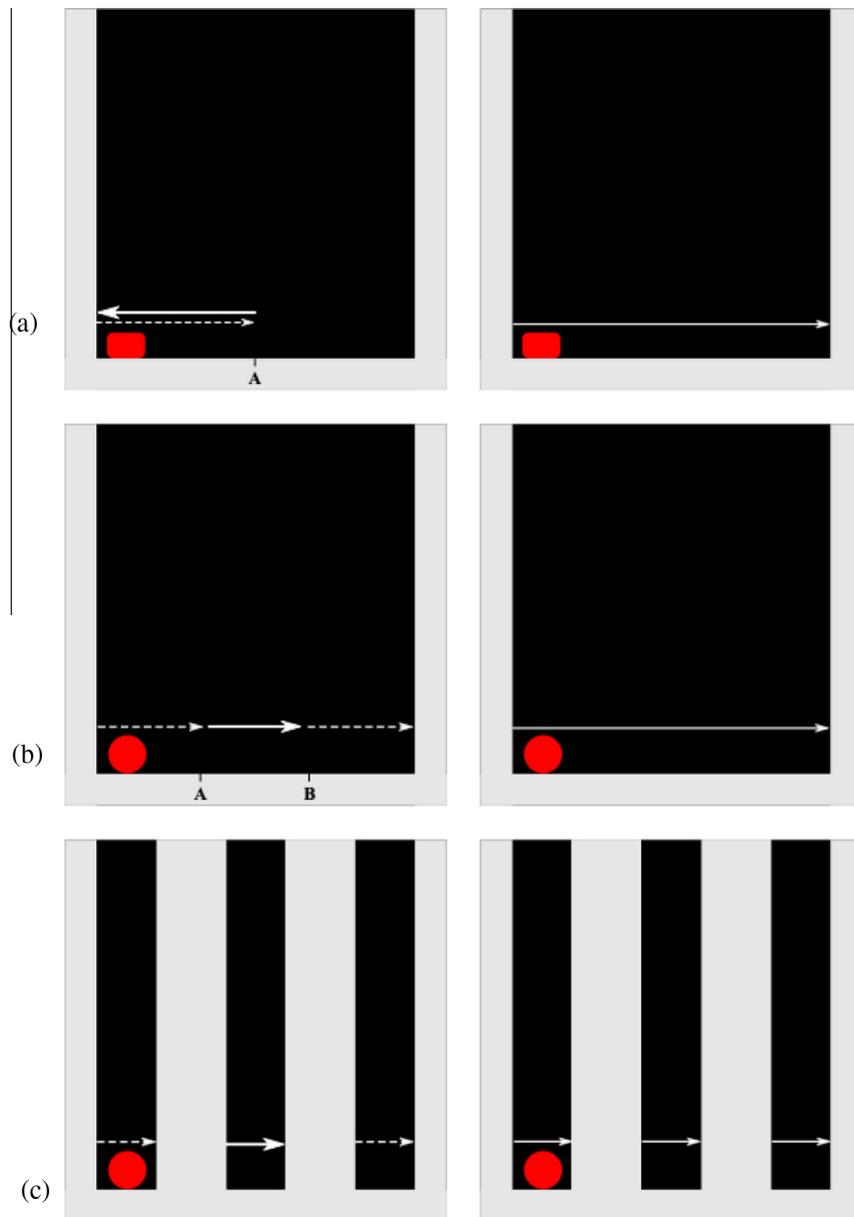


Fig. 1. Schematic representation of the stimuli used in Exp. 1 (panel a), in Exp. 2 (panel b) and in Exp. 5 (panel c). The speed-change (or speed-and-direction-change, for Exp. 1a) stimulus is always represented on the left and the speed-constant stimulus on the right. For Exp. 1 the point of visible speed and trajectory change is marked by the capital letter A. For Exp. 2 the two points of speed changes are marked by A and B (in Exp. 5 there are no points of visible speed changes, due to the additional occluders). The arrows represent the direction and the speed of motion of the red object for the represented motion cycle. Dotted arrows represent the lower speed, followed by solid thinner arrows, whereas the solid thicker arrow represents the faster speed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

All measures were scored online, but a 10% of all subjects were scored again offline by a second blind experimenter (unaware of the position of the two stimuli in the apparatus), in order to evaluate the inter-coder reliability (i.e. the correlation between the two coders). Overall we recoded videos of 30 animals randomly chosen from all the experiments, obtaining a Pearson's correlation of 0.987, $p < 0.001$ between the ratio calculated based on the original and on the offline coding.

2.5. Data analysis

The number of chicks that first approached the speed-change or the speed-constant stimulus was compared with the chi-square test of independence. The ratio of time spent near the speed-

change stimulus over the total test time was compared to what expected by chance (0.5) by a one-sample two-tailed *t*-test.

3. Experiment 1a

In this first experiment we contrasted chicks' preference for a display in which a single stimulus simultaneously displayed a change in speed and an inversion of motion direction ('speed-and-direction-change stimulus'), with respect to another in which the stimulus moved at a constant speed along a linear trajectory ('constant stimulus'). The rationale was to incorporate in the first stimulus both motion cues that, in previous research, increased animacy perception in human observers (Tremoulet & Feldman, 2000).

3.1. Subjects

Sixty-four domestic chicks (32 males) were used for this experiment.

3.2. Stimuli

In Experiments 1a and 1b the red moving stimulus was of rectangular shape, with rounded corners (3 × 2 cm). The stimulus moved along the direction of its longer axis. Each cycle of motion lasted for 6 s.

The two motion patterns for which chicks' preference was tested were the following. In the constant display, the red stimulus crossed the screen (e.g., from behind the left wall to behind the right wall) with constant speed. In the speed-and-direction-change display, the red stimulus moved with constant speed up to the middle of the screen where it reversed its motion. At the reversal the stimulus moved at constant acceleration (see Fig. 1a). Thus, in the speed-and-direction-change display the red stimulus employed 4.5 s to reach the middle of the screen, and

1.5 s to complete its motion in the opposite direction. The side of appearance/disappearance of the red stimulus (from the left or the right lateral wall) was counterbalanced between subjects.

For each of the two motion patterns, two types of loops were created. In one type, the motion pattern started always from the same side-wall. In the other type, the starting sides were interleaved. Each chick was tested for its preference between a constant and a speed-and-direction-change stimulus. The two types of loops were combined with the stimuli in so that for half of the subjects only the speed-and-direction-change stimulus was characterized by object constancy of the red shape (i.e., the red shape disappeared in one side and reappeared from the same side at the beginning of the next cycle). For the other half of the subjects the red moving shape was never characterized by object constancy (it disappeared on one side of the screen and reappeared from the other side in the next cycle). This was done to assess whether chicks would react differently to stimuli that presented object constancy. However, preliminary analyses revealed that this did not affect chicks' behaviour. Thus, the data from conditions with or without object constancy were pooled together in all further analyses.

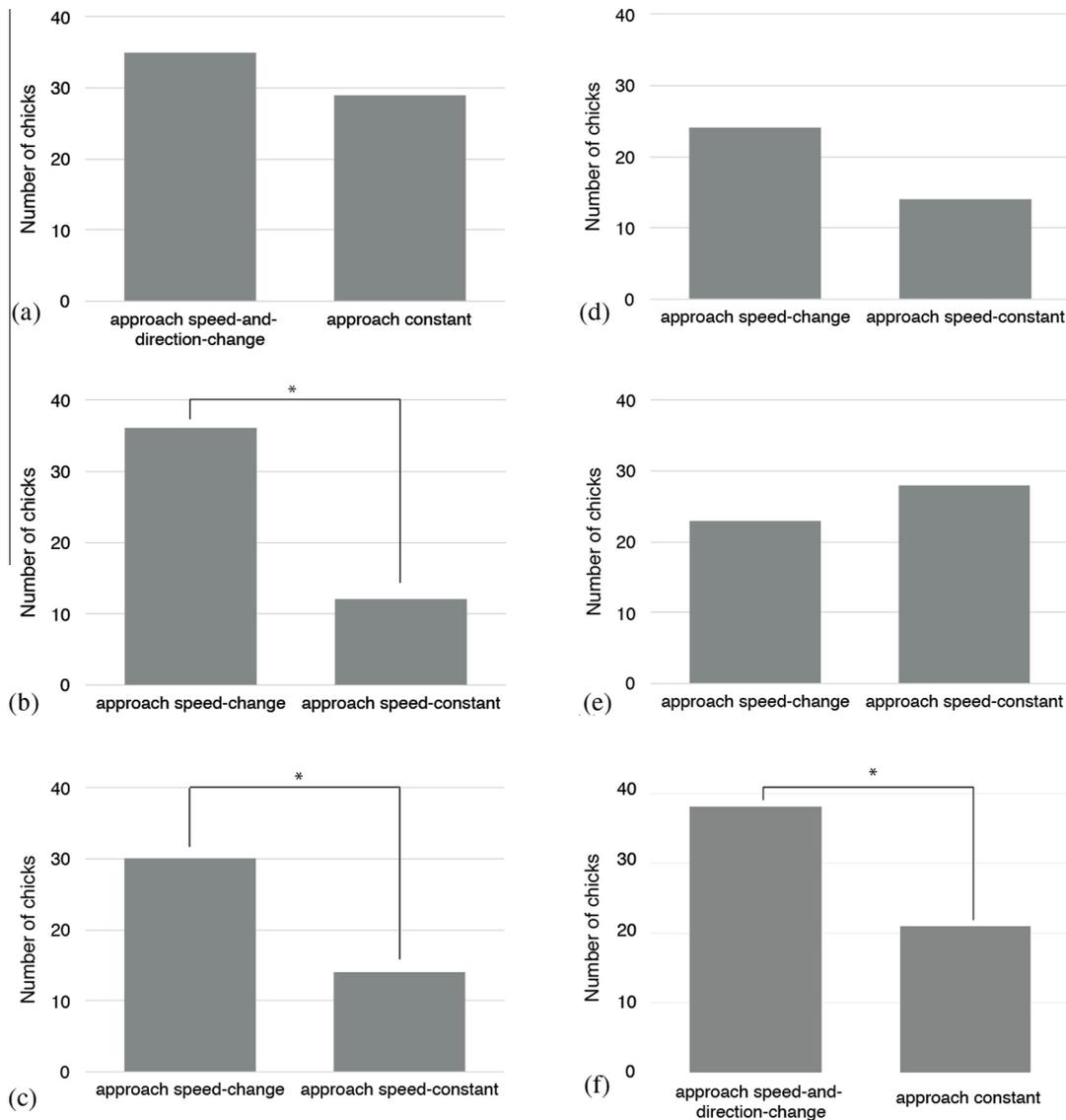


Fig. 2. Results for the dependent variable first stimulus approached for (a) Exp. 1a; (b) Exp. 2; (c) Exp. 3; (d) Exp. 4; (e) Exp. 5; (f) Exp. 6. The number of chicks is represented on the Y-axis, the left and right columns represent respectively the approach for the speed-change (speed-and-direction-change, for Exp. 1a and 6) and for the speed-constant (or constant, for Exp. 1a and 6) stimulus. Asterisks indicate significant differences ($\alpha = 0.05$).

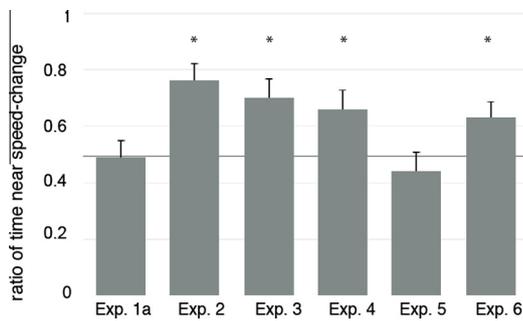


Fig. 3. Mean proportion of choice time spent by chicks near the speed-change (or speed-and-direction-change, for Exp. 1a and 6) stimulus in Exp. 1a, 2, 3, 4, 5 and 6. Asterisks indicate significant ($\alpha = 0.05$) departures from chance level, which is marked by the grey line at 0.5. Error bars represent the standard error of the mean.

3.3. Results

No significant preference for the speed-and-direction-change stimulus emerged, neither for the first stimulus approached (35 chicks approached the speed-and-direction-change stimulus, 29 the constant stimulus, $X^2_1 = 0.563$, $p = 0.453$, see Fig. 2a) nor for the ratio of time spent near the speed-and-direction-change stimulus (mean = 0.49, S.E.M. = 0.06, $t_{63} = -0.1$, $p = 0.921$, $d = 0.02$, see Fig. 3).

4. Experiment 1b

In Exp. 1a we were unable to demonstrate a significant preference for any of the two stimuli, even though we manipulated motion cues that, at least in human adults, should affect animacy perception. To interpret these results, in Exp. 1b we tested with adult observers how the perception of animacy in our stimuli was affected by the different motion cues that we manipulated in Exp. 1a (i.e., change in speed, change in motion direction and object constancy).

4.1. Subjects

Twenty adult participants (10 males mean age \pm S.E.M. 24.5 ± 3.6) participated to this experiment.

4.2. Procedure

In an initial familiarization phase the participant was asked to observe each of the video-stimuli, presented in random order. This provided a first general impression to what s/he would watch and judge after. Successively, the participant was told that s/he would be shown videos similar to those watched before. At the end of each video the participant gave a judgment of similarity between the movement of the red stimulus and the movement of an

unspecified living organism, using a 0–10 scale (0 = minimal similarity, 10 = maximal similarity). Every single video was shown four times to each participant. Videos were presented in random order.

4.3. Stimuli

Stimuli were similar to those of Exp. 1a. There were four types of motion patterns showing the red stimulus moving on the screen (Table 1). Again, all motion patterns lasted 6 s. In the first ('constant'), the red stimulus moved forward with constant speed starting from behind one of the two side-walls (e.g., left) and stopping behind the opposite wall. In the second ('speed-change'), the stimulus moved along the same path, however, in the first half of the path it moved at a constant speed, in the second part of the path it moved at a constant acceleration. In the third motion pattern ('direction-change'), the stimulus moved forward, starting from behind one of the two side-walls up to the middle of the path where it abruptly reversed the direction of motion and moved backward to the starting point, disappearing behind the side wall. The speed of the stimulus in both directions was constant. In the last motion pattern ('speed-and-direction-change'), the red stimulus reversed abruptly the direction of motion, however, before the reversal its speed was constant, whereas after the reversal it moved with constant acceleration. Each motion pattern was shown in a loop of four repetitions separated by a 1 s pause. For each motion pattern two types of loops were created. In the first type ('loop 1', see Table 1), the motion pattern started always from the same side-wall. In the other type ('loop 2'), the starting sides were interleaved. In synthesis, with the above stimuli we were manipulating three parameters: change in speed (no change vs acceleration); change in direction of motion (present vs absent); object constancy (present in those loops where the stimulus disappears on one side and reappears from the same side, or absent when it reappears from the opposite side), according to a $2 \times 2 \times 2$ design summarised in Table 1.

4.4. Results

A repeated measures ANOVA was calculated with *change in direction*, *change in speed* and *object constancy* as within subjects factors. The main effect of *change in speed* was significant ($F_{(1,19)} = 11.872$, $p = 0.003$, $\eta^2_p = 0.385$); all other main effects or interactions were not significant (main effect of *change in direction* $F_{(1,19)} = 0.735$, $p = 0.402$; main effect of *object constancy* $F_{(1,19)} = 0.544$, $p = 0.470$; *change in direction * change in speed* $F_{(1,19)} = 0.897$, $p = 0.356$; *change in direction * object constancy* $F_{(1,19)} = 0.097$, $p = 0.759$; *change in speed * object constancy* $F_{(1,19)} = 1.122$, $p = 0.303$; three-way interaction $F_{(1,19)} = 0.003$, $p = 0.959$). Animacy ratings were thus significantly affected by the presence of speed changes only, regardless of the presence of changes in motion direction and of object constancy. In particular, animacy ratings given by human observers were higher when the

Table 1
Summary of the properties of the eight stimuli employed in Exp. 1b, obtained by the combination of four motion patterns with two loop types.

Motion pattern	Loop type	Speed-change	Direction-change	Object constancy
Constant	1	No change	Absent	Absent
	2	No change	Absent	Present
Speed-change	1	Acceleration	Absent	Absent
	2	Acceleration	Absent	Present
Direction-change	1	No change	Present	Absent
	2	No change	Present	Present
Speed-and-direction-change	1	Acceleration	Present	Absent
	2	Acceleration	Present	Present

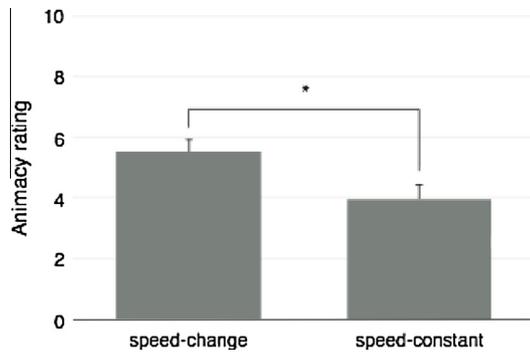


Fig. 4. Mean animacy ratings provided by adult observers to speed-change stimuli (on the left) and to speed-constant stimuli (on the right). Error bars represent the standard error of the mean. The asterisk indicates a significant main effect of the factor speed change ($\alpha = 0.05$).

stimulus displayed a speed change than when speed was constant (mean rating for speed changes = 5.529, S.E.M. = 0.427; mean rating for constant speed = 3.954, S.E.M. = 0.483, see Fig. 4).

5. Experiment 2

In the Exp. 1a we did not observe any significant preference for one of the two stimuli in chicks. Validation of the stimuli by human adults surprisingly revealed that only changes in speed increased the perceived animacy, whereas changes in motion direction were not effective (Exp. 1b). Thus, in Exp. 2 we tested chicks with a new pair of stimuli, in which the “animate” stimulus presented only speed changes, without any change in motion direction. As in Exp. 1a, in the control display the red stimulus moved at a constant speed and direction (i.e., along a linear trajectory). In order to maximise the effectiveness of this contrast we introduced two consecutive speed changes (an abrupt acceleration, followed by a sudden deceleration). This motion pattern, called “jump”, was shown to be particularly effective in eliciting animacy perception in human adults (Gyulai, 2004). Moreover, in the present experiment the red stimulus had a circular shape, rather than an elongated one. This was done in order to prevent any effect of the alignment between the object’s main symmetry axis and the direction of motion (see Tremoulet & Feldman, 2000). The rationale was the following: it is possible that even in the absence of direction changes, the fact that an object’s main symmetry axis is aligned with the motion direction contributes to the perception of animacy. If both stimuli presented in one experiment would share this feature, this could mask or weaken the effect of the other manipulation on which we decided to concentrate in Exp. 2–5 (presence of speed changes). The use of a circular shape was aimed at preventing this potential confound.

5.1. Subjects

Forty-eight domestic chicks (24 males) were used for this experiment.

5.2. Stimuli

In Experiments 2–5 the red stimulus was of circular shape (rather than elongated as in Experiments 1a and 1b) (diameter 3 cm) to neutralize any interaction between the direction of motion of the object and its orientation. Moreover, the stimulus always moved along a constant trajectory (never changing its motion direction). The only difference between the stimuli presented at the two sides of the corridor was that, while they both

moved at the same average speed, one always moved at a constant speed (~ 4.64 cm/s on our monitors), whereas the other displayed two changes in speed, abruptly accelerating at one third of its trajectory and decelerating back to the original speed at two thirds of the way (the slower and the faster speed being, respectively, of ~ 3.37 and ~ 19.64 cm/s, with a slower-to-faster speed ratio of ~ 0.171) (see Fig. 1b). In this and the following experiments, the two stimuli were called respectively ‘speed-constant’ stimulus and ‘speed-change’ stimulus.

5.3. Results

Chicks showed a clear preference for the speed-change stimulus, which was significant for both the dependent variables considered: the first stimulus approached (36 chicks approached the speed-change stimulus, 12 the speed-constant stimulus, $X^2 = 12$, $p = 0.001$, see Fig. 2b) and the ratio of time spent near the speed-change stimulus over the total choice time (mean = 0.76, S.E.M = 0.06, $t_{47} = 4.296$, $p < 0.001$, $d = 0.62$, see Fig. 3).

6. Experiment 3

In the previous experiment we demonstrated a significant preference for the stimulus presenting visible speed changes. However, the two stimuli did not differ only in the presence of visible speed changes, but also in the overall variability of each display. By virtue of the changes in speed, one of the two stimuli was also intrinsically more variable than the other, characterized by constant speed. In order to circumvent this problem, in Exp. 3 we employed the same speed-change stimulus of Exp. 2, paired with a new control speed-constant stimulus. In this new control display the red stimulus was still moving at a constant speed for the whole length of its trajectory, but alternating two different speeds in subsequent cycles. That is to say that when traveling in one direction (e.g., appearing from behind the left lateral wall and disappearing behind the right one) the stimulus was moving at a constant slow speed. Then, when it appears again from behind the right occluder the stimulus is traveling back in the opposite direction at a constant speed, which is faster than the previous one, and so on. Again, the average speed over a whole presentation was identical for the two stimuli.

6.1. Subjects

Forty-four domestic chicks (23 males) were used for this experiment.

6.2. Stimuli

The speed-change stimulus was that of Exp. 2 and the speed-constant stimulus alternated 2 different speeds (~ 6.99 and 3.48 cm/s, with a slower-to-faster speed ratio of ~ 0.50), while maintaining the average speed over one cycle identical in the two stimuli. After completing the movement in one direction the red stimulus remained hidden behind the lateral occluder for additional 1 s, before resuming motion in the opposite direction.

6.3. Results

Again, chicks revealed a significant preference for the stimulus displaying speed changes, confirming and extending the results of Exp. 2. This was evident both when considering the first stimulus approached (30 chicks approached the speed-change stimulus, 14 the speed-constant stimulus, $X^2 = 5.818$, $p = 0.016$, see Fig. 2c) and when considering the ratio of time spent near the speed-change

stimulus over the total choice time ($M = 0.70$, $S.E.M. = 0.07$, $t_{43} = 2.921$, $p = 0.006$, $d = 0.44$, see Fig. 3).

7. Experiment 4

The aim of this fourth experiment was to control, in a more stringent way, for the role of stimulus variability in chicks' preferences. Exp. 3 demonstrated that the presence of speed alternation per se was not sufficient to explain chicks' predisposition to approach the speed-change stimulus. In fact, also in the control speed-constant stimulus two different speeds were alternated, increasing its perceptual variability. Despite that, chicks were more attracted by the speed-change display, in which the acceleration and deceleration occurred along the visible part of the trajectory, thus providing a direct cue for the perception of animacy. However, one could argue that in Exp. 3 the speed-change stimulus was still more variable than the speed-constant one, since the relative difference between the two speeds being alternated was larger in the former than in the latter stimulus. Thus, in Exp. 4, we modified the two speeds used for the speed-constant control stimulus. In this new version, the relative difference between the two speeds was approximately matched in the two stimuli.

7.1. Subjects

Thirty-eight domestic chicks (21 males) were used for this experiment.

7.2. Stimuli

Again, the speed-change stimulus was identical to that of Exp. 2 and 3 and the speed-constant stimulus alternated 2 different speeds (~ 15.83 and 2.95 cm/s, slower-to-faster speed ratio of 0.18). However, the ratio between the two speeds displayed by the speed-constant stimulus was similar to that between the two speeds displayed by the speed-change stimulus (i.e., 0.17).

7.3. Results

Overall, the results confirmed and extended those of previous experiments. The analysis of the ratio of time spent near the speed-change display revealed a significant preference for this stimulus (mean = 0.66, $S.E.M. = 0.07$, $t_{37} = 2.152$, $p = 0.038$, $d = 0.37$, see Fig. 3). A non-significant trend in the same direction was observed for the first stimulus approached (24 chicks approached the speed-change stimulus, 14 the speed-constant stimulus, $X^2_1 = 2.632$, $p = 0.105$, see Fig. 2d).

8. Experiment 5

In Exp. 2–4 we demonstrated a robust preference for the stimulus characterized by visible changes in speed, with respect to stimuli with no visible speed changes, despite the fact that both stimuli had the same average speed (Exp. 2–4) and were characterized by a similar level of internal variability, defined by the ratio between the slower and the faster speed, that were, respectively, of ~ 0.18 and 0.17 (Exp. 4). Interestingly, the results of the last two experiments suggest that, in order to elicit chicks' preferential approach, the time of speed change must be perceptually available to the subjects, and not simply inferable from the dynamics of the scene. In fact, the alternation of different speeds in subsequent cycles of the control stimulus could have implied that an invisible change in speed was taking place behind the lateral occluders. Despite that, in Exp. 3 and 4, chicks showed a clear preference for the stimulus with visible changes in speed. In this last control

experiment we thus decided to test directly this hypothesis, by hiding behind two occluders the portion of screen where the speed change events took place. We predicted that this will be sufficient to abolish the preference observed in Exp. 2–4.

8.1. Subjects

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

8.2. Stimuli

Stimuli were obtained from those of Exp. 4, by introducing two rectangular grey occluders (5.6 cm) positioned at one third and two thirds of the red stimulus trajectory, occluding the speed changes. Identical occluders were present in both the speed-change and the speed-constant displays (see Fig. 1c).

8.3. Results

When the moment of speed change was occluded, no significant preference for any of the stimuli was observed, neither for the dependent variable first stimulus approached (23 chicks approached the speed-change stimulus, 28 the speed-constant stimulus, $X^2_1 = 0.49$, $p = 0.484$, see Fig. 2e), nor for the ratio of time spent near the speed-change stimulus over the total choice time (mean = 0.44, $S.E.M. = 0.07$, $t_{50} = -0.844$, $p = 0.403$, $d = 0.12$, see Fig. 3).

9. Experiment 6

Based on the results of Exp. 1a and 1b, in Exp. 2–5 we decided not to focus on direction changes, but rather on the more promising effect of speed changes. However, results of Exp. 1a revealed a paradoxical element, namely that the presence of direction changes was not only insufficient to elicit preferential approach in chicks, but also detrimental. In fact, in Exp. 1a we did not observe any preference for the direction-change stimulus despite the fact that it also contained a speed change. The aim of Exp. 6 was to determine whether this "detrimental effect" could be due to the unnatural combination created by the speed- and direction-profiles of the stimuli of Exp. 1a. In fact, when animate creatures invert their motion direction and move back on their original path they decelerate, stop, and only then they accelerate again moving in the opposite direction. On the contrary, in Exp. 1a the red stimulus inverted its motion direction abruptly, without any deceleration or pause, and immediately accelerated away. This could have originated the impression of an inanimate object bouncing back after collision with an invisible obstacle. In Exp. 6 we thus replicated Exp. 1a, but implementing the above described naturalistic speed-profile expected for biological entities that invert their motion direction.

9.1. Subjects

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

9.2. Stimuli

Stimuli were obtained from those of Exp. 1a by introducing a gradual deceleration and a brief pause (0.25 s), before the inversion of motion direction in the speed-and-direction change stimulus. For other respects the stimuli were identical to those of Exp. 1a: the inversion of motion direction happened halfway through the

screen and was followed by a gradual increase in speed while the red stimulus moved in the opposite direction. Also, the average speed was identical to that of the control display (constant stimulus) and the shape and size of the red stimulus was as described for Exp. 1a (a rectangular shape of 3×2 cm, with rounded corners).

9.3. Results

Chicks revealed a significant preference for the stimulus displaying speed and direction changes, confirming and extending the results of Exp. 2. This was evident both when considering the first stimulus approached (38 chicks approached the speed-and-direction-change stimulus, 21 the constant stimulus, $\chi^2 = 4.898$, $p = 0.027$, see Fig. 2f) and when considering the ratio of time spent near the speed-and-direction-change stimulus over the total choice time ($M = 0.63$, $S.E.M. = 0.06$, $t_{58} = 2.219$, $p = 0.030$, $d = 0.28$, see Fig. 3).

10. General discussion

In the present work we demonstrated, in naïve newborn animals, the presence of unlearned preferences for an elementary motion cue of animacy. This is, to the best of our knowledge, the first evidence that naïve animals respond to those cues when implemented in the motion of a single shape, without any interaction with other visual objects. This adds to previous reports that newly-hatched chicks preferentially imprint on stimuli characterized by another of the elementary motion cues that elicit animacy perception in humans (Mascalzoni et al., 2010): here we show that chicks respond also to changes in speed of already moving stimuli in addition to “start from rest”. Our results are also consistent with the evidence pointing to a crucial role of speed changes in infants’ and adults’ perception of chasing displays (Frankenhuis et al., 2013).

We want to add, however, a few notes of caution for the interpretation of our results. First of all, the paradigm employed here (and in numerous other studies with gallinaceous chicks Rosa-Salva et al., 2010, 2011; Vallortigara & Regolin, 2006; Vallortigara et al., 2005; non human primates, Sugita, 2008; and human infants Farroni et al., 2005; Frankenhuis et al., 2013; Rochat et al., 1997; Simion et al., 2008) only tests relative preference between two stimuli. Based on this it is not possible to determine the absolute level of preference for one stimulus. It is indeed likely that, for the experiments reported here, all stimuli are per se quite attractive for chicks. In fact, all have features which are socially attractive for chicks (appropriate size, rounded shape, red colour, presence of movement). Importantly, this also mirrors real-life visual processing: multiple stimuli are often present in the visual field, each characterized by various features. The preferential processing of one stimulus over another is going to depend on the relative weight of multiple relevant properties.

A similar point can be raised for the human observers tested in Exp. 1b. While it is clear that speed-changes are the ultimate winner of this task, eliciting higher animacy attributions than the other tested motion patterns, it is difficult to determine whether the other motion patterns are also perceived as animate, even though to a lesser degree. In favour of this hypothesis is the fact that the mean animacy rating for speed-constant motion was of nearly four points (if the subjects perceived no similarity between the motion of the speed-constant displays and that of a living creature one could expect a score closer to zero).

Another note of caution concerns the distinction between spontaneous preference and imprinting learning. We believe that the adaptive significance of predispositions is also to direct subsequent learning mechanisms toward appropriate stimuli (for a similar

argumentation regarding the human species and the predisposition for faces see Johnson, 2005). It is likely that, all else being equal, preferential approach of one kind of stimulus by naïve chicks will end up ensuring filial imprinting for the preferred stimulus, due to the increased exposure to it. However, these are for now only speculations, since the preference that we observed here does not automatically translate into animacy perception or preferential imprinting (indeed the current study was purposely designed to test spontaneous approach preference, rather than preferential imprintability, see below). For example, we cannot know whether chicks are attracted by the moving stimuli because they “perceive them as animate”. Even assuming that preferential imprinting will indeed occur, we do not know whether this will result from a direct social preference for that motion attribute or simply from an increased level of attention to it (an attentional orienting mechanism is believed to be at the basis of face preferences in humans Johnson, 2005; Morton & Johnson, 1991; Simion, Valenza, Umiltà, & Dalla Barba, 1998; Tomalski, Johnson, & Csibra, 2009). This issue could be tackled in future studies on the role of speed changes in attentional orientation, by implementing speed changes in visual search, learning or other tasks not based on spontaneous social preferences (e.g., using stimuli that are too small to be social companions, and thus categorised as potential food items).

A number of studies have revealed that human infants respond to different, and sometimes rather sophisticated, cues of animacy and agency (e.g., Csibra, 2008; Gergely, Nàdasdy, Csibra, & Bíró, 1995). However, in the present work we focus on chicks’ responses to a specific motion cue associated with animacy perception, that is speed changes, excluding other confounding factors. The construct of animacy is also clearly distinguished from that of agency and intentionality (see the Introduction). Thus, we do not address whether chicks might respond also to some other complex motion properties associated with agency or intentionality, even though the two are of course not mutually exclusive or antagonist phenomena.

The evidence obtained so far in chicks is nowhere near as extensive as that available for human infants in terms of the variety of motion properties that have been tested. Nevertheless, studies on human infants should be complemented by works such as the current one, in order to assess the fundamental mechanisms on which even more sophisticated processing is based. The present study offers a clear-cut demonstration of sensitivity to one fundamental perceptual property of animacy and it also investigates the evolutionary and developmental origins of this trait. Among the most important contributions of the present paper is that a preference for a property associated with human animacy perception has been obtained (i) in an animal model phylogenetically distant from humans and (ii) in the absence of any prior visual experience. This allows us to investigate the origins of this trait in a way that is impossible even when studying human newborns, for which a certain amount of previous visual experience is unavoidable. Studies on infants with months of visual experience cannot inform us on the inborn predispositions that characterise the initial state of the developing system and represent the building blocks for further cognitive development (Carey, 2009; Spelke, 2000; Spelke & Kinzler, 2007; Vallortigara, 2012).

In fact, a notable aspect of animacy perception is its automatic and irresistible nature, which raises questions on its developmental and phylogenetic origins. Overall, evidence from human adults and infants suggests the presence of core-knowledge mechanisms responding to the motion-cues indicating the presence of animate entities (Spelke & Kinzler, 2007). Along these lines is also the view proposed by Frankenhuis and Barrett (2013) that babies employ “a coarse, property-based attentional filter that navigates their attention toward social interactions. This filter could be

phylogenetically old, shared with other vertebrates, and respond to general properties of animate (anti-gravitational acceleration)". Moreover, children with autism have difficulties in learning to identify as "animate" abstract shapes on the basis of the above mentioned motion cues, suggesting a failure of the corresponding core-knowledge mechanism (Rutherford, Pennington, & Rogers, 2006). However, claims of unlearned core-knowledge mechanisms need to be supported by evidence from other animal species and especially from naïve models, allowing both to uncover the phylogenetic history of a given trait and to assess claims on its innate versus cultural origin, disentangling the role of inborn and experience-dependent factors in animacy perception. Our data offer direct support to this hypothesis showing remarkable similarity between the responses of 4-month-old human infants (Frankenhuis et al., 2013) and visually naïve domestic chicks to elemental motion properties that induce animacy perception in adult observers. Most importantly, the present study provides the first evidence that naïve animals respond to this elementary motion cue of animacy, which can be conveyed by the motion of a single visual object, indicating the presence of a mechanism to orient toward one of the general properties of animate creatures. This is also the first demonstration of a predisposition for speed changes in any non-human animal.

Another note of caution involves the relationship between speed-changes and other simple animacy cues, such as start from rest (Mascalzoni et al., 2010) and direction-changes. Both speed changes and start from rest are clearly effective cues for eliciting chicks' social preferences. However, the available evidence does not allow any prediction on the hierarchy and interaction between these two cues, whose effects have been demonstrated in two independent studies with different methodologies. Thus, it is currently unknown whether they can have additive effects and whether one is more powerful than the other.

As regards direction changes, results of Exp. 1a–1b, initially suggested that the presence of direction changes was not only insufficient to elicit perception of animacy in human adults or preferential approach in chicks, but also detrimental. In fact, in Exp. 1a we did not observe any preference for the direction-change stimulus despite the fact that it also contained a speed change. In Exp. 6, we tested whether this "detrimental effect" could be due to the unnatural combination of the profile of speed and direction changes of Exp. 1a's stimuli. In fact, when animate creatures decide to invert their motion direction they decelerate, stop, then accelerate again when moving away in the opposite direction. On the contrary, in Exp. 1a the object inverted its motion direction abruptly, without any deceleration or pause, and immediately accelerated away. This could have originated the impression of an inanimate object bouncing back after collision with an invisible obstacle (reported by some human observers exposed to the stimulus). In Exp. 6 we replicated Exp. 1a, but implementing the natural speed profile expected for animate creatures that invert their motion direction, finding a significant preference for the configuration that presented speed and direction changes. We can thus exclude that direction changes per se have a detrimental effect on chicks' preference for speed changes. However, it is unclear whether direction-changes can elicit chicks' preferences when presented in isolation (in the absence of any change in speed). The human literature reports contradictory results on this regard. On the one hand, human adults showed increased animacy perception for pure direction changes (Tremoulet & Feldman, 2000). On the other hand, in the study of Frankenhuis et al. (2013) infants' response to changes in speed did not depend on their level of engagement with the stimuli, contrary to what was the case for changes in trajectory. This can be interpreted as evidence that speed changes cause automatic orientation responses, whereas active (endogenous) engagement plays a role in the perception of

animacy from changes in trajectory. Similar to that, Tremoulet and Feldman (2000) reported acceleration to have a greater effect than trajectory changes on animacy ratings. These results are potentially suggestive of the presence of independent mechanisms for orienting towards speed changes and direction changes, which may involve to a different degree automatic and endogenous attention. If that would be the case, the presence of speed-changes would be detected in an automatic fashion, orienting attention towards the stimulus regardless of the current focus of attention and task demands, whereas the attention triggering effect of direction changes would be contingent on the presence of explorative behaviour (e.g., when attention has been endogenously directed at searching for animate entities).

Based on the main effect of direction change found by Tremoulet and Feldman (2000), we expected the human observers of Exp. 1b to respond also to pure direction changes. This was not the case, suggesting that some peculiarity of our stimuli could be involved in this lack of effect. This could be due to the fact that in both stimuli the red shape's main axis was always perfectly aligned with the direction of motion (Tremoulet & Feldman, 2000). Indeed, Tremoulet and Feldman report a reduced effect of speed changes in elongated stimuli whose main axis is aligned with motion direction, with respect to circular shapes (indicating that alignment of the main axis with the direction of motion could be already an animacy cue on its own). Moreover, during the second half of the motion of the red shape, the extremity that was initially facing forward with respect to motion direction, is now facing backward. This inversion of the "front" and the "back" of the stimulus is not expected from animate entities and could suppress the perception of animacy. Intriguingly, human infants have been shown to respond to similar cues, interpreting the anterior-posterior orientation of animate creatures in terms of a stable front-end and a stable back-end, defined with respect to the motion direction (Hernik, Fearon, & Csibra, 2015). However, we are well aware that non-significant results should be interpreted with caution and that there could be a number of reasons behind the non-significant results of Exp. 1b.

Of important implications for future studies, chicks' sensitivity to speed changes can be detected by a direct test of spontaneous preference (without the need to test for differential imprintability). This not only makes the procedure of the behavioural test more practical and efficient, substantially reducing the level of manipulations of the animals, as well as the time and number of subjects needed to perform an experiment, but also opens new interesting possibilities for the investigation of the neural bases of animacy preferences. This was not the case for the paradigm developed by Mascalzoni et al. (2010), based on the launching effect "à la Michotte" (1946), in which the focus was on chicks' preferential imprintability towards one of two distinct visual objects based on their causal interactions. In that work both the animate and the inanimate stimulus needed to be present simultaneously on screen and to interact with each other. This would make it difficult, even though not impossible, to disentangle the brain activation associated with the motion pattern of each of the two stimuli from the other, as well as from that associated with the physical causality of their interaction. On the contrary, with the present stimuli it would be quite straight forward to stimulate selectively different groups of animals, by exposing some only to the speed change stimulus and others only to the constant speed stimulus. On this regard, note also that the present work employs stimuli in which the visual objects are identical in appearance, differing only in their motion patterns (while in the study of Mascalzoni et al., 2010 the two visual objects necessarily differed in colour). A power analysis based on the effect size obtained in Exp. 2 ($d = 0.62$) indicates that a sample of 18 subjects would be sufficient to reveal a significant preference in a replica of this condition (one sample *t*-test against

chance level, one tailed, $\alpha = 0.05$, $\beta = 0.8$). This is significantly less than what required for most studies of this kind (e.g., corresponding analysis based on Exp. 1 from Mascalzoni et al., 2010, indicates a required sample size of 45 individuals), making it more attainable and ethical to conduct invasive studies of neural correlates. Thus, using the stimuli validated by the present work, future studies could verify which of the candidate brain areas suggested by the literature are indeed involved in the processing of this powerful motion cue of animacy. This could be done by staining immediate early genes' products (e.g. see Mayer, Pecchia, Bingman, Flore, & Vallortigara, 2016; Mayer, Rosa-Salva, Lorenzi, & Vallortigara, 2016) to map neuronal activity in chicks exposed to speed-changes and speed-constant stimuli. Once the involved brain regions would have been identified by this approach, their functional role in the expression of the predisposition could be tested by lesioning studies. Finally, a more specific characterisation of the response properties of the neurons in these brain regions could be achieved by electrophysiological recordings. As regards our predictions, we expect an involvement of areas hypothesised to have a role in unlearned social predispositions (Johnson, 2005; Rosa-Salva et al., 2015), among which the tectum opticum (avian homologue of the mammalian superior colliculus, that in chicks contains neurons responding to speed changes Verhaal & Luksch, 2016), the nucleus rotundus (homologue of the pulvinar nuclei of the thalamus in mammals) and the avian homologues of the mammalian amygdala (Martínez-García, Novejarque, & Lanuza, 2007; Yamamoto, Zhiqiang, Wang, & Reiner, 2005). We also expect involvement of the Social Behaviour Network that controls several different social behaviours and is rich in hormonal receptors for the homologs of oxytocin and vasopressin (Newman, 1999; O'Connell & Hofmann, 2011). The Social Behaviour Network incorporates various areas, including again amygdala and septum. Septum is a highly conserved region (Lanuza & Martínez-García, 2009; Puelles et al., 2000), which is also part of the Mesolimbic Reward System (O'Connell & Hofmann, 2011) and controls, among other things, gregarious behaviour in avian species (Goodson, Schrock, Klatt, Kabelik, & Kingsbury, 2009; Kelly & Goodson, 2014).

At a behavioural level, future studies with naïve animal models should further exploit the advantages of the approach implemented in the present work, testing the role of motion dynamics displayed by a single shape on a homogeneous background (Tremoulet & Feldman, 2000). Among the various motion cues associated with animacy perception in human observers (see Introduction; see also Rosa-Salva et al., 2015 for a review), some seem to be particularly promising for future investigations with our animal model, such as the alignment between the stimulus' major symmetry axis and the trajectory of motion, in relation to changes on direction, and the stable mapping of one the stimulus' extremities with its "front", i.e. the part facing the motion direction.

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