

Research report

Brain asymmetry modulates perception of biological motion in newborn chicks (*Gallus gallus*)



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HIGHLIGHTS

- Left-right asymmetries in biological motion processing in day-old domestic chick (*Gallus gallus*).
- Hemispheric specialization in perception of biological motion.
- The advantage of the right hemisphere in processing the biological motion.

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ABSTRACT

Few light-points on the joints of a moving animal give the impression of biological motion (BM). Day-old chicks prefer BM to non-BM, suggesting a conserved predisposition to attend to moving animals. In humans and other mammals a network of regions, primarily in the right hemisphere, provides the neural substrate for BM perception. However, this has not been investigated in avians. In birds the information from each eye is mainly feeding to the contralateral hemisphere. To study brain asymmetry, we recorded the eye spontaneously used by chicks to inspect a BM stimulus. We also investigated the effect of lateralization following light exposure of the embryos.

In Experiment 1, highly lateralized chicks aligned with the apparent direction of motion only when they were exposed to a BM-stimulus moving rightward first, monitoring it with the left-eye-system. In Experiment 2 weakly lateralized chicks did not show any behavioral asymmetry. Moreover, they counter aligned with the apparent direction of motion.

Brain lateralization affects chicks behavior while processing and approaching a BM stimulus. Highly lateralized chicks aligned their body with the apparent direction of the BM, a behavior akin to a following response, monitoring the stimulus preferentially with their left eye. This suggests a right hemisphere dominance in BM processing. Weakly lateralized chicks counter-aligned with the apparent direction of the BM, facing it during interaction, and monitored it equally with both eyes.

Environmental factors (light stimulation) seem to affect the development of lateralization, and consequently social behavior.

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1. Introduction

Movement is one of the most salient aspects of the world around us. Distinguishing different kinds of movement, such as that of living creatures and non-living objects, and reacting appropriately, is essential to survival [1–6]. An animation sequence, consisting of a dozen light points positioned to the major limb-joints of a walking person, already allows to recognize many features of the executed activity: a phenomenon known as biological motion (BM)

perception [7]. A variety of non-human animals are capable of discerning BM from non-BM, including chimpanzees [8], baboons [9], rhesus monkeys [10–12], common marmosets [13], cats [14], rats [15,16], bottlenose dolphins [17], pigeons [18–20], chicks [21,22] and medaka fish [23].

Crucially, studies in non-human animals proved that the BM perception can be independent from visual experience, prompting the subsequent investigation of sensitivity to BM in human newborns. Newly hatched chicks, incubated and hatched in darkness, and therefore having an extremely limited visual experience, exhibit a preference for BM over non-BM patterns [2]. Using the same stimuli employed with chicks – a walking hen (BM) and a rigidly moving (non-BM) hen – it has been shown that 2-day-old

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babies manifest a spontaneous preference for a display depicting BM compared with non-BM [3]. However, a subsequent study suggested that a preference for the translational component of movement may actually constitute the first step in development of visual preference for BM [24].

Overall, these data suggest that detection of BM is an intrinsic capacity of the visual system, presumably part of an evolutionarily ancient mechanism that predisposes animals to attend to and to interact with other animals.

Even more interestingly, naïve chicks align their bodies in the apparent motion direction displayed by the point light display (PLD) of a walking hen [25]. These results showed that inexperienced visual systems are able to extract the walking direction of PLD, and that the perception of BM stimulates a response akin to social interaction in the young animals [25].

Similarly to what occurs in face recognition, the perception of BM is orientation-dependent: when BM stimuli are presented upside down their perception is compromised [26]. Typically adult humans, observing an upright oriented BM display, report clearly seeing a walking figure, but such spontaneous recognition does not occur when the image-plane display is inverted [27,28]. Again this effect is likely to be independent from visual experience: day-old chicks, that align their bodies with the apparent direction of movement of the upright walking hen, oriented their bodies at random when presented with the upside-down version of the same stimulus [25]. Similar results have been subsequently obtained in human babies, that look longer at an upright than at an upside-down display [3].

Since walking is the most common type of movement in legged animals, it makes sense that sensitivity for this kind of motion develops very early in life, and that it is elaborated by a specific neural substrate [25,29,30]. The neural network engaged in visual processing of BM has been identified in adult humans and involves brain areas such as parietal cortices [31–34], the fusiform gyrus [33,35–37], portions of the frontal cortices [38] and especially, the posterior superior temporal sulcus, pSTS [35,37–43]. Moreover, neuroimaging studies in adult humans revealed a right hemisphere dominance in the perception of BM [42,44–48]. Event-related potentials (ERPs) revealed in both 8-month-old infants and adults, a similar activation of the parietal region of the right hemisphere during the vision of upright BM, indicating that the lateralized neural substrate for perceiving BM is mature at around 8 months of age [49]. This effect was confirmed by another ERPs study comparing upright and upside-down BM displays [50]. Thus, starting from at least 8 months of age, we can observe a differential neural response to canonical and inverted/distorted BM stimuli, and this seems to be particularly pronounced in the right hemisphere. However, it is unclear whether this hemispheric specialization is present at birth and extends to newborns' preferential attention to BM, or whether it emerges gradually during development with visual experience.

We have a limited amount of information about the functional organization of brain mechanisms underlying the processing of BM in non-human animals [51,52]. The existing evidence is mostly limited to adult primates. In macaques the superior temporal polysensory area plays an important role in the BM perception [10,53]. Watching a BM display elicits selective activation in the monkey superior temporal sulcus [12]. Moreover, the hemispheric specialization associated with the perception of BM has never been examined in non-human animals. With the present study, by taking advantage of animal models that might allow us to disentangle the role of maturational and experiential factors we aimed at filling this gap.

The sensitivity to BM in newly hatched chicks, together with their well-known lateralized visual pathways [54–56], makes them a suitable developmental animal model for investigating the neural

basis of BM processing [57–59]. Here, to disentangle the engagement of either hemisphere in inspecting the BM, we took advantage of the fact that birds with laterally placed eyes can process different aspects of the environment separately with the two eyes [60–62]. Since the avian brain does not have a corpus callosum and displays a virtually complete decussation of fibers at the optic chiasm [63], if one hemisphere is dominant in perception of BM, we would expect an asymmetry in the orientation of chicks' body, in order to view the walking hen display with the eye-system that can better process this kind of stimulus.

Moreover, we made use of a technique that allows us to manipulate the presence of brain lateralization in different groups of chicks. Avian studies have revealed that the level of lateralization of individual birds is influenced by an environmental factor, namely the quantity of light received by the embryo during a critical period, from Day 17 to 21 ([64–67]; but see [68] for new evidence of an effect of early-light stimulation). Chicks hatched from light incubated eggs are known to be strongly lateralized, whereas the lateralization is largely prevented in dark-incubated chicks [69,70]. In a first experiment, we tested the presence of lateralized responses to PLDs of conspecifics' motion in light-incubated chicks, investigating whether the lateralization profile was modulated by the stimulus orientation on the vertical plane. In the second experiment we explored how the degree of lateralization of chicks' visual system affects the responses to the upright PLDs, by testing chicks hatched from dark incubated eggs.

2. Experiment 1

In Experiment 1 we analyzed chicks' behavior to reveal asymmetries in the eye used by light-incubated (i.e., highly lateralized) chicks in biological motion (BM) processing. To do so we compared the level of body's alignment displayed by chicks in relation to the apparent direction of motion, either rightward or leftward, of a point light display (PLD) of a walking hen. In fact, to align their body with a stimulus moving rightward chicks must observe the stimulus with the left eye (right hemisphere); whereas, to align with a stimulus moving leftward chicks have to observe the stimulus with the right eye (left hemisphere).

If one hemisphere plays a dominant role in BM perception, we would expect that chicks behave differently with stimuli moving in opposite directions, aligning more readily with stimuli whose motion direction is consistent with the use of the dominant eye-system.

We also investigated whether lateralization was modulated by the orientation of the stimulus with respect to the direction of gravity (i.e., upright vs. upside down).

2.1. Materials and methods

2.1.1. Ethics statement

The experiments with chicks complied with all national laws and were approved by the Minister of Health.

2.1.2. Subjects

For the present experiment we re-analyzed behavioral data from a sample of 350 chicks (*Gallus gallus*; see [25]). Chicks hatched from fertilized eggs obtained from a local supplier (Agricola Berica, Montegald, Vicenza, Italy) at Day 14th of incubation. The eggs were incubated using a MG 70/100 incubator (45 cm × 58 cm × 43 cm), at controlled temperature (37.7° C) and humidity (about 50–60%), in the Comparative Psychology Laboratory of the Department of General Psychology, University of Padova. From Days 14th until Day 18th of incubation, the eggs were maintained in total darkness. From Day 19th of incubation to Day 20th included, the eggs were

exposed to light, provided by a 25 W incandescent light bulb, generating about 250 Lux, placed within the incubator. This was done in order to lateralize the embryos' visual pathways.

In the evening of Day 20th of incubation the eggs were moved into a hatchery (60 cm × 65 cm × 66 cm, with capacity of about 100 eggs), under the same temperature conditions and at a lower humidity level until hatching, which occurs on Day 21st. In the hatchery the light was switched off, to prevent any visual experience to the newly hatched chicks. After hatching, chicks were left into the hatchery for 24 h in complete darkness. Testing took place in the early morning of Day 2nd post-hatching.

2.1.3. Experimental stimuli

Stimuli consisted PLD obtained from walking hen movies [2]. These were created using the software Macromedia Director (Version 6.0). A point-light walking hen movie was obtained by carefully placing, frame by frame, 13 points of light on the main joints of the digitalized image of a video-recording of a real animal. To obtain a hen's complete step sequence 23 frames (each consisting in 13 bright dots, 95.71 candelas [cd]/m², on a black background, 0.03 cd/m²) were required. Each dot was composed of 16 pixels on a 640 × 480 resolution screen, and measured 0.12° of visual angle at the viewing distance of 68 cm. Each set of point-lights occupied a window of 237 × 220 pixels in the center of the computer screen, corresponding to 7.14 (width) and 6.54 (height) degrees of visual angle at the viewing distance of 68 cm. The hen's complete step sequence was looped to obtain a point-light walking hen movie. This was projected onto a computer screen after subtraction of translation components. As a result, the display was stationary in the central window of the screen, moving as if the hen was walking on a treadmill.

Two versions of the movie were created. In the first version (upright rightward-first), the point-light walking hen movie initially had an apparent left-to-right direction of motion. Then, at the end of the 4th minute, the display was mirrored along its vertical axis, so that in the remaining 4 min the apparent direction of motion was reversed (i.e., from right to left). Vice versa in the second version of the movie: upright leftward-first.

A second movie was created for the upside-down walking hen animation sequence. This was identical in all aspects to the upright version, with the only exception that the overall array of points of light was turned upside-down. Again two versions of this stimulus were created, counterbalancing the initial motion direction (upside-down rightward-first and upside-down leftward-first).

2.1.4. Test

Testing took place in an experimental room, adjacent to the hatchery room, in which temperature and humidity were controlled (25 °C and 70%, respectively) and which was kept dark except for light coming from the screen of a Macintosh I-mac computer, used to present the stimulus. The experimental apparatus consisted of a V-shaped arena, made of a plastic plate (thick 0.3 cm) black poli-plack® 25 cm high wall. The open end of the V-shape was made of a transparent glass sheet (40 cm high and 33 cm long), positioned in front of (and 15 cm away from) the monitor of the computer (see Fig. 1).

At the beginning of the test, the subject was positioned in the dead end of the arena (which was 53 cm away from the transparent wall), facing the computer screen (68 cm away) that could be clearly seen through the glass sheet. During the experiment, one of the four point-light walking hen movies was projected on the computer screen.

Each chick was tested only once, and different groups of chicks were exposed to a single version of the movie: upright rightward-first ($N=72$); upright leftward-first ($N=97$); upside-down rightward-first ($N=89$); and upside-down leftward-first ($N=92$).

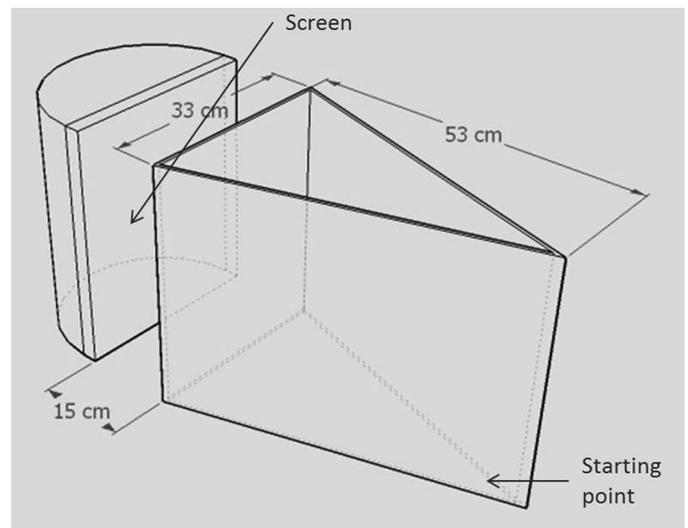


Fig. 1. Schematic illustration of the apparatus.

During the 8 min of movie presentation, each bird could move freely in the arena and approach the stimulus, while its behavior was video-recorded by an overhead infrared video-camera.

From the video-recordings, the angle formed by the chick's body and the apparent direction of motion of the walking hen was determined second by second for each minute of observation.

If the chick faced the screen perpendicularly, the angle was considered to be +90°, whenever the body of the chick was parallel to the screen the angle was considered to be 0°. Whenever a subject was oriented to the head of the stimulus and its body formed with the monitor an angle comprised between -15° and +75° (corresponding to chicks' visual field, [71]) it was considered aligned. Instead, when the chick was oriented to the tail of the stimulus and its body formed the same angle with the screen it was considered counter-aligned (see Fig. 2). As in previous studies, body orientation was used as a proxy for head orientation to maximize measurement precision, since the head orientation was not always clearly discernible [25].

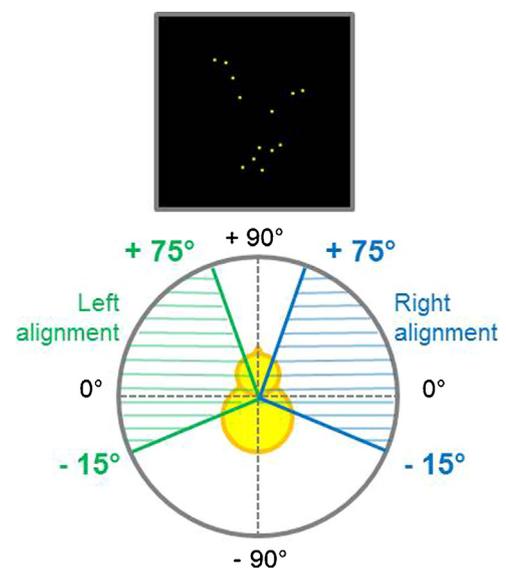


Fig. 2. Schematic illustration of the angles formed by the chick's body with the apparent direction of motion of the walking hen. Whenever the angle was comprised between -15° and +75° a chick was considered aligned, instead when the angle was comprised between +75° and +90° or between -15° and -90° the chick was considered not aligned.

All other orientation angles were discarded from the analysis, allowing us to exclude all the positions in which the stimulus was not visible to the chick (because the chick was turned). We therefore computed the percentage of alignment using the subsequent formula: $\text{time of alignment}/(\text{time of alignment} + \text{time of counter-alignment}) \times 100$. Values $>50\%$ indicated an alignment and values $<50\%$ indicated a counter-alignment with the apparent moving direction of the stimulus.

2.2. Analysis and results

A repeated measures ANOVA was performed on the percentage of alignment during the first and the last 4 min of the test (factor henceforth named *time*). Between subject factors were *stimulus orientation* (upright or upside-down) and *walking direction*: first rightward (the apparent direction of motion was from left-to-right in minutes 1–4 and leftward in minutes 5–8) or first leftward. A significant effect of *stimulus orientation* emerged ($F_{(1,346)} = 11.865$, $p < 0.001$), together with an interaction between *stimulus orientation* and *walking direction* ($F_{(1,346)} = 11.045$, $p = 0.001$). All other effects and interactions were not significant.

On the basis of the significant interaction, we analyzed separately the performance of the resulting four groups, comparing the alignment index of each group with chance level. Only chicks exposed to the upright walking hen moving first rightward and then leftward resulted to be overall significantly aligned with the stimulus walking direction ($N = 72$; mean = 62.100; s.e.m. = 3.400; $t_{71} = 3.603$, $p < 0.001$), with all other groups being at chance (upright-hen leftward first, $N = 97$; mean = 51.800; s.e.m. = 2.600; $t_{96} = 0.695$, $p = 0.489$; upside-down-hen rightward first, $N = 89$; mean = 48.500; s.e.m. = 2.8; $t_{88} = 0.536$, $p = 0.593$; upside-down hen leftward first $N = 92$; mean = 51.500; s.e.m. = 2.900; $t_{91} = 0.514$, $p = 0.609$, Fig. 3). The absence of alignment in chicks exposed to the upside-down stimulus had already been reported by Vallortigara and Regolin [25]. Interestingly, however, in the upright condition the alignment response was limited to chicks that were exposed to the stimulus that in the first part of the test was walking rightward, while chicks that were firstly exposed to the stimulus walking leftward did not align to it. Due to the peculiar organization of chicks' visual system (see Section 1), this suggests a different implication of the two hemispheres in processing this information, and

namely a right hemisphere dominance, in line with the human literature. In fact, when aligning themselves with the PLD depicting the rightward walking hen, chicks will keep the stimulus in the left monocular visual system. If this engagement of the left-eye/right-hemisphere system occurs in the first part of the test, then chicks seem to be able to re-align with the stimulus also in the second half of the test, when the stimulus must be monitored with the right-eye-system. On the contrary, if at the beginning of the test the hen's walking direction prevents a preferential engagement of the right hemisphere, chicks do not align with the stimulus even when it switches its direction and could be monitored by the left-eye system. The reasons of such a crucial role of the stimulation provided to the two eye-systems in the first half of the test is unclear. However, it seems reasonable to hypothesize that this might reflect the supremacy of the right hemisphere in processing social stimuli, that probably mediates the engagement of attention over protracted exposure to initially unfamiliar stimuli.

3. Experiment 2

The aim of Experiment 2 was to study if the pattern of hemispheric specialization for biological motion (BM) processing, reported in Experiment 1, can be observed also in dark-incubated (weakly lateralized) chicks.

3.1. Subjects, materials and methods

A new group of 161 chicks was used. The incubation conditions were the same as those described in the previous experiment, with the only exception that, in this case, the eggs were not exposed to light on Days 19th and 20th of incubation. Thus, chicks participating to this experiment are considered weakly or not lateralized.

Testing conditions were the same of those described in Experiment 1.

Two different groups of birds were exposed to different stimuli: upright rightward-first ($N = 84$) and upright leftward-first ($N = 77$).

Again, from the testing video-recordings, the angle formed by the chick's body and the apparent direction of motion of the walking hen was determined.

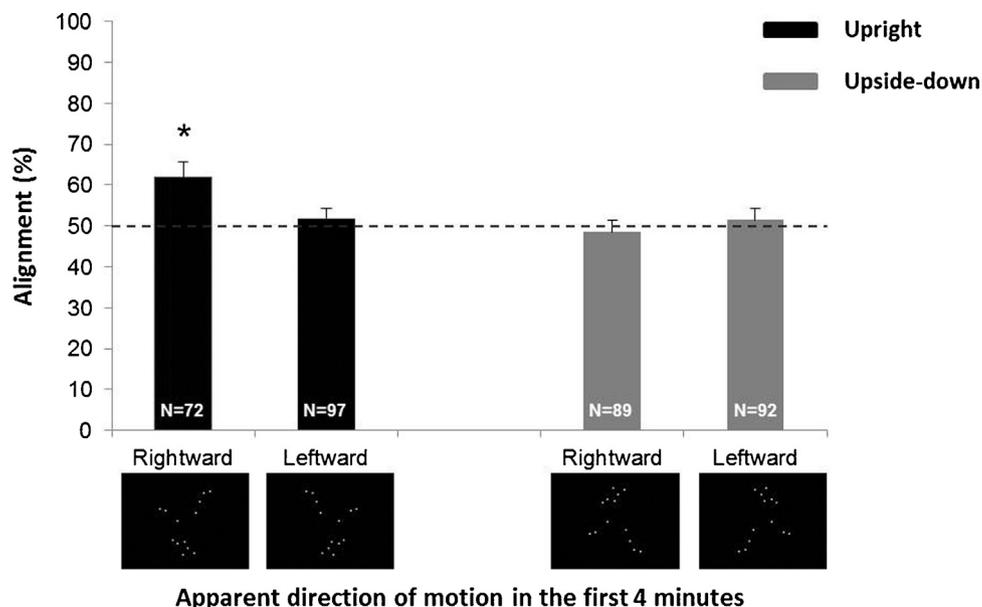


Fig. 3. Results of Experiment 1. Percentage of alignment (means with SEM) displayed at testing (considering the overall duration, i.e., 8 min) by each group of chicks.

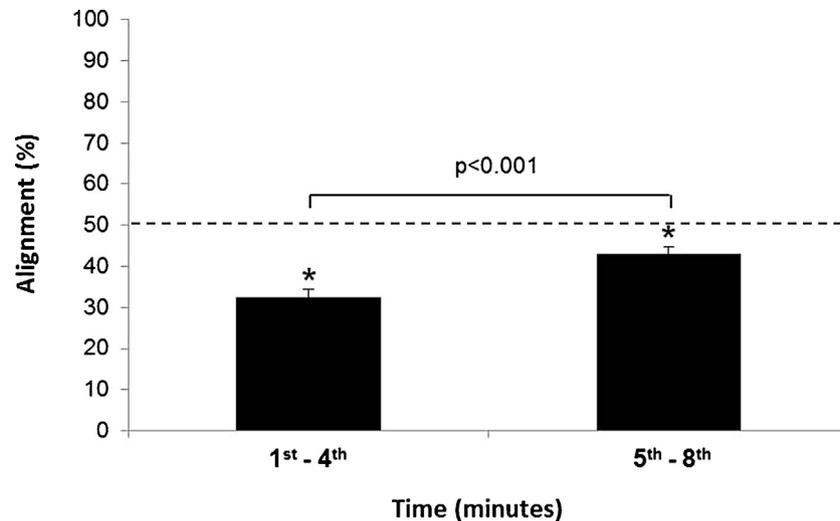


Fig. 4. Results of Experiment 2. Percentage of alignment (means with SEM) displayed in the first half (minutes 1st–4th) and in the second half (minutes 5th–8th) of test.

3.2. Analysis and results

Overall, dark reared chicks were able to extract the walking direction of the stimulus, since their percentage of alignment was significantly different from chance level ($N = 161$; mean = 37.300; s.e.m. = 0.020; $t_{160} = 8.786$, $p < 0.001$). Surprisingly, however, in this experiment chicks systematically counter-aligned their body axis with the apparent motion direction of the hen, appearing to “face” the hen rather than to “follow” it (as revealed by the below-chance value of the index representing the percentage of alignment). Even though the direction of this effect is in contrast with what observed in Experiment 1, this still proves chicks’ ability to discriminate walking direction of an upright PLD (Fig. 4).

In order to investigate lateralization effects, a repeated measures ANOVA was performed with *time* as within subjects factor and *walking direction* as between subject factor. As expected, dark-incubated chicks showed no significant effect of the factor *walking direction* ($F_{(1,159)} = 1.080$, $p = 0.300$), nor any interaction between *walking direction* and *time* ($F_{(1,159)} = 2.201$, $p = 0.140$), confirming their weaker lateralization level. Only a significant effect of the factor *time* emerged ($F_{(1,159)} = 14.489$, $p < 0.001$), revealing that chicks’ performance was significantly different in the first half of the test (mean = 32.400; s.e.m. = 2.000) than after the hen inverted its walking direction (mean = 43.000; s.e.m. = 1.900). Nevertheless, the percentage of alignment was still significantly below chance level also in the second part of the test ($t_{160} = 8.622$, $p = 0.020$). Thus, the counter-alignment was reduced but still present in the last 4 min (Fig. 4).

Chicks that have not been light-stimulated in the last days of embryonic development are still able to discriminate the apparent motion direction of an upright PLD of a walking hen, but seemed to employ equally both eye-systems in this task. This confirms the role of environmental factors such as light-exposure in modulating the development of functional lateralization in chicks.

4. Discussion

The goal of this work was to describe the engagement of the two hemispheres and the effect of brain lateralization in processing biological motion (BM). To this aim we employed two non-invasive techniques. On the one hand we inferred the eye-system spontaneously used by chicks to observe the BM display based on chicks’ body alignment with a stimulus depending on its apparent motion direction. On the other hand we manipulated the level of

lateralization of chicks’ visual pathways, by providing or preventing light exposure of the eggs.

We know that chicks tend to selectively monitor different kinds of stimuli with the eye system connected to the hemisphere specialized for the current task [54,58]. Therefore, hemispheric dominance for BM processing should result in differential alignment depending on the walking direction of the stimulus (i.e., depending on whether or not aligning with the stimulus allows inspection of it with the dominant eye-system). We found that highly lateralized chicks tend, to a significant degree, to inspect a BM-stimulus with the left-eye-system. On the contrary, weakly lateralized chicks did not show any behavioral asymmetry. Moreover, they counter aligned with the apparent direction of motion.

In particular, in Experiment 1, we investigated hemispheric specialization by observing the percentage of alignment with a rightward or a leftward moving hen stimulus and also if this could be modulated by the stimulus orientation (i.e., upright or upside down).

We already knew that chicks aligned their bodies with the apparent direction of motion of the upright walking hen, but oriented their bodies at random when presented with the upside-down version of the same stimulus, since absence of alignment in chicks exposed to the upside-down hen had already been established by previous work [25]. More surprisingly, significant alignment in chicks exposed to the upright hen was actually limited to subjects that, at the beginning of the test, experienced the hen walking rightward. Notably, in order to align themselves with the rightward walking hen, chicks will monitor it with their left eye (right hemisphere). If this happens at the beginning of the test, the chicks will maintain alignment with the walking hen stimulus and preserve it even when its direction was reversed. On the contrary, chicks first exposed to the leftward walking hen will never align with it, indicating that a failure to engage the dominant eye system early on during the first exposure to the stimulus results in compromised alignment also in subsequent time. It is relevant to note that no lateralization was observed of chicks exposed to upside-down stimuli. This inversion effect indicates that the mechanism of action observed here is specific for canonical biological motion processing.

The advantage of the right hemisphere in processing the movement of a living creature is not totally surprising. A general specialization of the right hemisphere for processing and storing visual information about animals is, indeed, testified in different species. For example in face recognition and in perception of facial

expressions the right hemisphere is proved to be dominant in humans [72], sheep [73], and chicks [74–78]. This suggested that the involvement of the right hemisphere in social cognition could be a phylogenetically conserved process (see [78] for a review on different species). More specifically, evidence obtained in human adults and infants indicated a prevalent involvement of the right hemisphere in specialized processing of canonical as opposed to upside-down or distorted BM [42,44–48,50]. Here we demonstrate for the first time that this precise pattern of lateralization is conserved also in non-human animals and can be observed in newborn subjects having a very reduced visual experience, excluding a role of experiential factors in the development of this specialization of function.

In Experiment 2, we limited our investigation to dark-incubated weakly (if at all) lateralized chicks exposed to the BM display of a upright walking hen (since no lateralization was observed for the upside-down condition even in light-incubated chicks). Contrary to individuals hatched from light-incubated eggs, non-lateralized subjects preferred to align themselves in the opposite direction with respect to the walking hen. This could indicate a tendency to face the walking hen, rather than to follow it. This would be consistent with the different social structure of groups of dark-incubated chicks, whose social hierarchies are less stable, implying an increased frequency of agonistic (face-to-face) encounters [79]. Most importantly, dark-incubated chicks did not show any lateralization effect. This confirms the crucial role of light exposure to determine functional asymmetries even in social-perceptual tasks. Despite the fact that the vast majority of studies reveal a causal role of light-exposure for the development of lateralization in chicks, a few papers have reported the presence of lateralized eye use in dark-incubated subjects ([80]; see [78] for a review). This suggested that the developmental mechanisms underlying the emergence of functional lateralization could be task or context specific. In particular, some cases of light-independent lateralization have been observed for chicks tested in social-discrimination tasks involving interaction with conspecifics (e.g., individual recognition, [81]). In contrast, we here observe the expected association of lateralization and light exposure, indicating that the developmental pathway of this functional specialization could be the same described for most other visual tasks in avian species.

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