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**(Background information: Gravity bias in the interpretation of biological
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Gravity bias in the interpretation of biological motion by inexperienced chicks

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Our ability to recognise biological motion in point-light displays is reduced when the animation sequence is upside-down, taken as evidence that past experience about direction of gravity influences the perception of biological motion. We exposed newly hatched chicks, reared in darkness and thus in the absence of previous visual experience, to point-light animation sequences of a walking hen either upright or upside-down: they responded by aligning their bodies in the apparent direction of motion in the former situation, but not in the latter, indicating that the vertebrate brain might be predisposed to make assumptions about direction of gravity.

When an animal moves, its limbs and torso move in characteristic synchrony. Johansson [1] first showed that an animation sequence consisting of just a few strategically placed points of light is sufficient to give a human observer the impression of an animal engaged in a coordinated activity. The detection and recognition of point-light walking is disrupted, however, when the display is turned upside down [2–4]. It has been suggested that difficulties with inverted displays arise, not because parts of the stimulus are not in their familiar relative locations, but because it is hard to recognize the action as the dynamic relations specified by the kinematics are unfamiliar [5]. For instance, in an upside-down display of a walking human, the normal pattern of acceleration shown by the limbs as they are pulling away from and then falling back toward earth is not detected.

Empirical evidence that assumptions about the direction of gravity play a crucial role in

interpreting biological motion has recently been reported. For instance, it has been shown that image inversion has a larger effect on performance than does image scrambling [6]. Even if human subjects had no idea about the kind of animal represented in a scrambled display, they could promptly and accurately indicate its walking direction; but, presenting the displays upside-down had a strong disrupting impact on the perceived direction, with performance dropping almost to chance level [6]. These data have been interpreted in terms of a sensory filter tuned to the ballistic movements of the limbs of an animal during locomotion [7]. Also, when detection accuracy was determined for upright and upside-down displays depicting a point-light human figure walking on his hands, detection was greater in the upright than in the upside-down display, even though the former had an unfamiliar object orientation [5].

These observations were taken [5] as evidence that biological organisms form, by observing the motion of objects in the natural world, a bias about the normal direction of gravity. An alternative, though seemingly unlikely, hypothesis would be that the apparent gravity bias does not require learning, but reflects a predisposition manifesting even in

the absence of visual experience. Developmental studies have been unable to address this issue, hard to prove or disprove unequivocally with human subjects [8].

Non-human animals have also been shown to respond to biological motion patterns [9–11]. We took advantage of the behaviour of the highly precocial domestic chick: chicks have been shown capable of discriminating point-light animation sequences [12], and are predisposed to preferentially approach biological motion patterns when first exposed to point-light animation displays [13]. Naïve, newly hatched chicks, lacking of any visual experience, were presented with a canonical (upright) or an inverted (upside-down) point-light animation sequence picturing a ‘walking hen’ (Figure 1A,B). The displays moved while staying in the same place on the screen, as though representing animals moving on a treadmill.

A single point-light stimulus display was presented to a chick, and for several minutes we scored the chick’s body orientation with respect to the apparent direction of movement of the point-light stimulus (see Supplemental Experimental Procedures available online). This procedure enabled us to measure a chick’s sensitivity to the features of a single biological

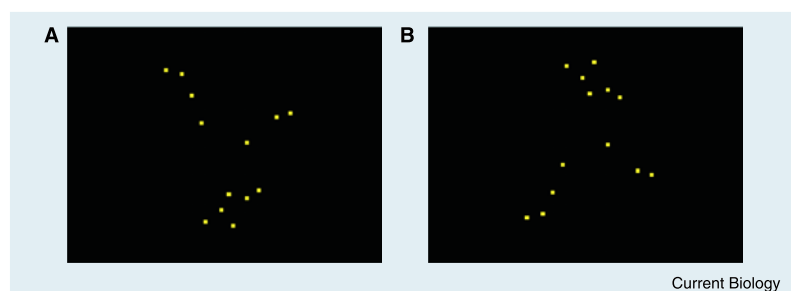


Figure 1. (A) The upright and (B) the upside-down version of the walking-hen animation sequence.

The walking hen animation was obtained by positioning 13 points of light on the main joints of the digitised video-recording of a real animal. The sequence was looped and projected on a computer screen after subtraction of translation, so that the display moved on the spot as if the represented hen was walking on a treadmill. The upside-down sequence was identical, except that the overall array of points of light was mirrored along its horizontal axis. The chick was positioned in front of the computer monitor and its behaviour was video-recorded for eight minutes. The initial direction to which the point-light hen stimulus was heading was randomised, and at the end of the fourth minute, the display was mirrored along its vertical axis, so that the apparent direction of motion changed from left to right or vice versa. 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. (For more details see Supplemental Experimental Procedures).

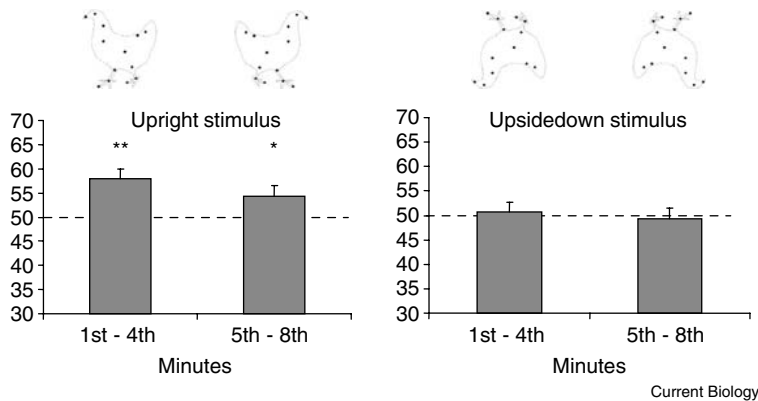


Figure 2. Percentage of time chicks kept their body aligned with the upright and upside-down walking hen stimuli.

Analysis of variance (Anova) was run on the percentage of time chicks kept their body aligned with the walking hen stimulus during the test. The two stimulus orientations were considered as the between-subjects factor, and time (first to fourth minutes *versus* fifth to eighth minutes) as the within-subjects factor. Results are shown with asterisks indicating significant departures from chance level: 50%, estimated by one sample two-tailed t-tests, * $p \leq 0.05$; ** $p \leq 0.0001$. There was a significant main effect of stimulus orientation ($F(1,348) = 9.118$; $p = 0.0027$); and no main effect of time ($F(1,348) = 1.461$; $p = 0.228$) nor of the orientation \times time interaction ($F(1,348) = 0.284$; $p = 0.594$). There were no significant differences between the two time periods in the upright condition ($F(1,168) = 2.394$; $p = 0.124$). A one-sample t-test on the overall eight minutes of the test for the upright position showed that in this condition chicks significantly maintained their body aligned with the stimulus ($t(168) = 2.905$; $p = 0.0042$). In contrast, no significant relation between chicks' body orientation and the walking hen stimulus was found for the upside-down display for the overall testing time ($t(180) = 0.0001$; n.s.). (For more details see Supplemental Experimental Procedures).

motion display in a very similar fashion to the 'direction' paradigm used with humans [7].

Half way through testing the apparent direction of movement of the point-light walking hen was reversed. The percentage of time the chicks maintained their body orientation in the same direction as the apparent motion of the animation sequence is shown in Figure 2. Chicks aligned their bodies with the apparent direction of movement of the upright walking hen — re-aligning themselves following the change in direction of the stimulus — but oriented their bodies at random when presented with the upside-down version of the same stimulus.

These results suggest that visually inexperienced chicks are spontaneously sensitive to the dynamic relations specified by the kinematics of motion of a walking hen, a response related in the more natural situation to filial imprinting [14–16]. Moreover, their sensitivity to the kinematics of the motion of a walking hen is abolished when the display

is upside-down. Previous work [13] has shown that sensitivity to the pattern of biological motion in visually inexperienced chicks is unrelated to the shape of the hen stimulus *per se*, but is purely associated with the kinematics of motion: the predisposition to approach was also observed for the pattern of motion of other vertebrates, even for that of a potential predator such as a cat, or for a scrambled hen in which the point-lights are spatially dislocated [13]. Our results suggest chicks hatch with a predisposition about the direction of gravity and use it to constrain the interpretation of the motion of visual objects. Though more difficult to assess in altricial species, we suspect a similar predisposition is embodied in the architecture of all animal neural systems responding to legged vertebrates, including humans.

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Supplemental data

Supplemental data including Supplemental Experimental Procedures are available at <http://www.current-biology.com/cgi/content/full/16/8/R279/DC1/>

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