Biological motion facilitates filial imprinting

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To study the functional role of the predisposed preference for Johansson's biological motion (BM) at an early stage of life, newly hatched domestic chicks, *Gallus gallus domesticus*, were exposed to a variety of motion pictures composed of light points (in red or yellow), and then tested for their learned colour preference. Point-light animations depicting the BM of a walking hen successfully facilitated both the approach activity during imprinting and the learned preference in the test, although significant positive correlations did not appear between these at the individual level. Furthermore, scrambling the light points did not significantly reduce the effects, whereas linear motion of a hen-shaped set of points had no effect. If pretreated with the linear motion, those chicks primed with a high BM preference score showed a high learning score in subsequent imprinting. We conclude that the local movement feature of the BM animation is critical in making chicks approach and learn the associated colour. We propose a scenario wherein naïve chicks have an innate preference for BM, which arises prior to imprinting through nonspecific visual experience in the early posthatch period. The induced BM preference then allows chicks to form a learned colour preference for the associated colour more effectively, leading to the development of tighter social attachment.

Animations composed of moving light points, if appropriately arranged to represent the major joints of a walking human, generate a vivid perception of locomotion. This phenomenon is known as the perception of biological motion (BM; Johansson, 1973). Highly simplified though the animation is, human observers detect not only the direction and type of the movement (Cutting, Moore, & Morrison, 1988), but also infer various features associated with the animation such as gender (Kozlowski & Cutting, 1977), age (Pavlova, Krageloh-Mann, Birbaumer, & Sikolov, 2002) and emotion (Dittrich, Troscianko, Lea, & Morgan, 1996), and can even identify the individual (Cutting & Kozlowski, 1977). The cognitive capability for BM perception has been thought to be limited only to human adults with mature visual-processing mechanisms, as it develops gradually and slowly in juveniles (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Freire, Lewis, Maurer, & Blake, 2006; Pavlova, Krageloh-Mann, Sokolov, & Birbaumer, 2001).

Recent studies have shown that BM perception might occur in taxonomically remote animals. Cats, *Felis catus*, were trained to discriminate BM animations from non-BM counterparts in an operant conditioning study (Blake, 1993). Marmosets, *Callithrix*

jacchus (although only females) inspected a BM animation of a walking hen more than the other patterns (Brown, Kaplan, Rogers, & Vallortigara, 2010). Further pioneering work reported that newly hatched domestic chicks, *Gallus gallus domesticus*, show a preference for the point-light animation depicting a walking hen (BM) over non-BM alternatives (Regolin, Tommasi, & Vallortigara, 2000; Vallortigara & Regolin, 2006; Vallortigara, Regolin, & Marconato, 2005). More recently, we confirmed these findings, as chicks showed a clear BM preference when they had been pretreated by any sort of point-light animation (Miura & Matsushima, 2012). The animation did not necessarily have to be a BM picture, and even an assembly of randomly moving light points was effective. We therefore agree with the idea that BM preference is predisposed (Rosa Salva, Mayer, & Vallortigara, 2015). Chicks may not learn BM, but the BM preference is induced through nonspecific visual experiences. Also, in Vallortigara et al.'s (2005) study, chicks ran in a running wheel in the darkness before the BM preference tests. Besides the visual experiences, chicks may thus have to execute motor activities in response to the stimuli. The critical factors required for the BM preference induction are yet to be specified.

We must stress that the BM preference arises at a very early stage of chick life. This early emergence is also found in humans, as 2-day-old babies prefer the walking hen animation in preference looking tests (Simion, Regolin, & Bulf, 2008). Although it is unclear whether chicks or newborn human babies have processes similar to

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those employed by human adults, the BM preference in the early postnatal (posthatch) period may be based on a common mechanism shared by birds and humans. In this respect, it is interesting that chicks have a similar pattern of functional lateralization of BM preference to that found in humans (Rugani, Rosa Salva, Roglin, & Vallortigara, 2015).

What functional roles might the BM preference play in early life? Imprinting, and the social bond formation that follows, might be a target. Precocial chicks follow conspicuous objects and learn their visual features (colour and shape in particular) after a brief exposure in the early posthatch period, a process referred to as imprinting (Lorenz, 1937; also see reviews in Bolhuis & Honey, 1998; Horn, 2004; Matsushima, Izawa, Aoki, & Yanagihara, 2003). Even though chicks can be imprinted with a variety of artefacts such as a rotating cylinder or a toy made of LEGO blocks (Izawa, Yanagihara, Atsumi, & Matsushima, 2001; Yamaguchi et al., 2012), the preference gradually shifts towards more natural objects such as a stuffed hen (Johnson, Bolhuis, & Horn, 1985), suggesting that filial behaviour is also influenced by a predisposition (Bolhuis, 1991; Rosa Salva et al., 2015). Possibly, imprinted chicks may gradually shift their preference to those objects with a predisposed nature, such as BM pictures, and/or the BM preference may arise earlier than the filial imprinting, allowing chicks to form a memorized attachment selectively to those objects.

In this study, we investigated the possible contribution of BM preference to imprinting. We did not address the possibility that the BM preference is strengthened after imprinting. Specifically, we asked (1) whether chicks would selectively learn the colour associated with BM animations and (2) if pretreated with nonspecific visual stimuli to show a BM preference, whether chicks would score higher in learned colour preference by imprinting. To do that, we recorded two behavioural parameters: the number of approaches to a single visual stimulus during imprinting and the learned colour preference in a binary choice test.

GENERAL METHODS

Subjects and Ethical Note

Domestic white leghorn chicks (Julia strain) were used at 24–48 h posthatch. Fertilized eggs supplied from a local hatchery (Iwamura Poultry Co. Ltd., Yubari, Japan) were incubated in the laboratory. The inside of the incubator was kept in darkness. To avoid posthatch visual experiences, hatchlings were individually housed and kept in another incubator in complete darkness. After the experiments, chicks were sexed and euthanized by carbon dioxide. A total of 221 chicks (111 males and 110 females) were used. We did not perform any potentially harmful manipulations, invasive sampling of blood or tissues or tagging. All experiments were conducted under the guidelines and approval of the Committee on Animal Experiments of Hokkaido University. The guidelines are based on the national regulations for animal welfare in Japan (Law for Humane Treatment and Management of Animals; after a partial amendment No. 68, 2005).

Apparatus

We used an I-shaped maze (9 cm × 70 cm) equipped with a 50 cm long treadmill consisting of a rubber belt at the centre and an LCD monitor at each end. During imprinting and pretreatment (Fig. 1a), an infrared sensor and a transparent Plexiglas partition were placed at a point 10 cm from the monitor, and the other monitor was occluded by an opaque partition. When chicks ran and hit the sensor, the rubber belt of the treadmill moved for 0.3 s, drawing the chick backwards by about 30 cm at a time. The
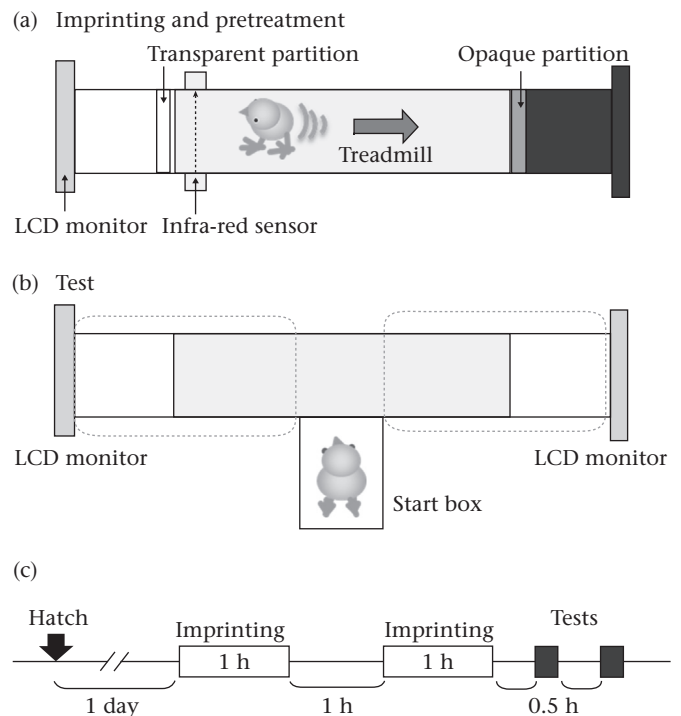
Figure 1. Apparatus used for (a) imprinting and pretreatment and (b) testing. (c) The procedure is shown schematically for experiments 1 and 2. Chicks were imprinted twice at a 1 h interval, and subsequently tested twice at 0.5 h intervals. During the first posthatch day and the intervals between the sessions, chicks were individually housed in a dark incubator at 37–38 °C. For experiments 3-1 and 3-2, see Figs 4a and 5a, respectively.

treadmill motion was digitally counted, and the number of approaches was recorded for each of the trials, which lasted for 1 h if not stated otherwise.

In the binary choice test (Fig. 1b), the partitions were removed and the treadmill was turned off. The subject chick was enclosed in a start box placed at the centre for about 10 s, and was then allowed to freely go out and choose between the two arms. We recorded the total stay time near each monitor for a period of 5 min, starting from the point when the chick walked out of the start box. The choice test was repeated twice with the side changed after 0.5 h (in experiments 1 and 2) or about 1–2 min (experiments 3-1 and 3-2). The behaviour of the subject chick was monitored through a CCD camera (250 kilo pixels) placed on the ceiling, and the videos were stored for offline analysis in a video recorder (DCR-SR60, Sony, Japan). The apparatus was placed in a soundproof wooden box, which was illuminated by infrared LED lamps.

Video Clips and Point-light Animations

For imprinting and pretreatment, we used a full-screen colour illumination (Plate), two realistic video clips (LEGO block and Real chick), and seven point-light animations (LEGO point, Walking hen, Stationary dots, Walking chick, Scrambled, Linear motion and Stationary chick). The colour preference was tested using a binary choice between two Plates with different colours (yellow and red). The BM preference was tested using a binary choice between a pair of point-light animations (Walking hen and Rotating hen). These are available in the Supplementary Material. The videos/animations were accompanied by sounds, except those used in the BM preference test (Walking hen and Rotating hen) and the colour preference test (test (red) and test (yellow)). The same sound source