



Experience during a period of right hemispheric dominance alters attention to spatial information in the domestic chick

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We tested the hypothesis that experience of moving out of sight of an imprinting stimulus during a period of right hemispheric dominance (11 days of age), but not during a period of left hemispheric dominance (8 days of age), biases attention to distal spatial cues. Domestic chicks, *Gallus gallus domesticus*, were trained to locate a hidden imprinting object behind one of two differently marked screens placed at either end of a rectangular arena, and then presented with five unrewarded probe tests with the arena rotated by 180°. Chicks that had experience of going behind opaque screens on day 11 chose the screen in the same direction as during training (i.e. using distal cues) significantly more often than chicks given experience with opaque screens on day 8 or chicks provided with two transparent screens on either of these 2 days. We conclude that the similarities between behaviour patterns of chicks in the laboratory and in seminatural environments suggest that moving out of sight of the mother at 11 days of age is an ecologically important behavioural pattern that requires dominance by the right hemisphere to shift the chick's response to distal spatial information for locating a hidden goal.

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The domestic chick, *Gallus gallus domesticus*, with its accomplished spatial memory, known lateralization of brain and behaviour and neuronal and behavioural plasticity, is a useful model for studying the development of brain and behaviour (e.g. Rogers 1995). Domestic chicks are able to detour around a barrier to obtain a goal (Regolin et al. 1995) and can use landmark, geometric (Tommasi & Vallortigara 2000) and magnetic (Freire et al. 2005) cues to locate a hidden goal. In the domestic chick, the hippocampus is involved in spatial memory formation (Nakajima et al. 2003), and the processing of geometric spatial features occurs in the right hippocampus (Tommasi et al. 2003), as has been found in other vertebrates (reviewed in Vallortigara et al. 2004). The right hippocampus of chicks has

longer dendrites and more synapses than the left hippocampus (Freire & Cheng 2004), further supporting a functional similarity between the avian and mammalian hippocampus (Colombo & Broadbent 2000).

Studies involving monocular tests of spatial memory in chicks suggest that the right hemisphere is primarily concerned with processing and responding to nonlocal spatial information (distal cues), whereas the left hemisphere is concerned with local cues (Rashid & Andrew 1989; Tommasi & Vallortigara 2004; Freire & Rogers 2005). For example, Tommasi & Vallortigara (2004) trained chicks to locate food hidden in the centre of an enclosure next to a landmark (a red cylinder) and then tested the chicks monocularly with the landmark displaced. The chicks that used the left eye searched in the centre of the apparatus (thereby using geometric spatial information) and those that used the right eye searched near the displaced landmark. Since input from the left eye is processed primarily in the right hemisphere (Rogers 1995), this result indicated use of the right hemisphere for controlling responses to geometric

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spatial cues. Lesioning of the hippocampus provided further support for this deduction (Tommasi et al. 2003); lesions in the right hemisphere removed the response to geometric cues, whereas lesions to the left hemisphere, or a sham procedure, did not. In another test, chicks were tested in a delayed-response task with local and positional cues (i.e. relative left and right positions) in conflict; the chicks that used the left eye preferentially used positional information, whereas those that used the right eye showed no preference for local or positional information, as predicted (Regolin et al. 2005). When these cues were not in conflict, the chicks using either the left or right eye were able to use both local and positional cues, suggesting that both local and positional spatial information are available to both hemispheres. Hence, the hemispheric differences seem to be at the level of decision making rather than there being specialized availability of perceptual information.

One technique that reveals the processing of local and nonlocal spatial information is the rotated floor test, in which chicks are trained to locate a goal hidden on one side of the apparatus, usually marked with distinguishing local features, and are then tested with the apparatus rotated by 180°, so that extra-apparatus (distal) cues are in conflict with intra-apparatus (local) cues (Rashid & Andrew 1989). The kind of distal spatial information that the chicks use in this latter test is largely undetermined, but is thought to include features of the ceiling, lighting direction, and possibly olfactory (Rashid & Andrew 1989; Freire & Rogers 2005) or magnetic cues (Freire et al. 2005). By presenting local and distal spatial information in conflict, the rotated floor test has consistently revealed a difference in response for chicks using the right or left eye, indicating that the right hemisphere preferentially responds to distal cues and the left hemisphere to local cues (Rashid & Andrew 1989; Freire & Rogers 2005).

Although it has been known for some time that the domestic chick shows sharply timed periods of bias in dominance of either hemisphere during development (Andrew 1991, 2002), the role of these shifts in dominance in these lateralized spatial responses is largely undetermined. Of particular relevance to spatial memory is the shift in dominance to the right hemisphere on day 11 (Rogers & Ehrlich 1983), a period when chicks in seminatural conditions actively move out of sight of the mother hen (Workman & Andrew 1989). Chicks in the laboratory also show a peak in moving out of sight of an imprinting stimulus on day 11 (Freire et al. 2004). Providing chicks with the opportunity to experience being out of sight of an imprinting stimulus by moving behind a screen on days 10–12 improves performance in a detour and a visual displacement tests (Freire et al. 2004) and increases dendrite length and linear spine density in the hippocampus (Freire & Cheng 2004), indicating that experience at this time affects both behaviour and brain development. Hence, particular experiences during this sensitive period shape spatial memory, and mark it as one of the known periods during development when it may be important that one or the other hemisphere is dominant for the appropriate, age-related control of behaviour.

The function of these shifts in hemispheric dominance is largely unknown; they may act to constrain behaviour

or to allow each hemisphere to learn particular responses (Andrew 2002). It is unclear whether the effectiveness of the experience of moving out of sight of the imprinting stimulus is restricted to day 11 or can occur at other ages or, perhaps more relevantly, during periods of dominance of the left hemisphere. The left hemisphere is dominant on day 8, as revealed by asymmetrical sensitivity to the action of cycloheximide (Rogers & Ehrlich 1983). We used a rotated floor test to test the hypothesis that experience of moving out of sight of the imprinting stimulus during a period of right hemispheric dominance (day 11), but not during a period of left hemispheric dominance (day 8), shifts attention to distal spatial information.

METHODS

We tested 24 layer chicks exposed to light throughout incubation (Nulkaba Hatchery, Cessnock, NSW, Australia) and obtained as day-old chicks. The chicks were reared in isolation from arrival until 7 days of age in grey, sheet-metal cages (25 × 25 cm and 30 cm high). A yellow tennis ball was suspended by string 10 cm above the floor in the centre of the cage to provide an imprinting stimulus. Temperature was maintained at 35°C for the first week after hatching and lighting from halogen strips was provided on a 12:12 h light:dark cycle. The floor of the cage was lined with white paper and sprinkled with chick starter crumbs to encourage eating; the chicks were also observed regularly throughout this time to ensure that they found the food and water. Brief isolation at this age did not cause distress and chicks were housed in pairs after the imprinting period to allow them to show social behaviour. Water was available *ad libitum* from a drinker placed outside the cage with the cup on the floor. In the first few days chicks were sexed by inspection of the wing feathers: primary and secondary wing feathers are the same length in females but different lengths in males.

When the chicks were 7 days old, we paired them (one male and one female as far as possible) and placed each pair into a home pen (50 × 50 cm and 60 cm high). Pairing at this age was undertaken to uphold the welfare of the chicks by providing access to litter and allowing them to express social behaviour. The chicks were observed regularly during this time to ensure that aggression did not occur and that welfare was not compromised: aggression was not observed nor were there any other signs that pairing at this age caused distress. A yellow tennis ball was suspended by a string in the centre of the pen, 10 cm above the floor. The floor was covered with wood shavings and food (starter crumbs) and water (from an externally placed drinker) were available *ad libitum*.

At lights-on on day 8, we added two screens (20 × 20 cm and 30 cm high) to each box centrally and 10 cm either side of the imprinting stimulus, and these were removed just before lights-on on day 9. Similarly, we added two screens to each box on day 11, and removed these just before lights-on on day 12. Some pairs of chicks were provided with opaque screens made of wood (0.5 cm thick) and painted grey and others with transparent screens made from acrylic sheet (0.3 cm thick). There were three treatments: T8 chicks experienced opaque

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