Lateralization of social learning in the domestic chick, *Gallus gallus domesticus*: learning to avoid

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Social learning occurs through the observation of conspecifics performing biologically relevant behaviours. Like other forms of learning, aptitude for such tasks may be influenced by cerebral lateralization. Social recognition is subject to lateralization and it seems highly likely that any lateralization effect would be transposed onto a social-learning situation. We used a social version of a passive avoidance task in which one chick (the demonstrator) pecked at a red bead while another chick (the observer) viewed the demonstrator's response. This bead was either coated in the bitter-tasting substance methylanthranilate (MeA) or was left dry. Thirty minutes later both chicks were presented with a similar, dry, bead to determine whether learning had taken place. Experiment 1 showed that chicks were able to learn, by observation only, not to peck the bead when it had been coated in MeA at training. Experiment 2 demonstrated a role of lateralization in performing the task; specifically, male observer chicks trained binocularly but tested monocularly had a poorer performance in this task with the left hemisphere than with the right. In experiment 3, we both trained and tested chicks monocularly. This time there was no difference between left-eyed and right-eyed chicks, suggesting a spontaneous bias for encoding relevant information available at training in the right hemisphere. In conclusion, chicks are able to avoid pecking just by observing a conspecific. The social learning appears to be lateralized to the right hemisphere in male chicks, females showing no bias in lateralization.

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The ability to learn from the behaviour of conspecifics confers an important adaptive advantage, allowing an individual to benefit from the experiences of others without the need for direct interaction itself. For example, social learning may result in increased foraging efficiency by reducing the costs required for learning, by direct experience, the features and edibility of different food sources (Nicol 2004, 2006). Chicks of the junglefowl, *Gallus gallus spadiceus* (the wild ancestor of domestic chickens) do not have an innate ability to recognize edible food items, and tend to peck at both food and nonfood objects (Hogan 1973). Learning to recognize edible items is thus required in this species, but direct learning arising from the consequences of ingestion does not seem to be possible shortly after hatching, increasing the importance of social learning (Nicol 2004, 2006). Birds including gallinaceous species, seem to be capable of learning about the availability and quality of food sources via social mechanisms. The mother chicken influences

the feeding behaviours of her chicks by attracting their attention towards suitable food sources in the environment (Moffat & Hogan 1992; Nicol & Pope 1996; Nicol 2004, 2006; Allen & Clarke 2005). The feeding behaviours of chickens are influenced not only by maternal food displays, but also by the behaviour of a peer demonstrator (McQuoid & Galef 1992, 1993, 1994; Nicol & Pope 1992, 1993, 1994, 1999; Gajdon et al. 2001; Sherwin et al. 2002; Caldwell & Whiten 2003; Nicol 2004; for similar evidence of social learning in chicks, but with an artificial demonstrator see Bartashunas & Suboski 1984; Suboski & Bartashunas 1984).

The ability to refrain from ingesting items that conspecifics avoid eating could have as much adaptive value as the tendency to consume food preferred by social partners by reducing the risk of consuming potentially poisonous items. When hens observe chicks pecking at a kind of food that they had experienced as being unpalatable, they increase behavioural displays to direct the chicks' attention towards other, palatable food (Nicol & Pope 1996; Nicol 2004; 2006). This result suggests that maternal displays and the consequent social learning of the chicks could serve to redirect the chicks' attention away from unpalatable food sources. Adult hens seem incapable of learning to avoid pecking at a food that elicited a 'disgust' reaction in another hen (Sherwin et al. 2002). This lack of avoidance may have been because although demonstrators eating

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the unpalatable food showed a disgust reaction, they continued eating, thus providing potentially conflicting information to their observers (Nicol 2004). This result is inconsistent with evidence indicating the presence of social learning for pecking avoidance in day-old chicks (Johnston et al. 1998). This difference may be a result of the different ages of the subjects: newborn chicks learning for the first time to distinguish food with respect to nonfood items could be more sensitive to social learning derived from the observation of the feeding behaviours of others. This sensitivity may be reduced as the chicks mature and the consequences of ingestion may become an important source of information about food palatability (Nicol 2004). In addition, Johnston et al's. (1998) procedure was radically different from that of Sherwin et al. (2002). Johnston et al. used a modified version of the one-trial passive avoidance learning (PAL) task described by Lössner & Rose (1983). This task exploits the tendency of young chicks to peck at any small object presented to them. The task involves the presentation of a coloured bead coated in a bitter-tasting substance (usually methylanthranilate, MeA) to a chick. Chicks usually peck at the bead but pecking MeA is an aversive experience, following which chicks display a disgust response, which includes behaviours such as head shaking and bill-wiping. After undergoing this training, chicks will subsequently avoid pecking at a bead of similar colour and size (but not at a bead of a different colour and/or size) for 24 h or more (Cherkin 1969; Lössner & Rose 1983).

In the PAL task, chicks are usually trained and tested in pairs (Ng et al. 1991), but social information transmission between cage-mates does not seem to be present when the standard version of the procedure is used (Gibbs & Ng 1977). Nevertheless, Johnston et al. (1998), who used a slightly different version of the procedure, found convincing evidence showing just such an occurrence. They used pairs of chicks in which one of the pair (the 'demonstrator') was presented with a chrome bead dipped in either MeA or water. The second chick in each pair was termed the 'observer', and was prevented from pecking at the training chrome bead. During the test phase the demonstrator and observer chicks were presented, one at a time, with a dry chrome bead, followed by the presentation of a dry white bead to determine whether the chicks' response was specific to the bead or a general inhibition of pecking.

With that procedure, it was possible to prove that both demonstrator and observer chicks avoided pecking at the dry chrome bead up to 24 h after the observer chick had seen its demonstrator pecking a similar bead coated in a bitter-tasting substance. In contrast, chicks continued to peck at the dry chrome bead if, during the training phase, the demonstrator had pecked a similar bead that was coated in water and that had not elicited any disgust reaction. This social learning occurred specifically during training.

The formation of a memory for the PAL task occurs over the course of several hours, with a range of biochemical, physiological and morphological changes (Rose 2000) associated with different memory phases (e.g. short-term, intermediate-term and long-term memory, see Gibbs et al. 2003) leading to a permanent memory. Localized brain circuits, such as those within the mesopallium and medial striatum, seem to be involved in these memory phases (e.g. see Freeman & Rose 1999) with the resulting activity lateralized in a time-dependent fashion (e.g. Andrew 1999; Rose & Stewart 1999; Rickard & Gibbs 2003a, b). A flow of memory has been hypothesized, with a transfer of memory from the left mesopallium through to the right mesopallium and then later to the left and right medial striata or to the basal ganglia (e.g. Patterson et al. 1990). Bilateral or left, but not right, pretraining mesopallium lesions interfere with the acquisition of this task (Patterson et al. 1990) consistent with biochemical evidence showing that the memory trace appears to consolidate first in the left mesopallium and then in the right (Sandi

et al. 1993). Other authors have hypothesized changes in linkages between distributed memory fragments, with different informational content in the two hemispheres, rather than a flow of memory with trace transfer over time (Andrew 1999). According to these models, successive phases of memory formation would be determined by changes in the left hemisphere trace, responsible for the performance at test, possibly with moments of integration with the contents of the right hemisphere trace (Gibbs et al. 2003). Existing evidence thus seems to indicate that the memory for the PAL task (in its standard nonsocial version) forms in the left hemisphere (Gibbs et al. 2003).

The predominant role of the left hemisphere in memory formation for the PAL task, in its standard nonsocial version at least, may be because of the importance of the left hemisphere in controlling motor responses towards objects (Andrew et al. 2000). In addition, the left hemisphere performs a role in the discrimination of local, specific cues associated with a target (such as the colour of the bitter-tasting bead; see Vallortigara et al. 1996; Tommasi & Vallortigara 2001). However, the social-learning task used by Johnston et al. (1998) was different, with respect to the standard PAL task, in that it involved the elaboration of social cues. In chicks, as well as other animals, the right hemisphere appears to be dominant for various aspects of social cognition, including the recognition of individual conspecifics (Vallortigara & Andrew 1991, 1994; Vallortigara 1992; Deng & Rogers 2002; Andrew et al. 2004) and gaze processing (Rosa Salva et al. 2007). This differential use of brain hemispheres is due to a structural lateralization in the chick's brain that is triggered by exposure of the embryo in the egg to light (Rogers & Sink 1988). During a critical period (Rogers 2008) exposure to light produces an asymmetrical stimulation of the two eyes and the consequent lateralization of projections of the visual pathways to the forebrain (Rogers & Bolden 1991; Rogers & Deng 1999; Koshiba et al. 2003).

Nevertheless, some behaviours, including social behaviours such as preferences to approach a social companion are known to be lateralized also in dark-incubated chicks (Deng & Rogers 2002; Andrew et al. 2004). An intriguing hypothesis in this regard is that some forms of lateralization involving the social domain may emerge independently from environmental cues such as exposure of the embryo to light. This in turn could result from within-population consistency in the strength and direction of lateralization being extremely relevant in the social domain (Vallortigara & Rogers 2005); thus mechanisms could have evolved ensuring that all individuals are similarly lateralized, despite changes in environmental conditions.

Thus, one issue to arise is that regarding the lateralization pattern expected for this social-learning version of the PAL task, which requires both elaboration of behavioural cues from the demonstrator (probably a right-hemisphere process) associated with the bead's visual cues (a left-hemisphere process) and also effective control of the pecking response (again a left-hemisphere process). Our main aims were to confirm that 2-day-old domestic chicks are capable of the social learning of pecking avoidance (Johnston et al. 1998), and to investigate the presence and direction of lateralization effects in observer chicks for the social version of the PAL task.

GENERAL METHODS

Subjects

We used domestic chicks of the 'Hybro' strain. For experiment 1 chicks were obtained weekly from a local commercial hatchery (Agricola Berica, Montegalda (VI), Italy) when they were only a few hours old. These chicks hatched from eggs incubated in the dark, so