



Swapping mallards: monocular imprints in ducklings are unavailable to the opposite eye



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Eutherian mammals are unique in that sensory input from each eye is exchanged and shared between left and right brain hemispheres through the corpus callosum. All other vertebrates lack this structure and hence interocular information exchange is more restricted, raising issues of how information acquired with each eye contributes to the control of behaviour. Studies of food hoarding, laboratory-based discrimination tasks and homing in birds show that information acquired with one eye is not immediately available for action guided by the opposite one. We investigated interocular transfer, using filial imprinting in pekin ducklings, *Anas platyrhynchos domestica*, as our experimental system. In experiment 1 we imprinted hatchlings on either of two duck decoys, in three treatments differing on whether (A) birds were trained and later tested for a following response binocularly, (B) trained and tested monocularly, with the same eye, or (C) trained and tested monocularly, with opposite eyes. Birds preferred the training decoy for at least 3 h after imprinting in treatments A and B, but were indifferent in C. In experiment 2 birds were imprinted sequentially with two decoys, in three treatments where they were (D) trained and tested binocularly, (E) trained monocularly with a different decoy for each eye and tested monocularly with each eye, or (F) trained monocularly with a different decoy for each eye and tested binocularly. In treatment D ducklings were close to indifference, with a weak preference for the most recent decoy. In treatment E preference weakly favoured the decoy used during imprinting with the eye being tested. Finally, in treatment F there was no evidence for dominance of either eye. Thus, imprinting information is laterally isolated for at least 3 h, the experience status of the opposite eye (naïve or with a competing imprinting) has a small effect and we found no evidence for eye dominance.

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Among vertebrates, only eutherian mammals have a corpus callosum, the main anatomical structure allowing a high level of rapid information exchange between the left and right brain hemispheres. In the case of birds, while several smaller commissures connect the two hemispheres (Parsons & Rogers, 1993; Rogers, Vallortigara, & Andrew, 2013), the relative independence (compared with mammals) of information processing between the left and right sides of the brain is interesting for a number of reasons. On the one hand, relating differences in neuroanatomy to differences in behaviour between mammals and birds allows for deeper understanding of how action is controlled by the brain in general. On the other, it makes birds a useful model for exploring hemispheric information integration, including how a system so

different from the mammalian one controls attention and use of acquired information to control action.

The avian visual system consists primarily of the tectofugal and thalamofugal pathways. In most birds, the optic nerves are completely decussated, and the inputs from each eye project only to the contralateral hemisphere. From there, in both the tectofugal and thalamofugal pathways, inputs remain mostly within the same hemisphere: in the tectofugal, the right tectum projects to the right nucleus rotundus and vice versa, and in the thalamofugal, the right dorsal lateral geniculate nucleus projects to the right wulst and vice versa. In both pathways, there are also smaller interhemispheric projections, which are generally smaller than the ipsilateral projections, and, in some species, lateralized, with one hemisphere sharing more information contralaterally than the other (Diekamp, Prior, & Güntürkün, 1999; Manns & Ströckens, 2014; Parsons & Rogers, 1993). This results in brains in which each hemisphere may have a better representation of the contralateral eye's inputs than the ipsilateral, and in which one hemisphere may have more ipsilateral eye information than the other.

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Monocular learning experiments have demonstrated varying levels of hemispheric integration of visual information in bird species. Experiments in marsh tits, *Poecile palustris*, have shown that food cached with one eye open is not found when searching with the other (Sherry, Krebs, & Cowie, 1981), but that information gathered with the left-eye system is apparently transferred to long-term memory in the right-eye system between 3 and 24 h following learning (Clayton, 1993). Incomplete contralateral visual input has been demonstrated in local area homing in pigeons, *Columba livia* (Martinho, Biro, Guilford, Gagliardo, & Kacelnik, 2015), and inter-hemispheric transfer of pattern discrimination fails in chickens, *Gallus gallus* (Gaston, 1979), although in the latter case, reinforcement with food enabled previously failed transfer (Gaston, 1984). This lack of complete access to the other hemisphere's visual memories has produced a similar pattern in binary discrimination and transitive inference tasks in pigeons (Diekamp et al., 1999; Manns & Römmling, 2012). In most cases, visual input seems to be restricted to the eye-contralateral hemisphere, with integration via interhemispheric transfer occurring some time later. Several studies in young chicks have suggested that this hemispheric independence may support task specialization in each hemisphere, with left and right eyes and hemispheres taking on differing roles (Deng & Rogers, 2002; Horn, 1979; Horn & Johnson, 1989; Rogers et al., 2013).

Most existing studies dealing with hemispheric integration in birds have used adult birds and protracted learning with the initial eye to develop memory contents: a homing pigeon requires at least eight to 10 flights over several days to develop a route, and binary choice and transitive inference require reinforcement over the course of many trials. The hoarding–retrieval experiments with adult marsh tits are an exception, because memory for the location of caches presumably takes place during the brief exposure to the hoarding site and its spatial context. Here we investigated interocular transfer in newly hatched pekin ducklings, *Anas platyrhynchos domestica*, using imprinting as the critical task.

Avian filial imprinting is recognized as a unique form of learning, notable for having an obvious major biological function, occurring without explicit reinforcement, being fast, relatively permanent and confined to well-defined critical or sensitive periods (Bateson, 1964, 1966, 1979b; Lorenz, 1937; Ramsay & Hess, 1954; Ratner & Hoffman, 1974). In its most characteristic natural form, imprinting manifests as a strong attraction by which young nidifugous birds tightly follow their mother (Bateson, 1966), her presence providing protection from predation, guidance to food sources and in the case of the Anatidae waterfowl, waterproofing of the chicks' feathers until their own preen glands develop.

An imprint is formed by exposure to some stimulus during the sensitive period (Bateson, 1979b), and forms in a relatively short amount of time, with preference for the imprinted stimulus over a novel stimulus in a binary test occurring after as little as 15 min of prior exposure to the imprinted stimulus (Bateson & Jaeckel, 1976). Imprints may be formed for multiple stimuli to which the chick is exposed during the sensitive period (Bolhuis & Bateson, 1990), and in such cases the multiple imprints are sensitive to primacy of formation and immediacy of exposure: more recently encountered stimuli are generally preferred to those encountered earlier, but equally recent exposure results in a preference for the imprint that formed earlier (Bolhuis & Bateson, 1990). Imprints can be formed of both visual and auditory stimuli (Boyd & Fabricius, 1965), and maternal auditory calls can enhance the strength of imprinted response to a visual stimulus (Dyer & Gottlieb, 1990).

Duckling imprinting is useful to investigate the autonomy of visual inputs and the timescale over which learned visual information may become available to the contralateral hemisphere, because multiple tests can be undertaken within minutes and hours of reliable acquisition, rather than after days of training.

Monocular imprinting has been investigated in ducklings before; Moltz and Stettner (1962) showed that a duckling imprinted monocularly on a moving duck decoy during several sessions would follow that decoy when only the contralateral eye was available (Moltz & Stettner, 1962). However, ducklings took several minutes to begin to follow the stimulus, and Moltz and Stettner rightly suggested that the following response exhibited during contralateral testing could be due to reacquisition of the imprint with the naïve eye, as the imprinted stimulus was the only moving object available to the duckling during testing (Moltz & Stettner, 1962). Furthermore, training occurred over 3 days, a span shown in other species to be sufficient for interhemispheric transfer, which may have allowed the ducklings access to interocular transfer not available immediately after initial imprinting.

We employed a protocol similar to that of Moltz and Stettner but included an additional, novel stimulus in the test phase to compete with the imprinted stimulus, and confined all training to 30 min and all testing to within 3 h of the conclusion of training. This allowed us to rule out reacquisition with the naïve eye, because if imprinting begins anew with the contralateral eye in the test phase, it would result in equivalent imprinting of the two decoys, regardless of the previous experience of the other (now occluded) eye. The very brief nature of imprint learning allowed us to investigate whether information gathered with one eye is available to the other in the interval before interhemispheric transfer occurs (3 h after acquisition, as in caching marsh tits). Furthermore, by testing at hourly intervals within this period, we probed the first hours after imprinting for evidence of interhemispheric transfer, which if present would result in increasing following fidelity to the originally imprinted stimulus.

Using moving imprinting stimuli shaped as adult duck decoys of indeterminate species, and identical to each other except for colour (see Fig. 1), in experiment 1 we investigated the capacity of ducklings imprinted with only one eye available to distinguish between an imprinted and novel stimulus at hourly intervals across the first 3 h following learning. In experiment 2, we explored intereye dominance and the influence of alternative eye experience by setting imprints formed with each eye at odds, allowing them to compete for control of the ducklings' preference.

METHODS

Ethical Note

These experiments were conducted according to the University of Oxford's Department of Zoology animal welfare standards. The experimental protocols were approved by the University of Oxford's Animal Welfare and Ethical Review Body. We used 88 1–2-day-old domesticated mallard ducklings of unknown sex in the experiments. They were incubated and hatched by Oxford University Farms and returned to their care upon completion of trials. They were housed together in a heated industrial brooding chamber before and after the experiments and in smaller social brooding baskets with overhead heat during experimental intervals. Handling was kept to a minimum to avoid disturbance, and consisted only of moving animals from one chamber to another (which occurred over a matter of seconds), and of fitting goggles. The goggles were designed with Velcro release to allow swift fitting and removal (again, on the order of seconds) and were lined with silk to avoid discomfort. No invasive procedures occurred in this study.

Experiment 1

Subjects

Subjects were 48 newly hatched pekin ducklings, from a variety of clutches within an established farm stock, between 15 and 31 h

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