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Research report

Effects of light stimulation of embryos on the use of position-specific and object-specific cues in binocular and monocular domestic chicks (*Gallus gallus*)

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Abstract

Chicks hatched from eggs incubated in the dark (D-chicks) or from eggs exposed to light during the last 3 days before hatching (L-chicks) were trained on day 4 to peck at small cones for food reinforcement. The cones had different patterns (checked or striped) and were located in different positions (either on the left or on the right of a rectangular arena) so as both object-specific (pattern) and position-specific cues could be used to discriminate cones that contained or that did not contain food. After learning, the position of the cones was reversed so that object- and position-specific cues provided contradictory information. No effect of light incubation was observed in binocular chicks that chose cones on the basis of object-specific cues. Monocular D-chicks also tended to approach and peck the cones with the correct pattern in the wrong position, whereas monocular L-chicks did not show any clear choice. Initial choices for one side or other of the arena were mostly determined by the first side visible through the non-occluded eye in D-chicks, particularly when using their left eye. These results suggest that light exposure of the embryo makes neural mechanisms that do not receive direct visual input (i.e., those of the occluded side) more available to be used in assessment of novelty.

Keywords: Light exposure; Embryo; Brain lateralisation; Asymmetry; Spatial cognition; Domestic chick

1. Introduction

The domestic chick is used widely as a model system for research on cerebral lateralisation of functions [2,19–21, 34,36,40]. This species possesses features such as a nearly complete decussation of the fibres at the optic chiasma, relatively poor interhemispheric connections compared to mammals (but see [6]) and independent scanning by the two eyes [2]. This makes it possible to study the separate functions of the two hemispheres using the simple technique of the temporary occlusion of one eye, which largely confines processing of visual information to the hemisphere contralateral to the stimulated eye.

Using monocular tests it has been proven that the chick's brain is lateralised for control of a range of visual responses. The right eye/left hemisphere system (RES) attends to categorisation of visual stimuli and it seems to be responsible for the visual control of a considered response (see for reviews [21,38]). The RES superiority in visual discrimination learning has been demonstrated in other avian species besides chicks [12], namely in pigeons [10], zebra finches [1] and quails [28]. The left eye/right hemisphere system (LES) seems to be more involved in certain aspects of spatial cognition [14,39,26,27], in the assessment of novelty [2] and in establishing identity with a past

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experience by attending to the details of individual stimuli [29,31,32].

Some of these behavioural asymmetries have been associated with neuroanatomical asymmetries caused by the exposure of the right eye of the embryo to light during the later stages of development before hatching. The chick embryo is oriented in the egg so that only the right eye receives light stimulation passing through the shell and the membranes, whereas the left eye is covered by the rest of the body [18]. This asymmetric light stimulation in embryo promotes asymmetric development of the visual projections that originate from the left side of the thalamus (fed by the right eye) and continue to the visual Wulst [23]. This has been revealed by injecting fluorescent tracers in the Wulst and then looking for ipsi- and contra-lateral labelled cell bodies in the thalamus. The exposure of the right eye to light leads to an increased number of visual projections from the left side of the thalamus (which receives inputs from the right eye) to the right Wulst region of the forebrain compared to the equivalent and opposite projection from the right side of the thalamus to the left visual Wulst [23]. Intriguingly, in the pigeon a similar asymmetry has been found, but in the tectofugal rather than in the thalamofugal pathway [9]. The exposure of the right eye to light leads to an increased number of visual projections from the right tectum to the contralateral rotundus. It could be that the difference in the pathway involved has something to do with the different developmental pattern of the two species, the pigeon being an altricial species the chicks being a precocial one [7].

Embryos incubated in completely dark conditions do not develop any asymmetry in the visual pathways [23]. Moreover, withdrawing the embryo's head from the egg 2 days before hatching, occluding the right eye with a patch and allowing the left eye to be stimulated by light, reverses the pattern of asymmetry, with an increased number of visual projections from the right thalamus to the contralateral Wulst (summarised in [7]).

Asymmetrical light exposure of embryos has been shown to affect some forms of behavioural lateralisation after hatching. For example, performance in the pebble floor task, in which chicks are required to categorise grains of food as distinct from pebbles, is impaired only by glutamate-treatment of the left (and not the right) visual Wulst in L-chicks; this asymmetry is absent in D-chicks [6,7]. Lateralisation of attack responses shows the same dependency on light exposure of the eggs [16,18]. In this case, the response is higher in chicks using their left eye than it is in chicks using their right eye, provided that the eggs have been exposed to light [24]. In chicks hatched from eggs incubated in the dark, the levels of attack are the same when they use the left or right eye.

There are other forms of lateralisation in chicks that, however, do not depend on light exposure of the embryo, and these include imprinting and social recognition [37,3,8], response to olfactory versus visual cues [22,33] and lateralisation of auditory responses [4].

Lateralisation of spatial cognition has yet not been investigated for possible effects of asymmetric light stimulation in embryo. This is in spite of the fact that spatial cognition is probably among the best studied lateralised functions in the chick (see for a review [35]). A well-established fact, that seems to hold also for other species of birds (see e.g., for pigeons [11]), is that the two hemispheres of the chick's brain tend to attend differently to object-specific local cues and to position-specific, large scale, global cues. For instance, Tommasi and Vallortigara [26] trained chicks to find food hidden below sawdust on the floor by ground-scratching in the centre of a closed uniform arena: the centre was indicated by a conspicuous landmark. After learning, the landmark was relocated to a novel position and chicks were tested binocularly or with only one eye in use. A striking asymmetry appeared: binocular chicks and chicks using only their left eye searched at the centre (ignoring the landmark), whereas chicks using only their right eye searched at the corner (ignoring purely spatial information). Clayton and Krebs [5] tested the memory of food-storing and non-food-storing birds for feeders that had a trial-unique location in an experimental room as well as a trial-unique colour pattern. When, after a short retention interval, birds were given dissociation tests in which the correct feeder changed its position and a different feeder was placed at the original location, all birds searched by preference using position-based cues when tested with only their left eye and using feeder-specific cues when tested with only their right eye. More recently, using a working memory rather than a reference memory test, Regolin et al. [15] found that both object- and position-specific information is available to the two cerebral hemispheres in working memory; however, when a conflict between cues arises, the right hemisphere preferentially attends to position-specific cues, whereas the left hemisphere tends to attend to object-specific cues (and see also [25,30,38]).

The aim of this paper was to investigate whether asymmetric light stimulation of the embryo may affect relative reliance on object-specific and position-specific cues in chicks hatched from eggs exposed to light in the last days before hatching or maintained in darkness.

2. Materials and methods

2.1. Subjects and rearing conditions

The subjects were 458 Hybro *Gallus gallus* chicks (a local variety derived from the White Leghorn breed). The fertilized eggs came from two local commercial hatcheries (Avicola Berlanda Edio and C. Snc, Carmignano di Brenta, Padua, Italy and Agricola Berica, Montegalda, Vicenza, Italy) and were delivered to our laboratory weekly when the eggs were at day 14 of incubation. Thereafter, and until day 18, the eggs were incubated in the dark in the laboratory in an automatically turning incubator FIEM snc, MG 100H (45 cm × 58 cm × 43 cm), under controlled temperature (37.7 °C) and humidity (about 50–60%) conditions. On day 18 of incubation, the eggs were separated into two incubators