

S21-4 Development of the two visual pathways and lateralized visual function in the chicken

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Abstract As lateralization of visual function has been shown in seven avian species, as well as in a broad range of both lower and higher vertebrates (Rogers and Andrew, 2002), it can be assumed to be a general characteristic of vertebrates even though it may be expressed in different ways in different species. Some evidence, mentioned here, indicates that a lateralized brain enhances cognitive performance; and this may be a reason why it evolved and has been retained across species. This paper discusses the asymmetrical organization of the visual pathways in birds and the role that exposure of the avian embryo to light plays in the development of lateralization of some visual functions. It considers species differences in transmission of light through the egg shell, and the intensity of light required to generate the asymmetry. The development of asymmetry in visual projections to the forebrain in the chicken is prevented not only by incubating eggs in the dark but also by exposing them to light of high intensity. The extent of light exposure received by the embryo depends on the color and construction of the egg shell, as well as on the location of the nest and the incubating behavior of the parent(s). Steroid hormones also affect light-dependent development of lateralization, mediating the influence of maternal stress on the strength of lateralization in offspring.

Key words Visual behavior, Lateralization, Light stimulation, Steroid hormones

1 Introduction

Visual lateralization was discovered in the domestic chicken (*Gallus gallus*) over two decades ago, as specialization of the left hemisphere for learning to discriminate grains of food from small pebbles and specialization of the right hemisphere to control attack and copulation responses (Rogers and Anson, 1979). Subsequent research confirmed this finding and extended it to demonstrating lateral biases in motor responses guided by left and right eyes (Andrew et al., 2000; Rogers and Andrew, 2002) and to the display of eye preferences to view different stimuli (McKenzie et al., 1998). A large body of empirical evidence now allows us to formulate a general model for lateralization of visual function in the chicken, namely that the right eye and its associated left hemisphere are used preferentially when responses have to be considered against alternatives, as in the case of learning, while the left eye and right hemisphere are used when the response must be given without hesitation (Andrew and Rogers, 2002; Rogers, 2002a). The latter system is demonstrated clearly by a recent study showing that chickens respond with shorter latency to a model predator when it is introduced into their left, not right monocular visual field (Rogers, 2000).

The pigeon (*Columba livia*) shows visual lateralization in terms of faster pecking to feed and superior memory of visual images when using the right eye (Güntürkün, 1985, 2000). This is consistent with findings in the chicken; and the same right eye preference for controlling feeding re-

sponses has been found in the zebra finch, *Taeniopygia guttata* (Alonso, 1998). Other studies of visual lateralization in avian species have measured eye preferences in wild birds monitoring their surrounds for predators or prey. The dark-eyed junco (*Junco hiemalis*) exhibits a right-eye preference for this, whereas the American tree sparrow (*Spizella arborea*), tends towards a left-eye preference (Franklin and Lima, 2001), the latter consistent with the chicken. The kookaburra (*Dacelo novaeguineae*), also shows a strong preference for using the left eye to scan the ground for prey several meters beneath its perch (Rogers, 2002b). Most impressive of all is the New Caledonian crow (*Corvus moneduloides*), which uses of its right eye preferentially when cutting its tools from pandanus leaves with its bill (Hunt, 2000).

All of these studies demonstrate lateralization at the species level; but the eye preferred varies, probably according to the specific processing being used by the bird in each context. Use of the left eye, for example, may indicate vigilance and readiness for a rapid response (either fight or flight) with processing of spatial information, since the right hemisphere is specialized for assessing spatial cues (Rashid and Andrew, 1998; Tommasi et al., 2000). Further research will be needed to clarify the differences among species in eye preferences.

2 Response of the embryo to light exposure

At least some features of visual lateralization in birds develop as a consequence of monocular stimulation of the visual system in the embryo, as shown first in the chicken (Rogers, 1982) and later in the pigeon (Güntürkün, 1993). During the final stages of incubation, the embryo in these species, and probably in most birds, is oriented in the egg so that the left eye is covered and the right positioned near the air sac where it can be stimulated by light passing through the shell and membranes (Rogers, 1990). As a consequence, the left side of the thalamus and its projections to the left hemisphere receive visual stimulation ahead of the right side of the thalamus and its projections. This establishes lateralization of feeding responses (right eye) and attack responses (left eye) since chickens hatched from eggs incubated in the dark during the final 3 days of incubation are not lateralized for such functions, at least during the first 3 weeks of life post-hatching (Rogers, 1997).

Likewise, pigeons not receiving monocular exposure to light lack asymmetry of their feeding responses (Güntürkün, 1993). In the chicken, in fact, it is possible to achieve a complete reversal of lateralization of feeding and attack responses by occluding the embryonic right eye and exposing the left eye to light instead (Rogers, 1990). Other expressions of lateralization (e.g., of social recognition) are not dependent on embryonic visual experience even though light experience after hatching is important (e.g., Deng and Rogers, 2002a).

3 Lateralization of the visual pathways

The lateralization of feeding and attack responses in the chicken has been traced to asymmetry in the thalamofugal visual system (see below). This system projects from the region of the thalamus known as the nucleus geniculatus lateralis pars dorsalis (GLd) to the visual Wulst of the forebrain (Deng and Rogers, 1997, 2002b). The other visual system, the tectofugal, which projects from the optic tectum via the nucleus rotundus to the ectostriatal region of the forebrain is not asymmetrical in the chicken (Rogers and Deng, 1999), unlike the pigeon (Güntürkün, 1997).

Rogers and Sink (1988) discovered asymmetry in the projections of the rostral thalamus to the visual Wulst of the chicken by injecting a retrograde tracer into the left or right Wulst regions of the hemispheres and counting the labelled cells on either side of the thalamus. The ratio of the number of labelled cells contralateral to the injection site to the number ipsilateral to the same site (*c/i* ratio) was higher for right-side than for left-side injections. A later study by Rogers and Deng (1999), using other tracers, confirmed that this asymmetry was located in the projections that cross the midline of the brain, from one side of the thalamus to the contralateral Wulst; there are more projections from the left thalamus to the right Wulst than vice versa (Fig. 1). This is the arrangement in chickens hatched from eggs exposed to light. Chickens hatched in the dark lack asymmetry in these projections, while in those stimulated by light to the left eye pre-hatching have the direction of lateraliza-

tion reversed (Rogers and Sink, 1988). This result was confirmed recently by Koshiba et al. (2002).

Koshiba et al. (2002) also discovered asymmetry in a region located in a rostral part of the pars dorsolateralis pars anterioris (DLA), which also develops after the embryo is exposed to light. This region sends primarily ipsilateral projections to the Wulst. The DLA contralateral to the light-exposed eye has more projections to its ipsilateral Wulst than does its equivalent on the other side of the thalamus. Hence, depending on the region of the GLd, there is asymmetry in the contralateral or ipsilateral projections to the visual Wulst (Fig. 1).

4 Egg shell transmission of light and lateralization

Most experiments investigating the effects of light exposure on the development of lateralization in embryos have used ambient, white light at intensities of 100 to 800 lux for 24 hours on day 19/20 of incubation in chickens (Fig. 2). I have found that asymmetry of the thalamofugal visual projections does not develop following exposure of eggs to only 1 300 to 1 500 lux, probably because sufficient light penetrates the egg to stimulate both eyes of the embryo. This result was obtained using white shelled eggs, which transmit approximately 8% of ambient light (Fig. 3). Brown egg shells transmit only 1% to 2% of ambient, white light. Hence, color and construction of the egg shell is a major factor determining whether embryos receive too little or too much exposure to light for lateralization to develop. In the natural environment, the position of the nest, the hours and intensity of sunlight, and the periods during which the in-

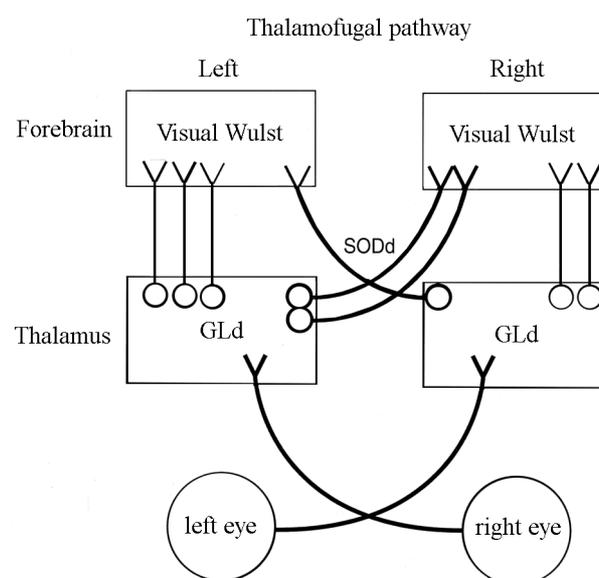


Fig. 1 The thalamofugal visual system showing the location of asymmetry in the projections from the GLd region of the thalamus to the visual Wulst region of the forebrain

There are more contralateral projections from the left GLd to the right Wulst than vice versa, and more ipsilateral projections from the left GLd to the left Wulst than vice versa.

cubating parent leaves the nest to forage, thereby exposing the eggs to light, will all have influences.

These data raise the possibility that species which nest in the open in full sunlight have eggs shells that minimize light transmission, such that it helps embryos to develop lateralization. As a first step in testing this idea, light transmission by the egg shell of the emu (*Dromaius novaehollandiae*) was determined; the results are presented in Fig. 3. It can be seen that the amount of light entering the emu egg is much less than that entering the egg of a domestic chicken: ambient intensities above 1 500 lux would not prevent the development of visual lateralization in emu chicks. It is not yet known whether emu chicks are lateralized but, given the ubiquity of lateralization, this is to be expected.

As to the advantages conferred by lateralization on visual behavior, some evidence shows that strongly lateralized chickens have superior ability in detecting an overhead predator as they feed (Rogers, 2000), and that strongly lateralized pigeons perform the pebble-grain discrimination task more successfully (Güntürkün, 2000). Thus there may be survival advantage in maintaining lateralization. If so, egg shell color and construction should affect the developmental process. Egg shell color, in particular, may serve this function in addition to its role in camouflage and for species and individual recognition.

5 Hormonal effects on lateralization

The level of steroid hormones also affects the development of lateralization, as shown in the chicken for testosterone (Schwarz and Rogers, 1992) and oestrogen (Rogers and Rajendra, 1993). Abnormally elevated levels of these hormones during the final stages of incubation prevent the

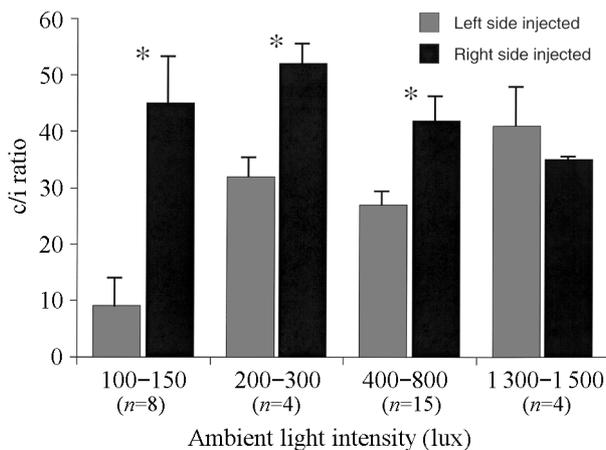


Fig. 2 The effect of variation in ambient light intensity on lateralization of the thalamofugal visual projections

The ratio of contralateral to ipsilateral projections (c/i ratio) is presented following injection of tracer dyes into the left or right Wulst. Note significant asymmetry (indicated by asterisks) for all intensities apart from the highest (1 300–1 500 lux), and a trend for the c/i ratio into the left Wulst to increase as light intensity increases.

light-sensitive development of asymmetry in the thalamofugal visual projections. Recent work has shown that corticosterone too has a similar effect (Deng and Rogers, 2002c).

The effect of steroid hormones on the embryonic development of asymmetry is of significance because of the influence that environment has on the level of testosterone that the maternal bird deposits in her eggs. Whittingham and Schwabl (2002) have shown that the concentration of testosterone in egg yolk either increases or decreases with laying order of the eggs in the clutch, the direction of change depending on the species. The level of testosterone deposited also depends on the number of aggressive interactions that the maternal bird experiences before or during egg laying, as shown in tree swallows (*Tachycineta bicolor*). This effect might well apply to other species and it suggests a means by which social conditions experienced by the female might influence the degree of lateralization of visual pathways and associated behavior patterns in her offspring.

Hence, light exposure and maternal hormonal contribution in the egg both influence the development of certain forms of visual lateralization. These influences, in response to social and ecological demands, must modulate the development of lateralization to cause individual differences.

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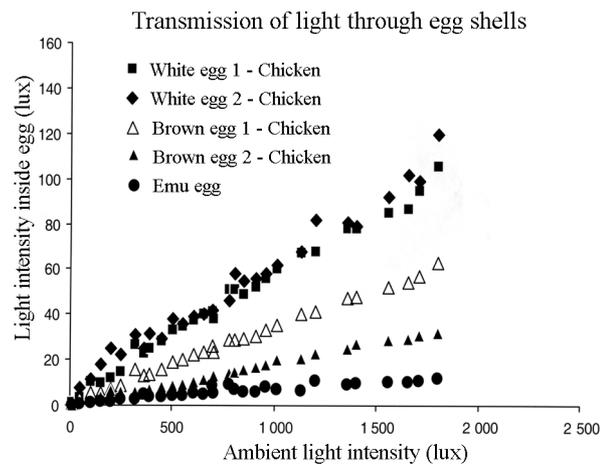


Fig. 3 Transmission of sunlight through egg shells

Light intensity inside the eggs is plotted against ambient light intensity. The white-shelled chicken eggs transmit a higher percentage of ambient light than brown chicken eggs and especially more than emu eggs.

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