

Research report

Development and function of lateralization in the avian brain

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Abstract

The avian brain is functionally lateralized. Different strategies of choice (within and between modalities) are adopted by each hemisphere. Visual lateralization has been studied most but attention to auditory, olfactory and magnetic cues is also lateralized. The left hemisphere (LH) focuses on cues that reliably separate pertinent stimuli from distracting stimuli (e.g. food from pebbles, odour cues from attractive visual cues, magnetic cues from other cues indicating location), whereas the right hemisphere (RH) has broad attention and is easily distracted by novel stimuli. The RH also controls fear and escape responses, as in reaction to predators. Exposure of the embryo to light just before hatching, when the posture adopted occludes the left eye (LE) but not the right eye (RE), leads to the development of asymmetry in the visual projections to the pallium and enhances the ability of the RE/LH to inhibit attention to distracting visual cues and of the LH to inhibit the RH, but has no effect on the RH's interest in novelty. Exposure to light before hatching has both short- and long-term consequences that are important for species-typical behaviour and survival. For example, on a food search task with a predator presented overhead, dark-incubated chicks perform poorly on both aspects of the task, whereas light-exposed chicks have no difficulty. Steroid hormone levels prior to hatching modulate light-dependent development of asymmetry in the visual projections and consequently affect neural competence for parallel processing and response inhibition. Differences between lateralization in the chick and pigeon are discussed.

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1. Introduction

This paper reviews research on lateralization in the avian brain. The domestic chick and the pigeon have served as models to investigate the mechanisms and development of lateralization [31] and the findings have relevance not only to other avian species but also non-avian vertebrates [74]. Some of the lateralized functions found in birds are remarkably similar to some aspects of lateralization in the human brain, as noted previously by Andrew and Rogers [4] and also mentioned in this paper. In fact, the avian brain is now serving as a valuable model to test some of the hypotheses developed previously to explain the presence of lateralization in the human brain. For example, empirical investigation of the function of lateralization can be conducted far more reliably in the avian model than in humans because the performance of lateralized and non-lateralized animals can be compared on ecologically relevant tasks, as opposed to the

artificial testing paradigms used so far to test the function of lateralization in humans. Some thoughts on possible advantages of having a non-lateralized brain are also offered.

Differential processing of neural inputs and control of outputs by the left and right sides of the brain is referred to as functional asymmetry or lateralization. Such differences located at the telencephalic level of neural organization are known as hemispheric specialization. Although the latter is a notable feature of the human brain it is certainly not limited to humans, as once thought, but is widespread among vertebrates [74,77]. Lateralization at the diencephalic level is also present in humans [106] and other vertebrates [8,55]. In fact, it has recently become apparent that even an invertebrate brain can be functionally lateralized, as shown in fruitflies [60], bees [40] and spiders [1]. Hence, it would seem that the central nervous system, no matter whether it is simple or complex, is functionally differentiated across the left-right axis.

The avian brain is no exception to this pattern and evidence indicates that it is as lateralized as the human brain. The earliest experiments revealing lateralization in the avian brain used either localised lesions, as in the case of lateralized control of

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song production in songbirds [56], or injection of a specific pharmacological agent into the left or right hemisphere, as in the case of processing visual information by chicks [35,78]. Unilateral lesioning or pharmacological treatment of one hemisphere has different effects on behaviour than the same treatment of the other hemisphere. For example, cycloheximide or glutamate treatment of the left hemisphere (LH) of the chick impairs the ability to find grains of food scattered on a background of distracting pebbles but the same treatment of the right hemisphere (RH) has no effect on this ability [35,78].

Somewhat later it was discovered that lateralization of the avian brain could be revealed simply by testing the bird monocularly [50], at least in those species with eyes positioned on the sides of the head. In such species the majority of visual input is relayed to and processed by the hemisphere contralateral to the open eye [26]. The chick tested using its right eye (RE), and so processing the inputs largely in the left hemisphere (LH), is able to peck at grain and avoid pecking at distracting pebbles, whereas the chick using its left eye (LE), and processing these inputs largely in the right hemisphere (RH), pecks pebbles and grain at random [50,72].

Now we know that without any treatment, not even applying an eye patch, lateralization can be revealed by introducing stimuli into the monocular visual field of the LE or RE and comparing the responses elicited. For example, chicks are more reactive to a model snake introduced into the left monocular field than they are to the same stimulus introduced into the right monocular field [44], as also shown in non-avian species [45,46]. Lateralization can also be revealed in birds by measuring the preference to use the LE or RE to view particular stimuli. For example, McKenzie et al. [47] scored the chick's eye preference to view an imprinting stimulus and found that the LE was preferred when the chick approached the stimulus and the RE was preferred when examining the stimulus on first encounter while deciding whether to approach. It appears that a bird chooses an eye according to the processing of the visual inputs that it brings to bear on the task, as also shown by Dharmaretnam and Andrew [16]. This can also be manifested as side biases displayed on approach to stimuli: Andrew et al. [5] found that chicks trained to lift a lid from a bowl to gain access to food approached the bowl along a leftward arc, which allowed use of the RE, whereas they approached along a rightward arc with use of the LE when the food was presented in a bowl without a lid. Turning direction to negotiate a barrier is also determined by the preferred eye to view a stimulus on the other side of the barrier [100].

Two avian species have been the focus of most research conducted so far on lateralization in birds, the chicken, *Gallus gallus domesticus*, and the pigeon, *Columba livia*. In addition to lateralized control of behaviour, structural asymmetry has been described in the visual pathways of both species, although not in the same neural projections in both species, as discussed below.

2. Lateralization in the chick

Although research on lateralization in the chick has been focused on visual processing, lateralization of olfactory and auditory processing has been investigated to some extent. The

left and right forebrain hemispheres are specialized to process sensory inputs in these modalities to different degrees or in different ways (olfaction [9,99] and audition [54]).

2.1. Right eye-left hemisphere

Some examples of functional lateralization have been mentioned above, in particular the ability of chicks using their RE to focus on pecking at grain and avoid pecking at distracting targets (pebbles), an ability not shown by chicks using their LE. An initial interpretation of this result might be that the RE-chick can discriminate grain from pebbles, whereas the LE-chick cannot. A number of subsequent tests have indicated that this simple explanation is not correct and that the difference results from interest in novelty by the RH, which receives most of its visual input from the LE. Since the pebbles have a much wider range of colours and textures than the grains, they are continually attractive to the chick using its LE, and RH, and elicit exploratory pecking. The neural circuits fed by inputs from the RE, by contrast, attend to the categories 'food' and 'non-food', rather than the small differences between individual pebbles, and so shift pecking away from pebbles to grain.

Two experiments have shown that the LH attends to categories, whereas the RH responds to small differences. One experiment tested chicks with a choice between a familiar companion chick and an unfamiliar chick [98]. Use of the LE (and so RH) led to approach to the familiar chick and avoidance of the unfamiliar chick. No such discrimination between the chicks occurred when the RE was in use, indicating the LH attends only to the category 'chick' and not to the small differences between individual chicks. The other experiment tested the chick's responsiveness to change in an imprinting stimulus [97]. Chicks were imprinted on a red ball with a horizontal white strip placed centrally on one side. They were then tested with a choice of this stimulus and a red ball with the white strip oriented either vertically or at 45° to the horizontal to see whether the chick noticed a small or large change, respectively, in the imprinting stimulus. When using the RE only, the chicks chose the imprinting stimulus over the ball with the vertical strip but showed no preference for it over the ball with the 45° strip. They responded only to the large change or, in other words, a category change. When tested using the LE, chicks chose the imprinting stimulus over both of the changed balls, showing that they detect and respond to small differences between stimuli.

Attention of the LH to category differences between stimuli means a focus on pertinent cues coupled with an ability to inhibit response to irrelevant stimuli. These categories might well be constructed on past experience (learnt) and we could say that the LH operates on a set of established rules, as is known to be the case for the LH of the human brain [92].

This ability of the LH to focus on relevant cues and avoid distraction by irrelevant cues, no matter how attractive they might be, is seen also in chicks presented with stimuli in two modalities. When presented with both visual and olfactory cues the chick responds to the olfactory cues provided they are processed in the LH; when the RH is used, olfactory cues are ignored if the visual stimulus is attractive, and hence distracts attention from

the olfactory cues, but not if the visual stimulus is unattractive [84]. Similarly, recent tests have found that chicks trained binocularly to follow magnetic cues to locate an imprinting stimulus behind a screen continue to do so when they use the RE only (and so the LH) but not when they use the LE (and RH) [87]. The results indicated that the chicks were able to detect the magnetic cues when the RH was used, because they followed them on some occasions, but were more readily distracted by other, non-magnetic cues.

2.2. Left eye-right hemisphere

Distraction of the RH by novel and other attractive cues, combined with the inability to inhibit responses to these cues, is consistent with the RH's interest in small differences between stimuli [3,97]. The RH also manifests broad attention, used in processing global, geometric cues in spatial tasks [94]. This is opposed to the attention of the LH to local features. Not surprisingly, therefore, the chick that is looking at the ground because it is engaged in searching for grain is more likely to detect and respond to a model predator, such as the image of a hawk moved overhead, when the stimulus is in the left visual field (RH) compared to the right visual field (LH) [17,73]. Even if the chick initially catches sight of the overhead predator using the RE it will turn to view it in more detail using the LE (and RH) [17].

One could say that the RH attends to stimuli as they are, rather than according to constructs or rules. In humans the RH is said to be the literal hemisphere [92], which describes a function not dissimilar to that of the RH of the chick.

Perhaps as a consequence of these functions of the RH, fear is expressed more strongly in chicks using the RH. The same is true of aggression. Agonistic pecks of one chick at another are preferentially delivered after viewing the opponent using the monocular field of the LE [101]. Also, impaired function of the LH, which means heightened control of responses by the RH, leads to elevated levels of attack and copulation [35,108]. It is worth mentioning that the same role of the RH in expression of hostility and aggression has been found in humans [4,13].

2.3. Lateralization of visual pathway

At least some of the lateralized visual behaviour of the chick depends on differential visual inputs to the hyperpallial region from the thalamus [79,82]. Provided that the chick has been exposed to light during the final stages of incubation (more below), the left side of the thalamus (now termed the lateral geniculate nucleus, LGN) develops more projections to both the contralateral [79] and ipsilateral [39] hyperpallium than does the right side of the thalamus (Figs. 1 and 2). Hence the RE has stronger thalamofugal connections to both hemispheres than does the LE. No such asymmetry is present in the other visual system, the tectofugal system, of the chick [79] (Fig. 1).

Although it is often said that the tectofugal system is more important than the thalamofugal visual system, especially in visual discrimination [27,33], this does not seem to be the case in chicks, at least, as shown by the effects of localized injections of

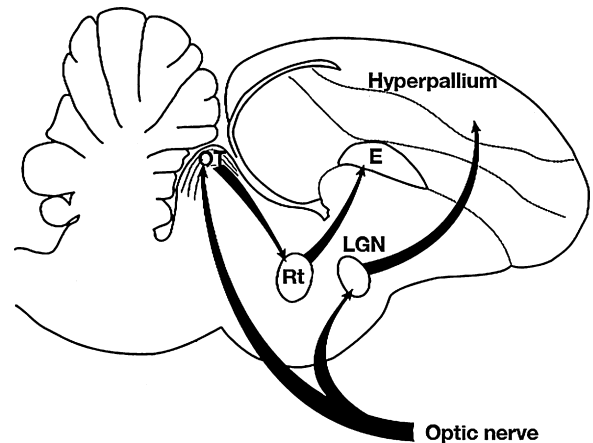


Fig. 1. A sagittal section of the domestic chick brain illustrating the two visual pathways but not showing the lateral asymmetry of these pathways. The tectofugal pathway is on the left and includes the optic tectum (OT), nucleus rotundus (Rt) and entopallium (E). The thalamofugal pathway is on the right and includes the lateral geniculate nucleus (LGN) and the hyperpallium.

glutamate into the hyperpallium, entopallium and nidopallium in the left and right hemispheres [14]. The chick's ability to peck at grain and avoid the distracting pebbles is impaired by such treatment of the left hyperpallium but not by treatment of any of the other regions. This finding links the superior ability of the RE in this task to the hyperpallium of the LH and demonstrates the importance of the thalamofugal system in this species.

3. Lateralization in the pigeon

The first demonstration of lateralization in the pigeon more or less repeated the finding for the chick: pigeons presented

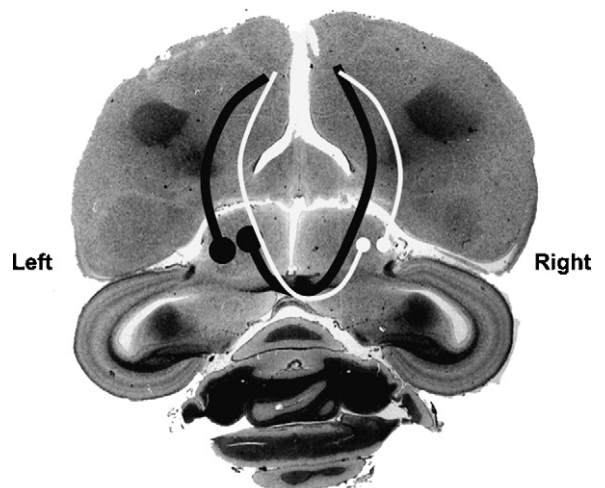


Fig. 2. A horizontal section of the domestic chick brain showing the asymmetrical organization of the thalamofugal visual projections to the hyperpallium. The pathways with greater numbers of fibres are in black and those with fewer fibres are in white. Note that the lines are a rough guide only since the ipsilateral projections far outnumber the contralateral projections. It can be seen that the left side of the thalamus (left LGN in Fig. 1), which receives input from the right eye, sends more projections to the left and right hyperpallium than does the right side of the thalamus (right LGN), which receives inputs for the left eye.

with a dish containing food grains mixed together with pieces of grit peck more rapidly and consumed more grains in a fixed period of time when they use the RE than when they use the LE [28]. Further experiments showed that pigeons use the RE for detailed visual analysis of objects [26,28] and, as do chicks, they seem to assign categories to visual inputs received via the RE, and processed by the LH. This is suggested by the finding that pigeons using the LH acquire strategies of learning when they are tested on successive colour discrimination reversals [18]. Moreover, the specialization of the LH to operate according to learnt strategies, as suggested above for the chick, seems to apply to the pigeon also: pigeons use the LH to acquire and store memory of a conditioning task requiring them to discriminate between visual symbols [58].

Until recently, there was little evidence of the pigeon showing a superior role of the RH on tasks requiring global/broad attention and attention to details, as demonstrated in the chick. In fact, on a spatial task using global cues pigeons were shown to use both eyes and hemispheres equally [61,62] and homing pigeons use the LH to navigate, as shown by hippocampal lesions [6] and monocular testing [63]. The homing pigeons showed a LH advantage to use visual memory in snapshot tracking to follow a pre-learned route [95]. Recent research has, however, shown that pigeons using the RH exhibit superior performance on a task requiring global attention to visual images [107].

These results point to a species difference of greater LH emphasis in the pigeon compared to the chick. It is quite possible that evolutionary adaptation has resulted in the pigeon being more LH-dependent than the chick.

At the anatomical level, the chick and pigeon differ markedly. Whereas asymmetry in visual inputs to the pallium is located in the thalamofugal visual system of the chick, it is located in the tectofugal visual system of the pigeon [26]. The retinorecipient neurons of the left optic tectum of the pigeon are larger than their counterparts in the right optic tectum [25,91] and this is also the case for GABAergic, and hence inhibitory, cells in this tectal layer [52]. A parvalbumin-positive subset of these neurons is larger on the right than the left side [52]. The right optic tectum sends more projections to the left nucleus rotundus than does the left optic tectum to the right nucleus rotundus, and the cell bodies of the neurons giving rise to efferent projections, both contralateral and ipsilateral, are larger in the right optic tectum than the left [25,91]. In other words, the left nucleus rotundus receives equal numbers of projections from the left and right optic tecta, whereas the right nucleus rotundus receives more projections from the right than the left optic tectum. Consistent with this, cell bodies of the left nucleus rotundus are larger than those of the right nucleus rotundus [51]. It seems, therefore, that the LH, which receives visual input from this system via the left nucleus rotundus, receives strong representation from both eyes. The RH, on the other hand, which receives its input from the right nucleus rotundus receives a strong representation from the LE but weaker from the RE [26,29]. This particular asymmetry is not present in the chick and it may explain why the pigeon appears to be LH dominant, whereas this is definitely not the case for the chicken.

4. Lateralization in other avian species and in wild birds

Similar to the chick and pigeon, the LH focuses pecking at food grains and away from distracting pebbles in zebra finches [2] and quails [96]. The marsh tit, which stores food items, uses the LH to recall the location of caches specified by object-specific cues, such as markings on the feeder, whereas the RH is used to recall location using spatial cues [12]. In addition, as in the chick, use of the RE, and not the LE, to orient using the geomagnetic field is known to be characteristic of two migrating species, European robins [105] and silver eyes [104]. Unlike the domestic chick, however, the latter two species, tested in the laboratory, were entirely unresponsive to magnetic cues when using the LE and showed no preferred direction of orientation. Chicks using the LE appear to be able to detect the magnetic cues but choose to ignore them in preference to using other non-magnetic indicators of direction. The difference between the chick and the two migrating species may depend on the nature of the tasks since the chicks were trained in the testing apparatus and could have learnt to use both magnetic and other extraneous cues indicating spatial position, whereas the migrating species had no such training prior to being tested. In other words, the apparent lateralized responsiveness to the geomagnetic field appears to result from attentional/processing differences between the hemispheres and not to the presence or absence of magnetic field detectors in the RE and LE, respectively [87].

A chick using its RH is more readily distracted from searching for food grains by an auditory stimulus, as found using a non-specific noise [78]. Distraction by unfamiliar auditory stimuli might be a general property of the RH since Palleroni and Hauser [59] found that playing recordings of howler monkey calls and pure tones to naïve, juvenile harpy eagles from behind the head caused the bird to turn to use its left ear (and hence RH) to attend to the sounds. Playing recordings of familiar sounds (e.g. of harpy eagle calls or of howler monkey calls to experienced adult harpy eagles) caused turning of the head to the right and so preferential use of the right ear, and LH. Nottebohm et al. [57], on the other hand, found that both hemispheres of the songbird process song but in different ways. Without more research on auditory lateralization it is impossible to draw a general picture across species but there is clear indication of ear preferences that might mirror known eye preferences.

Specialization of the RH for control of copulation responses, found originally in the chick [86], has been shown recently to be present also in the quail [24]. Specialization of the RH to control agonistic interactions with a simulated conspecific [86] and a real conspecific [101] has been demonstrated in the chick and also found in amphibians [65,66] but, so far, this interesting lateralization has not yet been investigated in other avian species.

All of the examples of lateralization discussed so far have emerged from tests on captive animals tested in the controlled laboratory situations. It is, therefore, valid to question whether lateralization is manifested in birds behaving naturally in their usual habitat. Until quite recently, only the knowledge of foot preference in wild parrots [32,67] suggested that lateralization could be manifested in natural behaviour. Now we have exam-

ples of eye preferences expressed in five avian species in their natural habitats. Franklin and Lima [22] reported that wild juncoos prefer to use the RE to maintain vigilance during feeding, a result opposite to the chick's use of the LE for this purpose. The kookaburra uses its LE to scan for moving prey at a distance [75], which could be similar to the chick's use of the LE (and RH) to process distal cues. The black-winged stilt uses the RE for foraging and the LE in copulation attempts [102], which is identical to chick's specializations for these behaviours. New Caledonian crows make more tools on the left than on the right side of pandanus leaves and, given the orientation they adopt when cutting the tool from the leaves using the beak, it has been deduced that they show a RE preference for guiding this behaviour [36,37], which is consistent with the chick's use of the RE when it has to manipulate a lid to remove it from a dish [5]. Finally, recent research on the Australian magpie has revealed several types of lateralization consistent with those shown in the chick [34,38]. Before the magpie approaches a model predator it views the stimulus with its RE and before it withdraws it views with its LE, see [38] for details and more examples.

5. Development of lateralization

The domestic chick was found to be an excellent model in which to study the development of lateralization. Later the pigeon was found to be a valuable comparison to the precocial chick, since the pigeon is an altricial species [31].

5.1. Effect of light on development of lateralization

The embryo of almost all avian species is oriented in the egg during the final stages of development so that it turns the head to the left side and so occludes the LE but not the RE [71]. It has been well established, first in the chick and then in the pigeon, that the resultant stimulation of the RE generates lateralization of the visual pathways and lateralization of several types of visual behaviour. Chicks hatched from eggs incubated in the dark during the final few days of the incubation period fail to develop asymmetry of the thalamofugal visual system [79,82]. Pigeons hatched from eggs incubated in the dark fail to develop asymmetry of the tectofugal visual system in any of its aspects, including cell size [52] and numbers of projections from the optic tecta to the rotunal nuclei [27].

A sensitive period for the effect of light has been determined in the chick. As little as two hours of light exposure during the last 3 days of incubation is sufficient to generate lateralized behaviour measured in the second week of life [68,69,76]. Light exposure prior to the final 3 days of incubation has no effect on lateralization [108].

This sensitive period for light-generated asymmetry of the visual pathways provides a possible explanation for the species difference in which pathway is lateralized. Chicks hatch at a precocial stage of development and their tectofugal pathway has completed development before the sensitive period, whereas the thalamofugal pathway is still developing during the sensitive period [15]. This may be the reason why the chick's tectofugal

visual system escapes the effects of lateralized light stimulation but the thalamofugal visual system does not. By contrast, the pigeon is an altricial species and the tectofugal visual system is still developing during the sensitive period to light just before hatching. It is therefore vulnerable to the lateralized stimulation by light. The pigeon's thalamofugal would continue to develop after hatching and escape any lateralizing effect of light stimulation because both eyes are exposed to light after hatching.

If this explanation is correct, monocular eye occlusion after hatching should lead to the development of asymmetry in dark-incubated pigeons, which it does [51], although I am not aware of any investigation that has yet been made to see whether this treatment causes asymmetry to develop in the pigeon's thalamofugal system.

The asymmetry of the thalamofugal visual projections that follows light exposure of the chick embryo persists through the first 3 weeks after hatching but no longer [82], whereas the tectofugal asymmetry generated by light exposure of the pigeon embryo persists into adulthood [26,27]. Despite the transient nature of the asymmetry of the visual projections in the chick, we know that lateralized attack responses, which are also generated by light exposure of the embryo [69,108], remain present in adult chickens [70] and adult chickens show eye preferences for viewing particular stimuli [47]. This behaviour must therefore rely on more subtle asymmetries, or ones located outside the thalamofugal visual projections, also caused by stimulation of the RE by light before hatching. Lateralized discrimination of grains from pebbles is more closely associated with the asymmetry in the visual projections, as shown by a lesioning study [14] and by the fact that it is no longer present in 3-week-old chicks [70].

The precise nature of the light-dependent asymmetry of the chick's performance on the grain-pebble task has recently been clarified [85]. This particular lateralization is present in chicks in their first and second weeks of life and it is not present in dark-incubated chicks of the same age provided that the chicks peck as the usual fast rate (i.e. use of the RE and not the LE allows the chick to focus on pecking only at the grain). If pecking is very slow, however, even dark-incubated chicks can focus on pecking at grain only when they use the RE. In other words, the lateralization is present in dark-incubated chicks pecking slowly. Hence, it seems that the light exposure does not cause the LH to develop a pattern of behaviour that would otherwise not be present but it enhances the ability of the LH to avoid distraction by the inedible targets, pebbles. At the same time the RH retains its interest in novelty, and hence is easily distracted, regardless of exposure to light before hatching [85].

The effect of light exposure on behaviour of the chick is, therefore, quite specific. As one would expect, it is also confined to visual behaviour, and has no effect on lateralization of olfactory responses [84] or auditory responses [unpublished observations]. Perhaps a more general effect resulting from light exposure is, however, manifested in unihemispheric sleep [48]. Birds are known to perform unihemispheric sleep, during which one eye is closed and the contralateral hemisphere shows a slow wave EEG pattern [49,64,71]. One- and two-day old chicks

hatched from eggs exposed to light show a preference toward RH unihemispheric sleep: they close the LE and open the RE to monitor the environment [48], possibly to detect only large, categorical changes. Chicks hatched from eggs incubated in the dark show the reverse preference [48]; their preference to open the LE may be another manifestation of the attention to novel stimuli by the RH and, as mentioned above, this is unaffected by light exposure prior to hatching. In contrast, monitoring for large changes by LH is dependent on light exposure of this eye system prior to hatching. Viewed in this way, these results are consistent with the effects of light/dark incubation on the pebble-grain task [85]. Exposure of the embryo's RE to light enhances its ability to guide behaviour using relevant cues. This does not mean that chicks using the LH are inattentive to cues/stimuli other than the pertinent ones, but rather that they can inhibit responding to them, as revealed when chicks are trained using two cues and then tested with these cues separated and in conflict [10,11], meaning that response to one of the cues has to be inhibited.

5.2. Effect of hormones on development of lateralization

Elevated levels of the sex steroid hormones and corticosterone prevent the influence of light on the development of visual lateralization in the chick (testosterone [90]; oestrogen [81]; corticosterone [80]). No asymmetry of the thalamofugal visual projections develops if the level of any one of these hormones is elevated during the final stages of incubation even though the eggs are exposed to light. The effects of elevated steroid hormone levels on lateralization of behaviour post-hatching has not been investigated in any detail but it is known that chicks exposed to elevated levels of corticosterone during the sensitive period before hatching have enhanced ability to form a memory of the passive avoidance learning task [93] and are less vigilant for overhead predators than untreated chicks [23]. The reduced vigilance following corticosterone treatment of the embryo was shown when the chick was searching for food grains on a background of pebbles. The fact that dark-incubated chicks not treated with corticosterone also show reduced vigilance in this situation (discussed further below) suggests that it could be due to the absence of visual lateralization since both treatments prevent the development of asymmetry of the visual projections, although corticosterone has wide-ranging effects on neural development [103].

These effects of hormones on the development of lateralization raise the possibility that lateralization could develop differently from one clutch of eggs to another and, even within a clutch, from one egg to another. Schwabl [89] has shown, in canaries, that corticosterone level varies systematically with the order of eggs laid in a clutch. It is also known that oestrogen levels vary according to order of laying in domestic chick eggs [20]. In fact, the levels of all the steroid hormones vary both within and between clutches and so provide a means by which individuals may vary in degree of visual lateralization. That variation, it seems, may have adaptive significance since it may be the way in which an individual or a group of siblings attunes to environmental demands.

6. Function of lateralization

The widespread occurrence of brain lateralization suggests that it is beneficial in evolutionary terms, despite the immediately apparent disadvantages of being more responsive to predators on the left side and to prey, or other food items, on the right side. One of the suggested benefits, proposed originally to explain the adaptive advantage of lateralization of the human brain [19,41,42], is parallel processing in each hemisphere. To test this hypothesis as applied to the chick, Rogers et al. [88] tested chicks on a task that demanded simultaneous use of the LH, to search for food grains against a background of distracting pebbles, and the RH, to detect and examine a model predator moved overhead in repeated presentations. Of course, the chick might alternate rapidly between food searching and vigilance for a predator rather than performing both tasks at exactly the same time but even with the head down birds can detect an advancing overhead predator [43] and, overall, it can be said that they are being asked to perform the two aspects of the task in parallel.

The performance of chicks hatched from eggs that had received exposure to light during the final stages of incubation was compared to that of chicks hatched from eggs incubated in the dark. According to the hypothesis, because the former are lateralized for these tasks, they should be able to perform the two tasks simultaneously, whereas the latter, having no lateralization for these tasks, should have difficulty in doing so. This was found to be the case (Fig. 3). The lateralized chicks were able to peck at grain and avoid pebbles and they also detected the predator but were not unduly disturbed by it once it had disappeared. Next day they remembered the pebble-grain task well. The dark-incubated chicks performed strikingly differently. They were unable to avoid pecking at the pebbles and, in fact, pecked at them more often relative to grain as the task progressed. Sometimes they missed seeing the predator but, when they did catch sight of it, they were more disturbed by it and made more distress calls [17]. Next day they had no apparent memory of the pebble-grain task. Clearly, they were unable to perform the two tasks simultaneously but, when tested on the pebble-grain task without presentation of the predator, their performance did not differ from that of the lateralized chicks either during the task or on the next day, when they had a good memory of it.

Originally, the poorer performance by the chicks hatched from eggs incubated in the dark was interpreted as showing confusion between the tasks because these chicks were unable to process each task separately in parallel. There is another slight variation on this explanation. Because the dark-incubated chicks pecked more frequently at pebbles as the dual task progressed, it could be said that response to the predator locks them into RH functioning and so they are increasingly unable to inhibit responding to the distracting pebbles. Of course, this still means that they are unable to perform parallel processing but their performance is not due to confusion between hemispheres but opting to use only one hemisphere, the RH, for both tasks. One might ask why would they choose to use the RH and not the LH and the answer is likely to be simply that a predator is a more pertinent stimulus than food. As we know from field studies, animals are vigilant for predators while they are foraging but

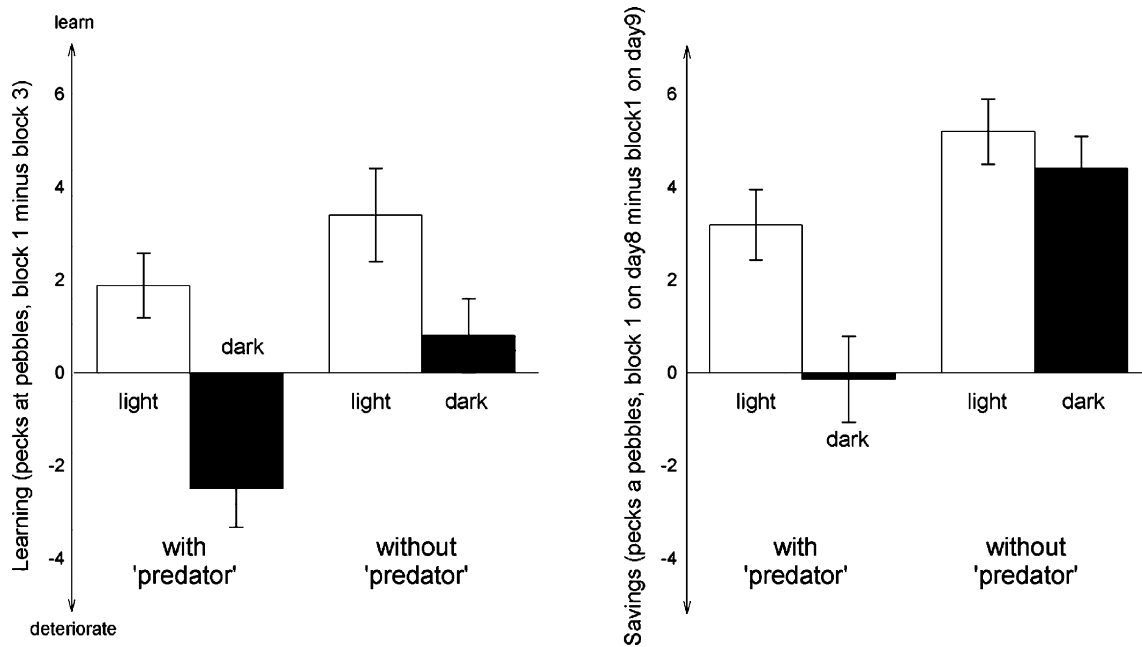


Fig. 3. The results of testing chicks on the pebble-grain task either with or without simultaneous presentation of a model hawk (predator) moved overhead [88]. Comparison is made between the performance of chicks hatched from eggs exposed to light before hatching (lateralized for both aspects of the task; white bars) and chicks hatched from eggs incubated in darkness (non-lateralized for both aspects of the task; black bars). Means and standard errors are plotted. The graph on the left side shows the learning ability on day 8 of life post-hatching by comparing the number of pecks at pebbles in the third block of 20 pecks with the number of pecks at pebbles in the first block of 20 pecks. A positive score indicates that the chicks have learnt to peck at grain in preference to pebbles and a negative score indicates deterioration of performance. The latter was shown only by the dark-incubated chicks tested when the predator was presented. The graph on the right side presents the results of testing the chicks for retention of the pebble-grain task on day 9. On this day no predator was presented (the labels 'with predator' and 'without predator' on this graph refer only to the training condition on day 8). Memory of the task is measured as a 'savings' score determined by subtracting the number of pecks at pebbles in the first block of 20 pecks on day 9 from the same score in the first block of 20 pecks on day 8 (Y-axis). A positive score shows memory of the task. Note that the only group not showing memory of the task is the dark-incubated group trained with presentation of the predator. Dark-incubated chicks trained without presentation of the predator showed memory of the task to the same extent as the light-exposed (lateralized) chicks. Hence, chicks not lateralized for these tasks performed as well as lateralized chicks when they could concentrate on searching for grain but, when they had to attend to the predator as well as search for food, they were unable to form a memory of the task.

they cease foraging immediately a predator is detected [21,53]. If the dual task were redesigned so that food searching took on higher priority than the task demanding use of the RH, the dark-incubated chicks might default to use of the LH and so be less vulnerable to distraction.

Comparison of these results with a test of the function of lateralization in the pigeon is appropriate. In pigeons, Güntürkün et al. [30] found a positive correlation between performance success on the grain-grit discrimination task and degree of lateralization determined in monocular tests. This differs from the results with chickens since there was no difference in the performance of light-exposed and dark-incubated chicks on the pebble-grain task when no predator was presented. Most likely the differing results depend on the testing conditions. If the pigeons were tested in conditions in which there were extraneous stimuli that could distract them from the task, whereas this was not the case for the chicks, this would explain the difference.

It is worth noting that a recent study compared the performance levels of humans on various tasks with their degree of lateralization on that task and found convincing correlations [7]. Depending on the task, the correlation was negative or positive. For example, performance on auditory linguistic and

spatial positional tasks increased with increasing lateralization, whereas performance on visual lexical and spatial quantitative tasks decreased with increasing lateralization. The researchers ascribed the differences in the direction of correlation to the age at which the particular type of lateralization develops. Regardless of the reason for the differences, the evidence that lateralization affects the performance of humans one way or another is strong. Based on the results obtained with chicks, it would be valuable to examine the human data taking the presence or absence of distracting stimuli into account.

7. Is there any advantage in not being lateralized?

Considering that the development of lateralization can be influenced by environmental stimulation, as well as certain hormones, during sensitive periods, one would expect to find variation between individuals in the strength and even the presence or absence of lateralization. Despite the complication that these effects on development are specific to certain types of lateralization, and lateralization in different modules may be stronger or weaker within the same individual, we can begin to address the question whether there are any advantages to being weakly lateralized or less lateralized.

Two studies of chicks give some indication of possible benefits from not being lateralized in those aspects of visual behaviour influenced by exposure of the embryo to light and both relate to social behaviour. Chicks not exposed to light before hatching form less strongly stratified social hierarchies than do chicks exposed to light, as measured by amount of access to a food source positioned so that not all of the group could reach it at the same time [83]. In groups comprised of dark-incubated chicks, the lower-ranking chicks gained more access to the food source than did their equivalents in groups comprised of light-incubated chicks. The lower-ranking, dark-incubated chicks were more persistent at pushing between their companions to reach the food source. Hence, if chicks are not lateralized by light exposure, all members of the social group have a better chance of survival.

Vigilance in a group is also influenced by lateralization. Groups of dark-incubated chicks are slower to detect a model predator presented overhead when they are feeding but, once the predator has been detected, all members of the group respond to it by looking up (Wichman, Freire and Rogers, submitted). This compares to fewer chicks looking up at any one time in groups comprised of light-exposed chicks. Whether or not this difference in the reactivity of the group is beneficial would, of course, depend on specific circumstances that require further investigation. The result could, however, indicate stronger social cohesion in chicks that are not lateralized. If so, depending on context, the cognitive benefits to the individual of having a lateralized brain could be sacrificed for the social benefits of having a non-lateralized brain.

8. Potential role of the light/hormone interaction in the natural habitat

Since only 2 h of light exposure is sufficient to establish visual lateralization in the chick [68,69,76], it is likely that, in the natural habitat, the hen would leave the nest often enough for eggs to receive the required amount of light. Moreover, low intensities of light are effective [76], which indicates that eggs in nests laid under vegetation are likely to receive enough light exposure to allow the development of visual lateralization. However, avian species that lay eggs in hollows that receive no light or incubate their eggs underground (as in the case of the Australian brush turkey) would not be lateralized by light exposure. A potential for species differences dependent on opacity of the eggshell also exists [76].

The interplay between the influences of light exposure and steroid hormones is likely to be most important in natural conditions. Stress could influence the development of lateralization not only by altering the time intervals during which the hen leaves the nest and exposes the eggs to light but also by elevating corticosterone levels in the egg. For example, a hen experiencing social stress or predation stress might nest in darker/thicker cover, leave the nest less often and deposit higher levels of corticosterone in her eggs. All of these factors would prevent the development of visual lateralization of the offspring. A possible outcome of this could be that all chicks have a better chance of survival in terms of food intake and

group cohesion but the ability to carry out parallel processing is sacrificed.

9. Concluding remarks

Now that we know a good deal about lateralization of visual processing and performance in two avian species, in my opinion, there are three ways to proceed. First, it would be informative to learn a considerable amount more about lateralization in the other sensory modalities in these two species so that comparisons can be made to visual lateralization and, moreover, lateralized integration of sensory inputs in the different modalities can be determined. Such studies might lead us to a better understanding of the benefits of having a lateralized brain. Secondly, expanding the investigation of lateralization to other avian species will allow comparisons that are likely to be most informative not only about the nature of lateralization but also about its development in species with different organization of their visual systems (e.g. in avian species with frontally placed eyes) and in species with different nesting behaviour and hatching at differing stages of development. Thirdly, knowledge of the interactive effects of light stimulation and steroid hormones on the development of lateralization is in its infancy and awaits further study, particularly at the cellular and subcellular levels using, for example, the techniques of molecular genetics coupled with a thorough recognition of the importance of the influence of experience. The known effects of experience on the development of lateralization make the avian brain an excellent model in which to study the events essential for neurone growth, survival and loss. In fact, the avian model is, I believe, poised to play a pivotal role in enhancing understanding of central nervous system development.

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