

Advantages of having a lateralized brain

Lesley J. Rogers^{1*}, Paolo Zucca²
and Giorgio Vallortigara^{2,3}

¹Centre for Neuroscience and Animal Behaviour,
University of New England, Armidale, NSW 2351, Australia

²Department of Psychology, and ³B.R.A.I.N. Centre for Neuroscience,
University of Trieste, Via Anastasio 12, 34123 Trieste, Italy
(vallorti@univ.trieste.it)

* Author for correspondence (lrogers@une.edu.au).

Recd 02.03.04; Acceptd 15.03.04; Published online 14.05.04

Brain lateralization is common among vertebrates. However, despite its implications for higher-order cognitive functions, almost no empirical evidence has been provided to show that it may confer any advantage to the functioning of the brain. Here, we show in the domestic chick (*Gallus gallus domesticus*) that cerebral lateralization is associated with an enhanced ability to perform two tasks simultaneously: finding food and being vigilant for predators. This finding suggests that cerebral lateralization enhances brain efficiency in cognitive tasks that demand the simultaneous but different use of both hemispheres.

Keywords: brain lateralization; advantages; foraging; vigilance; simultaneous tasks; chicks

1. INTRODUCTION

Lateralization of the brain is widespread in vertebrates (Rogers & Andrew 2002). Many species share a general pattern of using the right hemisphere to attend to novelty and execute rapid responses, whereas the left hemisphere is used to categorize stimuli and control responses requiring consideration of alternatives (Vallortigara 2000; Rogers 2002). Some of these lateralized functions are manifested as side biases that would be disadvantageous for survival, as in the case of enhanced reactivity to predators approaching on the animal's left side (Rogers 2000; Lippolis *et al.* 2002), which leaves prey more vulnerable to predators on their right side. The elevated agonistic responses directed at other members of the species on the animal's left side (Deckel 1995; Robins *et al.* 1998; Rogers 2000; Vallortigara *et al.* 2001) might also be disadvantageous, as also would the right side preference for responding to prey (Rogers 2002; Robins & Rogers 2004). Hence, we may question why lateralization is so common among vertebrates. Here, we show that these disadvantages are counterbalanced by an enhanced ability to perform two tasks simultaneously: finding food and being vigilant for predators.

Chicks were tested on a dual task requiring them to find food grains against a distracting background of small pebbles and simultaneously to attend to a model predator overhead. Lateralized chicks are able to engage their left hemisphere (and right eye) in discriminating the grain from the background (Rogers 1990) and their right hemisphere (and left eye) in monitoring overhead for a model

predator (Rogers 2000). They were compared with chicks without lateralization on such tasks. The lateralized chicks performed both tasks better than the non-lateralized chicks. In fact, the demands of the dual task impaired the performance of the non-lateralized chicks to such an extent that their performance deteriorated as they continued to search for food. The advantage conferred by lateralization in being able to carry out qualitatively different types of processing simultaneously in the left and right hemispheres may, therefore, explain why this specialization is conserved across vertebrate taxa.

Chicks were chosen for this study because we are able to manipulate their lateralization on visual tasks by exposing the eggs to light for a brief period during the last 3 days before hatching (Rogers 1990). The light exposure leads to the development of lateralization of some visual functions and generates asymmetry in the thalamofugal visual projections to the forebrain (Rogers & Deng 1999) because the late-stage embryo is turned in the egg so that it occludes its left eye but not its right eye (Rogers 1990). Chicks hatched from eggs exposed to light during the last days of incubation can discriminate grain from the background of pebbles when they are tested monocularly using their right eye but not when they use their left eye, whereas chicks hatched from eggs incubated in the dark are not lateralized in this way (Rogers 1990, 1997). The same occurs for lateralization of attack responses: chicks exposed to light before hatching show elevated levels of attack following treatment with testosterone provided that they are using their left eye but not when they use their right eye, and this lateralization is not present in chicks that are incubated in the dark (Rogers *et al.* 1985). The light exposure also generates a left-eye advantage in latency to detect an overhead predator, which is not present in dark-incubated chicks (Rogers 2000). Hence, light-exposed chicks are more strongly lateralized for processing visual information than are dark-incubated ones.

2. MATERIAL AND METHODS

We tested 27 chicks exposed to light (400 lx) from day 17 of incubation to hatching (Li chicks) and 24 dark-incubated chicks (Da chicks). The chicks were all raised in visual isolation from each other and with light exposure after hatching. They were deprived of food for 4 h before testing on days 8 and 9. The testing apparatus (figure 1) consisted of a central compartment with a floor to which small pebbles had been adhered at random and onto which food grains had been scattered, and two compartments, one on either side, containing mirrors angled at 45° so that the chick's behaviour could be monitored using an overhead video camera. About half of the chicks (16 Li and 14 Da) were tested with a model resembling the silhouette of a flying raptor (width of 8 cm) that was moved over the cage. By using a motor, the 'predator' was presented at 18 s intervals and at a speed of 12 cm s⁻¹. The chick was placed into the central compartment and its pecks at grain and pebbles were scored for a total of 60 pecks by direct observation through a small window at floor level. Responses to the 'predator' were scored from the video recordings. The remaining chicks (11 Li and 10 Da) were tested on the pebble-grain task without the overhead 'predator' being presented.

It is well known that learning to discriminate pebbles from grain is a function of the Wulst region in the left hemisphere in chicks exposed to light before hatching; in particular, glutamate treatment of the left Wulst impairs this learning, whereas the same treatment of the right Wulst has no effect (Deng & Rogers 1997, 2002). By contrast, monitoring for novel stimuli, including aerial predators, engages the right hemisphere (Evans *et al.* 1993; Rogers 2000; Rogers & Andrew 2002). Hence, the task demanded simultaneous but different use of both hemispheres. Our prediction was that Li chicks would have no difficulty in performing both aspects of this task, whereas Da chicks would perform poorly both in finding the grain and in responding to the predator.

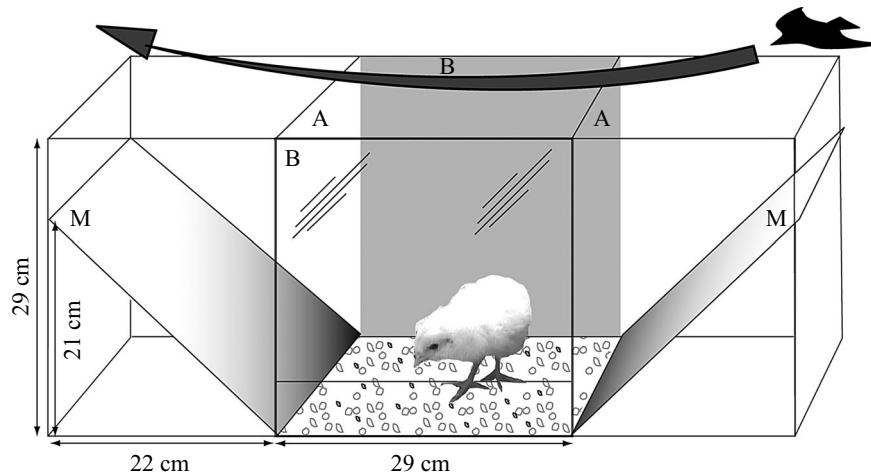


Figure 1. The testing apparatus with dimensions indicated. The chick pecks on the pebble floor (grain is scattered among pebbles adhered to the floor). A panels are transparent, B panels are opaque apart from a window at the bottom of the front B panel. The chick's choice of targets is scored by direct observation through the slit at floor level. Responses to the model predator are scored from a video recording made from directly overhead, and with the aid of the mirrors (M), which allowed accurate measurement of the angle of the chick's head when it viewed the predator.

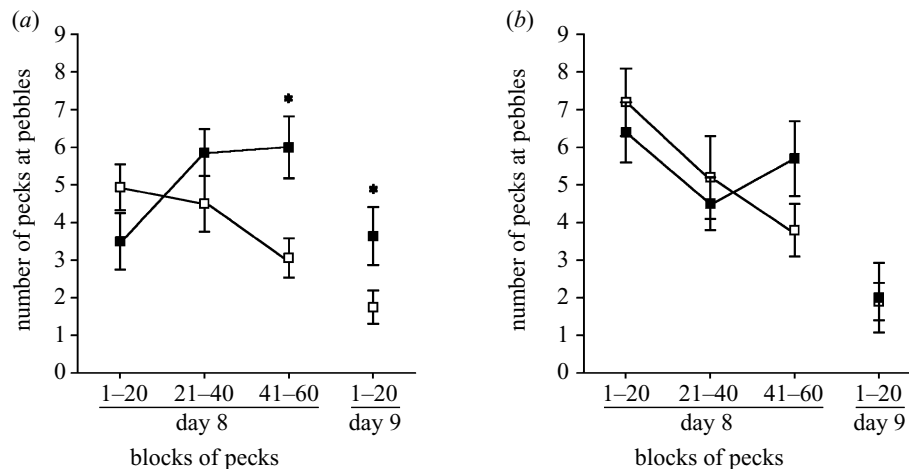


Figure 2. The results for the pebble-floor task both (a) with and (b) without presentation of the model predator: open squares, light-exposed chicks; filled squares, dark-incubated chicks. On the left sides of each *x*-axis are the scores for learning (on day 8) to find grain, expressed in terms of the numbers of pecks made at pebbles in each block of 20 pecks (total of 60 pecks). A decreasing score shows that learning has occurred (as was found in both of the groups exposed to light). An increasing score shows deterioration of the ability to find grain among the pebbles, as in the case of the dark-incubated chicks tested with presentation of the predator. On the right sides of the *x*-axes, the retention of performance on day 9 is indicated in terms of the numbers of pecks at pebbles in the first block of 20 pecks. Memory retention of the task is found for all groups except for the dark-incubated group trained with the predator being presented. Note that retention was tested on day 9 without presentation of the predator.

3. RESULTS AND DISCUSSION

Learning on the pebble-grain task is indicated by a decrease in the number of pecks at pebbles over the three blocks of 20 pecks (figure 2). When tested on this task and when the model predator was presented at the same time, Li chicks showed significant learning (paired one-tailed *t*-test between pecks at pebbles in the first and last block of pecks: $t = 2.68$, d.f. = 15, $p = 0.009$). By marked contrast, the ability of the Da chicks to avoid pecking pebbles deteriorated as the task progressed; they pecked at more pebbles in the last 20 pecks than they did in the first 20 pecks (two-tailed: $t = -3.04$, d.f. = 13, $p = 0.01$; figure 2). This deterioration in Da chicks did not occur

when the chicks were tested on the same task without the simultaneous presentation of the predator. The Da chicks did not show significant learning without the predator being presented (two-tailed: $t = 0.95$, d.f. = 9, $p = 0.36$) but their performance did improve in the second block of 20 pecks (two-tailed: $t = 2.68$, d.f. = 9, $p = 0.025$) and there was certainly no evidence of the deterioration in performance seen when the predator was present. Without the predator, Li chicks learnt to avoid pecking at pebbles (one-tailed, based on many of previous studies (Rogers 1990, 1997, 2000): $t = 2.93$, d.f. = 10, $p = 0.003$) just as they had done when the predator was presented. This better performance by Li compared with Da chicks matches

a finding in pigeons that the strength of lateralization correlates positively with efficiency in finding food grains (Güntürkün *et al.* 2000).

Retention of the task was measured by allowing the chicks to peck 20 times on the same floor with pebbles and grain on day 9 and again after 4 h of food deprivation. No model predator was presented. As shown in figure 2, only the Da chicks trained on day 8 with the predator failed to show recall of the task: they pecked as many pebbles as they had done in the first block of 20 pecks on day 8 (i.e. they showed no savings/memory). The Li chicks trained in the presence of the predator, in contrast, did show significant memory. Following training without the predator being presented, both Da and Li chicks showed good retention (memory).

In the test on day 8, all of the chicks detected the overhead predator on its first presentation and most showed startle followed by fear responses, which included the startle trill call followed by distress peeps, looking overhead, circling and crouching. The Li chicks detected the stimulus, as shown by an interruption of pecking, as soon as it appeared overhead (on a mean of 79% of presentations), whereas the Da chicks did so on a mean of only 63% of occasions (unpaired two-tailed *t*-test: $t = 2.49$, d.f. = 28, $p = 0.018$). In fact, the Li chicks usually stopped pecking and tilted their heads to view the predator with the left eye (left eye on 72% of occasions), whereas the Da chicks showed no such eye preference and were more inclined not to look up. Also, the Li chicks continued to respond to the predator over significantly more presentations than did the Da chicks: the mean (\pm s.e.) number of presentations to habituation (no interruption of pecking) in Li chicks was 10.9 ± 3.1 and in Da chicks it was only 4.3 ± 1.3 (one-tailed *t*-test (since the direction of difference was predicted): $t = 1.84$, d.f. = 28, $p = 0.03$). We conclude that the Li chicks were more vigilant than the Da chicks.

Hence, the lateralized (Li) chicks were able to perform both tasks better than the non-lateralized (Da) chicks. In fact, even though the non-lateralized chicks were less vigilant and less attentive to the overhead predator, their performance in finding food grains was affected by the presence of the predator to a greater degree than was the performance of the lateralized chicks. This demonstrates interference between the tasks in non-lateralized chicks and a clear advantage of having a lateralized brain.

The effect of being incubated in the dark seems to be quite specific, as Da chicks do not appear to be generally disadvantaged: an earlier study (Rogers & Workman 1989) has shown that, when in groups, they compete for access to a food bowl more successfully than do Li chicks.

We are not suggesting that the hemispheres of a lateralized brain operate entirely independently of one another: that would seem to be disadvantageous. Split-brain humans can attend to two tasks at once (Luck *et al.* 1989), but in most respects having a split brain is not an advantage. The avian brain has no large interhemispheric connecting pathway, as in the case of the corpus callosum in humans, but its smaller commissures may well serve to keep each hemisphere informed of the other.

We believe that our results have relevance to behaviour in the natural environment, and note that lateralized eye use for vigilance has been reported in birds in the wild (Franklin & Lima 2001; Rogers & Andrew 2002). Given that simultaneous processing of and attention to very different stimuli are demanded in the natural environment and that prey species of birds would meet situations very similar to those that we used in testing, our results show that having a lateralized brain would enhance survival. We have thus found one explanation for the ubiquity of brain lateralization.

Acknowledgements

This research was conducted at the University of New England and supported by funds from the Australian Research Council to L.J.R. The experiments were conducted by P.Z. and L.J.R.

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