Correspondence

A left-sided visuospatial bias in birds

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Humans primarily attend to objects in the left side of space, as shown in cancellation tasks routinely used during neuropsychological testing [1,2]. This asymmetry is thought to arise from a right hemispheric superiority in the control of spatial attentional resources [3], and is assumed to depend on the corpus callosum which mediates fast communication between two specialized hemispheres of the brain [4]. We tested two species of birds in a task that closely matches the cancellation task: the birds were required to explore an area in front of them and to sample grains. Birds displayed a clear bias into the left hemispace, as evident in the pecking activity or the order in which pecks were placed in the left or right hemispace. Birds thus exhibit a similar left-side bias to that of humans, but as birds have no corpus callosum, transcallosal interactions cannot be a critical prerequisite for spatial asymmetries. Lateralization of spatial attention is thus common to humans and birds, and may have evolved before their last common ancestor more than 250 million years ago [5].

Following right hemisphere damage, many patients display indifference to the left side of the world, attending primarily to the right hemispace ('spatial hemineglect') [6,7]. The neglect syndrome entails difficulty in reporting, responding or orienting towards stimuli within the hemispace contralateral to a unilateral brain lesion [8]. Left hemispatial neglect, caused by damage to the right hemisphere, occurs more frequently than right hemispatial neglect, caused by damage to the left hemisphere [6,8,9]. The syndrome has attracted considerable interest as it may shed light on the neural mechanisms underlying the spatial allocation of attention.

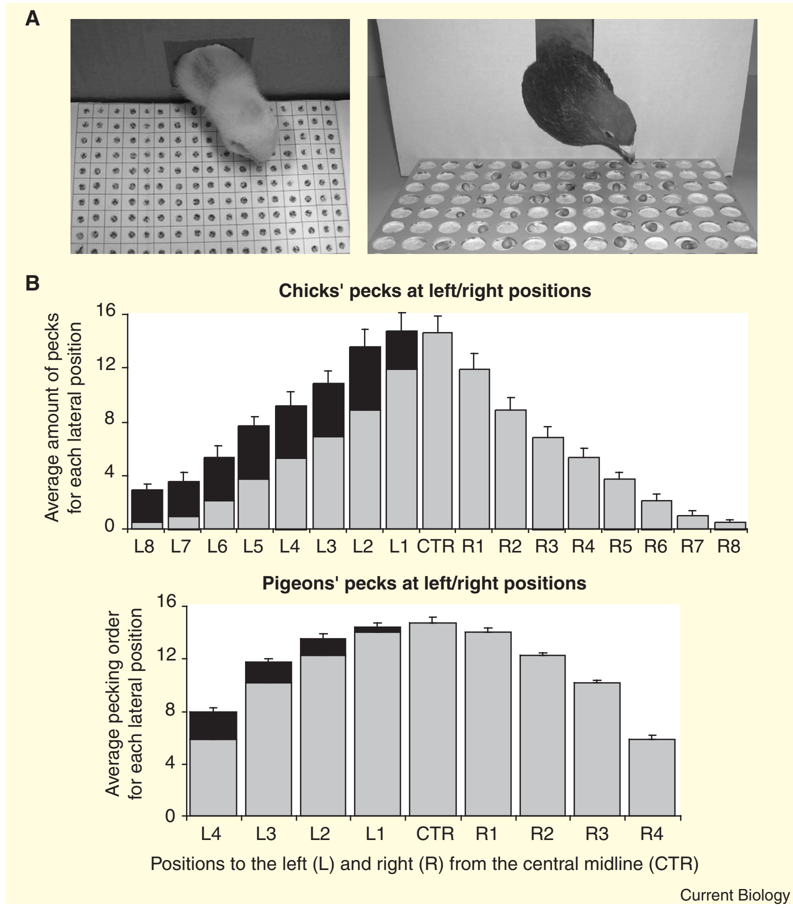

Figure 1. Left-right visuospatial bias in birds in a food cancellation task.
(A) Two-week-old chicks (left, N = 31) and adult pigeons (right, N = 14) were allowed to peck for uniformly spread grains of food (chicks: one piece every 1 cm square area over a surface of 17 x 10 cm; pigeons: one grain every other 2 cm square area, 23 grains total over a 18 x 10 cm surface). For analysis, the surface was divided into an array of identical vertical sectors (in chicks: 17 sectors; in pigeons: 9 sectors). For each chick, all pecks within each sector were counted. In pigeons, which make only a few pecks, the spatial position of pecks was scored based on the order in which they occurred, with the first peck given the highest score of 23. (B) The average amount (± standard error) of pecks made by chicks and the average score for the order in which pigeons pecked in each sector. Highlighted is the number of left over right pecks for chicks and the earlier pecks within left compared to corresponding right sectors for pigeons. Data were analyzed in a repeated measures ANOVA, with distance of each sector from the centre (8 in chicks, 4 in pigeons) and left/right position of these sectors as factors. For chicks, the analysis yielded a significant effect of distance ($F_{(7,30)} = 88.70$, $P < 0.0001$), indicating lower amounts of pecks with distance from the centre, and a significant left/right effect ($F_{(1,30)} = 45.35$, $P < 0.0001$), indicating an overall greater amount of left (8.5 ± 1.2) compared to right pecks (5.1 ± 1.0). The interaction between the two variables (distance x left/right) was not significant ($F_{(7,30)} = 1.92$, $P = 0.682$). Similarly, in pigeons the effect of distance was significant ($F_{(3,39)} = 262.59$, $P < 0.0001$). Sectors close to the centre were chosen earlier than distant sectors. A significant effect of the order of left/right pecks ($F_{(1,13)} = 9.68$, $P < 0.009$) indicated an overall greater tendency to choose food first from left (11.9 ± 0.4) and later from right sectors (10.6 ± 0.3). The interaction between the two variables was significant ($F_{(3,39)} = 6.49$, $P < 0.0011$), with significant differences between the three most lateral sectors (L4 vs. R4, L3 vs. R3 and L2 vs. R2; all Bonferroni post hoc tests $P < 0.01$). As shown, chicks placed more pecks in left than in corresponding right sectors and pigeons, on average, attended first to the left as compared to the right side.

A related phenomenon in healthy subjects is 'pseudoneglect' [10,11]: the slight systematic leftward bias in the allocation of attention in tasks, such as the cancellation task, in which subjects are asked to 'cancel' visual targets on a sheet of paper placed midline in front of them. This is one of the tests used to diagnose visuospatial attention deficits in human patients. In this test, normal subjects show right lateralized inattention [12]. We devised an adapted version of this task and administered it to two model bird species: the domestic chick (*Gallus gallus*) and the pigeon (*Columba livia*). The birds were given a free choice to orient towards and peck at grains spread evenly over an area in front of them. They could freely move their head, while their body was restrained and aligned centrally in front of the search area (Figure 1A). Chicks and pigeons both showed a strong and significant leftward bias, spread uniformly across the left hemispace (Figure 1B).

Spatial hemineglect is more frequent and severe after damage to the right hemisphere in right-handed humans; this asymmetry is usually explained assuming that neural circuits in the right hemisphere are capable of attending to and representing both sides of space, whilst the left hemisphere would be concerned only with the contralateral right side [13]. Our results suggest that a similar asymmetry is present in the bird's brain.

The presence of a corpus callosum is usually claimed to be at the base of the emergence of these asymmetries [4], but such a brain structure is not present in birds. Hence its role in spatial asymmetries is not clear.

It remains to be explained, however, why birds should show such a pronounced bias in spite of obvious ecological disadvantages (grains of food are unlikely to be located systematically to the left of an animal's midline in the natural environment). Very likely, lateralization enhances brain efficiency and counteracts ecological disadvantages. For instance, it has been shown that individual pigeons show a correlation between the degree of asymmetry and the efficiency in visual discrimination learning [14] and that not-lateralized chicks perform worse than lateralized ones in double tasks (such as finding food and being vigilant for predators) involving the simultaneous but different use of both hemispheres [15]. In the present context, the reason why the right eye system seems to be not as good as the left eye system at finding targets in rapid search is likely to be that the right eye system is specialised for something else. In search tasks, this has been shown to be approach to the selected target (pursuit if the target is alive) and its seizure [16,17].

In conclusion, birds show a strong leftward bias in the spatial distribution of attention related to food detection. The bird brain — and very likely the brains of other non-mammalian vertebrates with laterally placed eyes [18] — may offer an excellent model system for the investigation of visuospatial attention mechanisms in normal or pathological conditions and for studying aspects of the neglect syndrome in a comprehensive way.

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Supplemental data
Supplemental data containing further details of the experimental procedures are available at http://www.current-biology.com/cgi/content/full/15/10/R372/DC1/

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