Asymmetry pays: visual lateralization improves discrimination success in pigeons

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Functional cerebral asymmetries, once thought to be exclusively human, are now accepted to be a widespread principle of brain organization in vertebrates [1]. The prevalence of lateralization makes it likely that it has some major advantage. Until now, however, conclusive evidence has been lacking. To analyze the relation between the extent of cerebral asymmetry and the degree of performance in visual foraging, we studied grain–grit discrimination success in pigeons, a species with a left hemisphere dominance for visual object processing [2,3]. The birds performed the task under left-eye, right-eye or binocular seeing conditions. In most animals, right-eye seeing was superior to left-eye seeing performance, and binocular performance was higher than each monocular level. The absolute difference between left- and right-eye levels was defined as a measure for the degree of visual asymmetry. Animals with higher asymmetries were more successful in discriminating grain from grit under binocular conditions. This shows that an increase in visual asymmetry enhances success in visually guided foraging. Possibly, asymmetries of the pigeon's visual system increase the computational speed of object recognition processes by concentrating them into one hemisphere while preventing the other side of the brain from initiating conflicting search sequences of its own.

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Received: **28 June 2000**
Revised: **14 July 2000**
Accepted: **14 July 2000**

Published: **25 August 2000**

Current Biology 2000, 10:1079–1081

0960-9822/00/$ – see front matter

Results and discussion

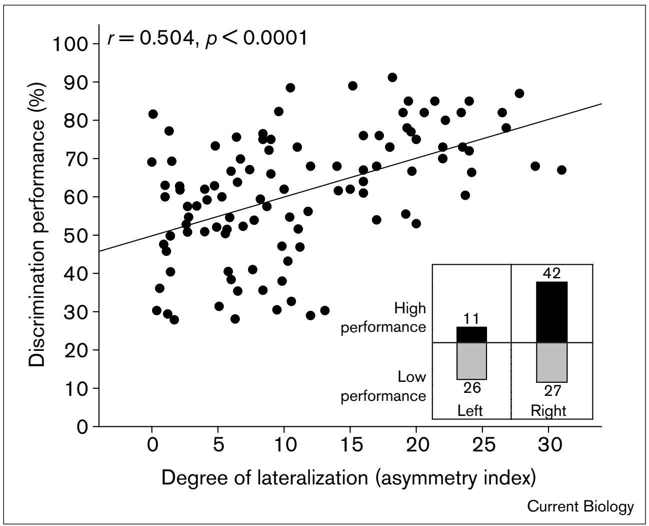
One hundred and eight adult, food-deprived pigeons were accustomed to the grit–grain discrimination test which requires the birds to peck within 30 seconds from a trough filled with 30 grains and 30 grams of grit (~1000 pieces) similar in color and shape [4]. In this task, percent discrimination performance is calculated as the number of consumed grains to total number of pecks. Using eyecaps, the pigeons alternatingly performed binocular, left- and right-eye seeing sessions. Thirty sessions were conducted altogether (10 for each condition, 1 session per day). The absolute individual degree of lateralization was expressed as the asymmetry index, AI, which is calculated as $|AI| = |\text{right} - \text{left eye performance } (\%)|$.

In most of the pigeons, binocular discrimination level was superior to either monocular one. Right monocular levels were higher than left monocular levels in 65% of the birds. This population asymmetry is virtually identical to the two-third/one-third division typical for human handedness [5,6]. Discrimination accuracy between left eye (mean = 46.1%) and right eye (mean = 51.7%) differed significantly ($t_{107} = 4.58$, $p < 0.001$). The correlation between AI and discrimination level under binocular conditions was also highly significant ($r = 0.50$, $p < 0.001$), showing that the level of lateralization was positively related to visual object discrimination performance (Figure 1). When AIs of animals with right- ($n = 70$) or left-eye dominance ($n = 37$) were correlated separately (one animal was not lateralized) with binocular discrimination levels, only values for animals with right-eye superiority reached significance (right: $r = 0.57$, $p < 0.001$; left: $r = 0.31$, $p = 0.067$), indicating a closer relation between asymmetry and discrimination performance for pigeons with the usual right-eye dominance.

Separate consideration of birds with a dominant left or a dominant right eye (small insert in Figure 1) shows differential distribution of subgroups (median-split) with high and low performance: whereas the number of left-eye and right-eye dominant birds is virtually equal within the low-performance group, high performance is related to right-eye dominance in the majority of birds (χ^2 $(df = 1) = 9.34$, $p < 0.003$).

Numerous theories have tried to explain why brain lateralizations evolved in so many organisms [1]. Cerebral asymmetries were suggested to allow for more efficient parallel processing [7], to decrease redundancy of neural operations [8], to facilitate neural processes by avoiding delays resulting from slow interhemispheric interactions [9], or to eliminate interhemispheric conflict during initiation of behavioral alternatives [10,11]. These theories would demand an increase of asymmetry to be significantly related to a higher level of performance. This is what the present study shows, using a task that directly tests the processes of the lateralized visual system (see also [12,13]).

Figure 1



Relationship between the degree of lateralization and binocular discrimination performance. Pearson's product moment correlation (scatter plot) reveals higher performance in more lateralized individuals. The small insert shows the differential distribution of pigeons with left- or right-eye dominance in subgroups (median-split) with high and low performance. While numbers of left-eye and right-eye dominant birds are about equal within the low-performance group, high discrimination accuracy is mainly related to right-eye dominance.

Two questions follow from these results. How does an increase of visual lateralization create an advantage in discrimination performance? Why is a reversal of the usual asymmetry pattern less advantageous?

Birds show higher levels of performance with the right eye when discriminating visual patterns [2,3]. Because of the virtually complete decussation of the avian optic nerves, a right-eye superiority reflects a left hemisphere dominance for visual object processing. This is also the case for grain–grit discrimination, in which performance differences between the eyes were repeatedly shown not to depend on visuomotor pecking speed but on discrimination accuracy [4,14].

Visual lateralization in pigeons depends on the left hemispheric superiority of the ascending tectofugal visual system. A nodal point of this pathway is the thalamic nucleus rotundus, which receives bilateral afferents from the tectum opticum and projects to the ectostriatum of the forebrain [15]. The rotundus of the visually dominant left hemisphere receives a significantly higher degree of bilateral tectal input whereas tectal afferents to the subdominant right rotundus mainly arise from the ipsilateral tectum [16]. Due to this wiring pattern, the dominant left rotundus integrates visual information from both eyes, whereas the subdominant right rotundus primarily processes left-eye input [17].

During feeding, pigeons select their next targets mainly within three visual 'hot-spots', one in the lower center of their binocular visual field, and two displaced laterally on either side [18]. The central hot-spot corresponds to the dorsotemporal fovea-like area of each retina pointing binocularly into the frontal field, whereas the two other spots are related to the areae centralis of each retina, which point to the monocular lateral fields on either side [19]. The visual input from both eyes enables the left rotundus to integrate all three critical hot-spots to a significantly higher degree compared with the rotundus on the subdominant right side. Therefore, the left visual hemisphere integrates visual input from the whole visual field. As it also reaches a higher performance in discriminating visual patterns [4,14], both the visualization and selection of the next grain to peck as well as the discrimination of grains from pebbles is superior on the left side. An increase in individual asymmetry should result in a concentration of this selection and discrimination process in one side of the brain, thereby increasing the computational speed of this neural process by a massive reduction of wiring lengths. Within the very short time frame of 30 seconds, as used in the present study, an increase of computational speed could be directly proportional to a higher efficiency of foraging.

An inrease of visual asymmetry could, however, additionally increase grain–grit discrimination efficiency by reducing interhemispheric conflicts during initiation of pecking movements to different grains. The tecto-tectal interaction is known to be mainly inhibitory [20] with the dominant left tectum modulating right tectal processes to a significantly higher degree than vice versa [21]. An increase in individual lateralization could therefore additionally augment this tecto-tectal asymmetry, resulting in a reduction of interhemispheric conflict during selection of the next pecking target. Thus, an individual increase in visual lateralization processes could concentrate discrimination and selection processes into the specialized hemisphere, while at the same time inhibiting the subdominant hemisphere from initiating behavioral alternatives.

About one third of the pigeons displayed a reversed left-eye dominance and these birds were on the average less efficient foragers. It is conceivable, however, that a reversed asymmetry pattern might constitute an advantage in other visual tasks, such that frequency-dependent natural selection could maintain this minority [22]. In pigeons, visual lateralization with the usual right-eye superiority depends on an asymmetrical prehatch position of the embryo. Avian embryos bend forward and keep their head turned to the right so that the right eye is exposed to the light shining through the translucent shell, while the left eye is occluded by the body [23]. This posture results in a stronger light stimulation of the right eye, which then establishes visual lateralization with a left hemispheric superiority in object discrimination [24,25]. Early light stimulation not only triggers asymmetry, however, but also organizes the developing visual system [26]. Any condition, genetic or epigenetic, that interferes with this developmental sequence not only disturbs the usual asymmetry pattern but could also result in slightly altered neural wiring patterns, which might result in differences in visual processing. In our sample, an increase of left-eye superiority was also positively related to discrimination success, although the relation was considerably weaker and of only marginal significance. For the majority of pigeons, however, an individual increase of right-eye dominance considerably increased discrimination achievement. In these birds, a 10-point rise in asymmetry resulted in a 10% increase in discrimination success. Thus, asymmetry pays.

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