

AVIAN CEREBRAL ASYMMETRIES: THE VIEW FROM THE INSIDE

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Research on human cerebral asymmetries has a long tradition (Broca, 1865). Although comparative studies on left-right-differences in non-human animals started shortly after Broca's initial discovery (Ogle, 1871; Cunningham, 1892), this tradition ceased and was slowly replaced by the erroneous assumption that lateralization is a uniquely human attribute, associated with language and higher cognitive abilities (Corballis et al., 2000). Up to now, asymmetry research has suffered from this long period of neglect that has been overcome only recently (Rogers and Andrew, 2002). As a result, cerebral asymmetry research is presently characterized by a detailed understanding of its functional architecture but an extremely limited knowledge of its neuronal basis. Since cerebral asymmetries are documented in all vertebrate classes (Bisazza et al., 1998) and seem to follow a comparable pattern (Vallortigara and Bisazza, 2002), the time is ripe to focus on animal models to gain detailed insights into the neuronal processes governing lateralized function. These analyses will uncover fundamental aspects of asymmetries that can hardly be answered by experiments with human subjects. One of the yet unanswered essential questions is whether functional asymmetries result from bottom-up lateralizations of ascending sensory systems that shape associative forebrain processing, or from top-down projections of forebrain structures that impose an asymmetrical control over sensory and motor systems.

Avian species like chicks and pigeons show a left hemispheric (right eye) superiority in object discrimination tasks and a right hemispheric (left eye) dominance during topographical learning that involves the utilization of relational configurations (for review see Güntürkün, 2002). In pigeons, this asymmetry primarily results from morphological and physiological left-right differences within the tectofugal system (retina → tectum opticum → n. rotundus → entopallium; Güntürkün, 2002), that is homologous to the extrageniculocortical visual system of humans (retina → superior colliculus → pulvinar → extrastriatal visual cortical areas; Shimizu, 2000). By recording from the left or the right n. rotundus while using a standardized visual stimulation paradigm of the ipsi- or the

contralateral eye, Folta et al. (2004) were able to distinguish between left-right differences that emerged bottom-up from the retino-tecto-rotundal system and those that were derived top-down from the forebrain. Both bottom-up and top-down systems contributed to visual asymmetry, but with a striking difference.

Left-right differences within the bottom-up system were due to variations in the latency and the tonic spike duration of rotundal neurons after stimulation of the contralateral eye. Visual signals arrived on average 18% faster in the right thalamus, but cellular activation lasted 27% longer in the left rotundus. These lateralized effects may underly the fact that pigeons are faster with the left eye (right hemisphere) in simple visual reaction paradigms (Di Stefano et al., 1987) but are superior with the right eye (left hemisphere) in pattern learning and discrimination (Güntürkün, 2002). While the asymmetries within the bottom-up system were a matter of degree, those of the top-down cells displayed an all-or-none organization. Without a single exception, all thalamic cells that were activated by descending forebrain systems were under control of the left hemisphere. Thus, although visual input reaches both hemispheres, at least the modulation of the diencephalic relay of the tectofugal system is under the executive control of only the left hemisphere.

If these results from pigeons also apply to other lateralized animals including humans, a couple of implications emerge. First of all, it is obvious that asymmetries arise both from bottom-up as well as top-down asymmetries, albeit with different contributions. The more moderate left-right differences of the ascending system are possibly already able to promote hemisphere-specific modes of visual processing. But since the top-down signal from the forebrain derives exclusively from the left hemisphere, we have to assume that asymmetrical modes of analyses within both hemispheres are ultimately funneled to a single hemisphere that then generates executive control over subtelencephalic sensory and motor structures. Theories on the evolutionary advantage of cerebral asymmetries have always revolved around the concept of a singular executive control to decide between two behavioral alternatives that result from processes

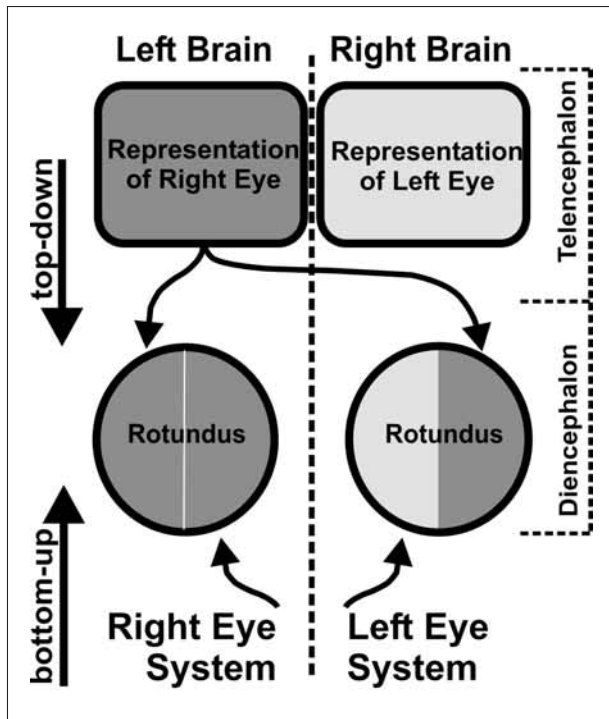


Fig. 1 – Schematic functional diagram of the bottom-up and the top-down inputs to the *n. rotundus* in pigeons. Due to the asymmetrical top-down influence from the telencephalon, the left diencephalic *n. rotundus* mainly represents the afferents from the right eye, while the right *n. rotundus* integrates input from both eyes. The figure is based on the single unit data of Folta et al. (2004).

within the two hemispheres (Vallortigara and Bisazza, 2002; Doty, 2003). Very likely, the virtually complete unilateral control of language in humans as seen in split-brain patients as well as in other complex motor behaviors results from such a process (Gazzaniga, 2000). It is conceivable that the complete unilaterality of top-down control in pigeons represents the neurobiological realization of such a unihemispheric executive control.

A second implication from the study of Folta et al. (2004) concerns left-right differences of visual representation at thalamic level. If descending forebrain signals arrive within the rotundus only from the left hemisphere, they should create cellular response patterns with diverse combinations of bottom-up and top-down influences depending on the thalamic side. Within the left thalamus most bottom-up and all of the top-down effects are communicated by the right eye system. This is different for the right rotundus, where bottom-up input derives from left eye stimulations while all of the top-down effects originate from the right eye input (Figure 1). Thus, bilateral integration predominates at right thalamic level but not at left. This electrophysiological pattern could explain some of the well known asymmetries on spatial orientation and attentional control. In most species studied, the right hemisphere dominates visuospatial orientation and attention, a cognitive feature that generally requires the integration of information

from widespread areas of the visual field (Rogers and Andrew, 2002). Several studies have reported that these tasks are associated with an activation of the dominant right superior parietal lobe after left and right sided attentional shifts, while the subdominant left hemisphere is only active while attending to contralateral right stimuli (Corbetta et al., 1993; Nobre et al., 2004). Consequently, hemispatial neglect is associated more often with right sided than with left sided cortical lesions (Weintraub et al., 1996). This condition is paralleled by birds that show a right-hemisphere prevalence in configurational processing of spatial information that span the visual field (Prior et al., 2002; Vallortigara et al., 2004).

The view from the inside is changing our perception of cerebral asymmetries. Like in all other fields of Cognitive Neuroscience, neurobiological and neuropsychological approaches will stimulate each other, resulting in an understanding of lateralized systems, that is beyond our present possibilities.

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