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Review

Memory-related brain lateralisation in birds and humans

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ABSTRACT

Visual imprinting in chicks and song learning in songbirds are prominent model systems for the study of the neural mechanisms of memory. In both systems, neural lateralisation has been found to be involved in memory formation. Although many processes in the human brain are lateralised – spatial memory and musical processing involves mostly right hemisphere dominance, whilst language is mostly left hemisphere dominant – it is unclear what the function of lateralisation is. It might enhance brain capacity, make processing more efficient, or prevent occurrence of conflicting signals. In both avian paradigms we find memory-related lateralisation. We will discuss avian lateralisation findings and propose that birds provide a strong model for studying neural mechanisms of memory-related lateralisation.

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1. Introducing lateralisation

Lateralisation is the asymmetric representation of functions in the body. This may be expressed overtly, as in the case of left- and right-handedness in humans and lateralised limb preferences in other animals (Rogers, 2009; Rogers et al., 2013; Vallortigara et al., 2010). A more extreme example in an invertebrate is claw asymmetry in male fiddler crabs (*Uca pugnax*). These crabs have one major claw that is large and predominantly used in conflict, and a smaller minor claw. This asymmetry is also reflected in the motor control of the claws; nerves to the major claw are enlarged and outnumber those of the minor claw (Young and Govind, 1983).

Cerebral lateralisation is a difference in the functional contribution of the two brain hemispheres. Anecdotal accounts characterising human phenotypes as “left-brain dominant” (logical, rational, analytical, objective, and sensitive to component parts of concepts) or “right-brain dominant” (random, intuitive, subjective, and sensitive to the whole concept) are widespread. However, while there is considerable evidence for lateralisation in numerous cognitive functions, there is little evidence for differential representation of such functions according to personality type (Nielsen et al., 2013). There is commonly a right-sided dominance for spatial cognition in primates (Oleksiak et al., 2011). Music perception occurs predominantly in the right hemisphere, although the different components of music (rhythm, pitch, tonality, etc.) have different neural representations and lateralisation patterns (Parsons, 2001). Another well-known example of functional brain asymmetry is speech and language lateralisation in humans. In the majority of people, language structure and meaning are processed in the left hemisphere predominantly, while syllable-stress cues for example are processed in the right-hemisphere predominantly (Friederici, 2011). Also many other animals show lateralisation for production and perception of vocalisations (Ocklenburg et al., 2013a,b).

Functional lateralisation is an ancient phenomenon, occurring both in subcortical structures and throughout vertebrate phylogeny (Bisazza et al., 1998; Frasnelli et al., 2012; Harris et al., 1996; Vallortigara et al., 1999). Examples of asymmetry in behaviour and in brain function have been reported in numerous lower vertebrate species. It should therefore be expected to benefit the individual or population. So what are the advantages conferred by neural lateralisation? It has been suggested that lateralisation might enhance the brain’s capacity for neural processing, by reducing conflict and interference between simultaneous neural processes, and thereby enhancing task performance (Vallortigara and Rogers, 2005). As an illustration of the principle, in teleost fish the escape response is mediated by two large, reticulospinal neurons, the Mauthner cells, which project to motor neurons innervating the contralateral body musculature. The response involves activation of the muscles of one side while inhibiting the other. The crucial function of the response is to distance the fish from the source of threat by fast contraction of the muscles along one side and simultaneous inhibition of the contralateral side. The direction of escape is secondary. Clearly the process would be restricted by bilateral activation, and this is prevented by a spinal inhibitory pathway (Korn and Faber, 2005). In the Goldbelly topminnow (*Girardinus falcatus*) the escape response is lateralised, the majority of adults escape in a rightwards trajectory on initial exposure to a potentially threatening stimulus (Cantalupo et al., 1995). In the Shiner perch (*Cymatogaster aggregate*) escape reactivity is fastest for individuals in which the response is most strongly lateralised (Dadda et al., 2010). Similarly from an adaptive perspective, in domestic chicks, more strongly lateralised individuals are better able to simultaneously search for food and predators (Rogers et al., 2004). A further suggestion is that hemispheric specialisation is a necessary adaptation to the inter-hemispheric delay imposed by axonal conduction velocity, this

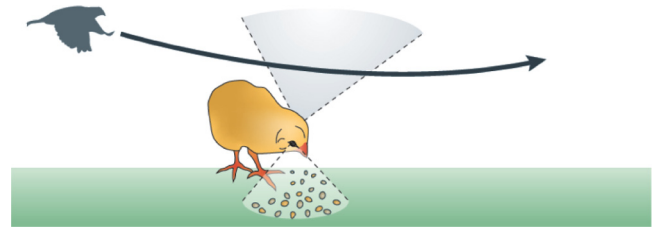


Fig. 1. Visual lateralisation in domestic chicks. The right eye (left hemisphere) is better at tasks such as discriminating grain and the left eye (right hemisphere) is better at tasks such as detecting moving predators.

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constraint on time-critical processing increasing with increasing brain size (Ringo et al., 1994).

Visual information processing is commonly lateralised in species in which the visual fields of the two eyes have little or no overlap, as documented in both vertebrate species (Vallortigara, 2000) and invertebrates (Jozet-Alves et al., 2012). Lateralisation of visual brain regions was first investigated in the domestic chick (*Gallus gallus domesticus*) by closing one or other eye. With the left eye occluded, the left hemisphere of chicks and pigeons, receiving visual input largely from the right eye, has been found better at processing visual details, such as small food particles, while the right hemisphere (right eye occluded) is more efficient at scanning for predators (Fig. 1; Concha et al., 2012; Güntürkün et al., 2000; Rogers et al., 2004; Rogers, 2012). Another example is eye and foot lateralisation in a cognitive task in parrots. The strongly lateralised individuals (either left-dominant or right-dominant) performed better than symmetrical individuals (Magat and Brown, 2009). However, a study in humans found that lateralisation did not facilitate parallel processing of a typically right-hemispheric face recognition task and simultaneously a typically left-hemispheric language recognition task. Instead, subjects with symmetric neural activation outperformed asymmetric subjects (Hirnstein et al., 2008).

Lateralisation also occurs in memory processes across a broad phylogenetic range. In honeybees, initial olfactory memory recall is lateralised towards the right antenna, while later, from 6 h after training, the memorised odour is recalled more efficiently when the left antenna is used (Rogers and Vallortigara, 2008). In human subjects, motor control of arm movements is lateralised; while the left hemisphere is more important in learning new movements, the right has a more important role in real-time updating and control of established movements (Mutha et al., 2012). Birds in particular show pronounced lateralisation in a wide range of mnemonic functions. It has been suggested that while the left hemisphere is associated with memorised tasks and environments, the right is involved in novelty detection (MacNeilage et al., 2009; Rogers, 2012).

In this review we will focus on song learning and visual imprinting (Fig. 2a and f). There are strong similarities between visual imprinting in the chick and song learning in zebra finches (Moorman et al., 2012), which are shared also with language acquisition in human infants (Dehaene-Lambertz et al., 2006; Peña et al., 2003). Each is guided by predispositions, for appropriate sounds in vocal learning (Doupe and Kuhl, 1999), and for appropriate visual cues in imprinting (Bolhuis and Honey, 1998; Vallortigara et al., 2005). In each case sleep is important in the consolidation process (Bobbo et al., 2006; Brawn et al., 2010, 2013; Dave and Margoliash, 2000; Derégnaucourt et al., 2005; Gobes et al., 2010; Gómez et al., 2006; Henderson et al., 2012; Hupbach et al., 2009; Jackson et al., 2008; Moorman et al., submitted for publication; Shank and Margoliash, 2009). Foremost here, in each case there is pronounced lateralisation of function (Horn, 2004; Bolhuis and Honey, 1998; Tervaniemi and Hugdahl, 2003; Friederici, 2011; Moorman et al.,

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