Introduction

Mechanisms and functions of brain and behavioural asymmetries

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For almost a century the field of brain and behavioural asymmetries has been dominated by studies on humans, resting on the evidence that the anatomical structures underlying language functions are asymmetrical, and that human handedness is lateralized at the population level. Today, there is not only evidence of population-level lateralization of brain and behaviour across a variety of vertebrate and invertebrate species, but also a growing consensus that the comparative analysis of the environmental and developmental factors that give origin to neural and behavioural laterality in animal models, together with theoretical analyses of their costs and benefits, will be crucial for understanding the evolutionary pathways that led to such a multifaceted phenomenon. The present theme issue provides a survey of theoretical, review and research work cutting across the biological and the cognitive sciences, focusing on various species of fishes, birds and primates (including humans) and emphasizing an integrative approach to the study of lateralization encompassing neural, behavioural, cognitive, developmental and environmental aspects.

Keywords: lateralization; brain asymmetries; laterality; behavioural laterality; hemispheric asymmetries

Brain asymmetries are (and most probably will continue to be) one standard chapter in every respectable neuroscience handbook. Typically, such a chapter focuses mainly on hemispheric asymmetries in humans and one will almost certainly find it in the second half of the handbook, in between chapters on the neural bases of language and other cognitive processes. There is a historical reason justifying this tendency: some of the scientific discoveries on brain asymmetries that have been achieved in humans can be considered authentic milestones in the history of the neurosciences from their early infancy to their adulthood. Noticeably, these discoveries have involved the faculty of language and its interaction with other higher cognitive processes.

The key findings that paved the way to the localization of human brain asymmetries are epitomized by the well-known case of a patient (nicknamed Tan), studied by the French neurologist Paul Pierre Broca at Bicêtre Hospital in Paris during the second half of the nineteenth century. Broca discovered that a lesion of a circumscribed region of the left frontal lobe was responsible for Tan’s inability to produce articulate speech (Broca 1861). The link between language disorders and lesions in the left hemisphere had been proposed at least two decades before Broca by another French neurologist, Marc Dax, although his clinical investigations (titled as unequivocally as ‘Observations aiming at proving the systematic coincidence of disturbances of speech with a lesion of the left brain hemisphere’) went basically unnoticed both before and after his death (but see Cubelli & Montagna (1994), for a historical reassessment of the relative weight of Dax and Broca). Further seminal discoveries on the relationship between the left hemisphere and language comprehension (rather than production) came later, thanks to the work of Wernicke (1874), a German psychiatrist. All of this evidence pointed clearly to a role of the human left hemisphere in the control of speech production and perception. Another moment in the history of studies on human brain asymmetries that became a classic landmark for the entire neurosciences deals with a more general idea of functional hemispheric specialization, and with the phenomenon of interhemispheric transmission: it is the work carried out by Sperry (1974) and his students on patients that had their corpus callosum surgically severed to prevent the diffusion of epileptic seizures. These patients, better known as ‘split brains’, were tested by presenting lateralized stimuli to their visual fields and asking them to perform specific motor, linguistic or purely visual tasks based on the content of the stimuli presented. As the tasks sometimes posed requests that made the transmission of information across the hemispheres necessary (such as in the case of naming a visual object presented to the left visual field, which projects to the right hemisphere), and the division of the corpus callosum prevented such transmission, the resulting inability of split-brain subjects to complete such apparently effortless tasks was astonishing even to the

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general public, and largely boosted interest for the study of functional hemispheric specializations of the human brain (see Gazzaniga (2005) for a current survey of split brain research).

The hemispheric asymmetry underlying language processing has been considered a clear signature of the human brain, together with the hemispheric asymmetry responsible for handedness, which is a strongly asymmetrical behavioural manifestation in the human species, with a distribution of approximately 90 per cent right-handers. Despite the relevance of these aspects and their clear value to human neuropsychology, we still have a limited understanding of the general origins of morphological and functional asymmetries in the brain and of their importance for behaviour. This is in part due to the fact that adequate model systems have been lacking until quite recently, lateralization of brain and behaviour having being considered an exclusively human trait for a long time. The change of perspective was reached gradually during the last century, with evidence accumulating in the 1970s that left–right paired nerves innervating the avian syrinx have different roles in the control of song production (Nottebohm 1971; Nottebohm & Nottebohm 1976), and that the left and right hemispheres of the chicken brain have different roles in visual behaviour (Rogers & Anson 1979). Asymmetries in behaviour exhibited by birds, fishes, amphibians, rodents and primates have since provided a strong argument for functional lateralization being a universal and evolutionarily ancient trait of the vertebrate brain (Bisazza et al. 1997). In an increasing number of cases behavioural biases have been directly linked to anatomical asymmetries, and today we can count on excellent animal model systems of brain and behavioural lateralization (Halpern et al. 2005), rivalling the well-established studies of human asymmetries (Toga & Thompson 2003). Importantly, the growing empirical evidence of brain and behavioural lateralization in animals has progressed in parallel with explanations of lateralization as a natural phenomenon, from its proximate manifestations to the factors determining its evolution and widespread distribution across vertebrate and invertebrate species (Vallortigara et al. 1999). In the last decades, thus, an increasing number of studies on non-human species have been carried out, expanding our knowledge about the universality of lateralization in behavioural processes and cognitive tasks, running in parallel with a more and more refined elucidation of the structural asymmetries that underlie these differences across the animal kingdom. Evolutionary pressures that brought the emergence of brain and behavioural lateralization have been hypothesized and the functional advantages that this general biological trait would convey have also been suggested (Andrew et al. 2000; Rogers & Andrew 2002; Vallortigara & Rogers 2005).

Among a number of advantages, the specialization of the two sides of the brain has been supposed to increase neural efficiency. Despite the fact individual brain efficiency does not require the alignment of lateralization in the population, directional preferences in the use of limbs or eyes (and the underlying brain asymmetries) usually occur at the population level, with most individuals showing similar direction of bias. Only recently it has been suggested that alignment of the direction of behavioural asymmetries in a population can arise as an evolutionarily stable strategy if individually asymmetrical organisms must coordinate their behaviour with that of other asymmetrical organisms, and a model was presented that accounted for the population-level lateral biases observable in prey–predator interactions (Ghirlanda & Vallortigara 2004). The present theme issue starts with an extension of that model. In the article by Ghirlanda et al. (2009), in fact, a new game-theoretical model is presented that takes into account not only agonistic interactions but also synergistic ones, showing that population-level lateralization can be established and maintained at equilibrium by means of strategic factors emerging from purely intraspecific interactions among individuals. The improvement of the model presented by Ghirlanda et al. (2009) rests on the fact that by accommodating phenomena of intraspecific social cooperation alongside with interspecific competition, the model can explain more easily human lateralization than a model based on purely agonistic interactions.

The following group of articles offers variable support to the theoretical hypothesis set forth in the model. Corballis (2009) emphasizes the fact that benefits of asymmetry might not necessarily be due to shared directionality (as the previous article assumes), but rather to the degree of expression of the trait. By showing that genes and environmental factors are inadequate to predict the distribution of two alternative asymmetrical phenotypes, and that lateralization is a trait varying along a continuum rather than a truly dichotomous variable, Corballis suggests that advantages of lateralization degree can be measured along cognitive and personality dimensions, disregarding the direction of its expression. Llaurens et al. (2009) focus on the issue of human handedness, reviewing specifically the literature concerning left-handedness and the costs and benefits that influence the conservation of its frequency in the human population. The evolutionary history and geographical variation of left-handedness, as witnessed by human palaeoanthropological and ethological data, suggest that the low frequency of left-handedness in humans can be explained both by its likely benefits (i.e. fact that it confers some advantage in fighting behaviour due to unpredictability) and by its associated costs (i.e. the fact that a number of health problems are consequent to its possession). Brancucci et al. (2009) keep the focus on human lateralization but shift the attention to functional asymmetries of the brain hemispheres. Reviewing the rich literature on social perception including visual, auditory and olfactory representations of self and other individuals, they show that the right-hemispheric lateralization pattern underlying the analysis of human faces, voices and smells (including the processing of pheromones), which is commonly revealed through both behavioural and neuroimaging research, despite the structural symmetry of the neural structures capable of supporting such representations, might be driven by other well-known types of right-hemispheric specialization.
In the following two articles, we are first offered a general overview about the relative weight of genes and the environment on the development of brain and behavioural asymmetries in humans and other animals, and then a detailed analysis of a specific environmental factor, namely the effect of prenatal exposure to testosterone on the development of asymmetries. Schafsma et al. (2009) clearly show that pre-, peri- and post-natal environmental factors, such as light exposure, body posture, or the side preferentially taken by parents while cradling infants, are important in influencing the development of the degree of lateralization, despite the fact their exact mechanisms have not been fully understood. Data obtained in domestic chicks (Gallus gallus) are presented to convey the idea that social rearing can be considered another environmental factor modulating lateralization. Pfannkuche et al. (2009) carry out a meta-analysis concerning the effects of prenatal exposure to testosterone on the degree and direction of lateralization in mammals and birds, testing four hypotheses and demonstrating a partial relationship between prenatal testosterone levels and asymmetry, emphasizing a higher correlation with the extent of the asymmetry rather than the direction of its expression.

Handedness has classically constituted one test bench for theories on both the development and the evolution of lateralization (MacNeilage 1991; Annett 2002). Rogers (2009) returns to the topic of handedness but she expands the scope to primates in general. Reviewing recent data on the preferential use of limbs/paws in a number of monkey species (including prosimians) and the growing evidence of asymmetrical anatomical correlates of such side preferences, Rogers argues that lateralization patterns might depend in the first place on hemispheric asymmetries in sensory processing, and that both sensory and motor biases might correlate with more general behavioural traits, such as response to novelty, coping and temperament. These traits, finally, would be mediated by the hemispheric asymmetries underlying the regulation of aggression and the control of stress responses. Data obtained in common marmosets (Callithrix jacchus) are presented to support the hypothesis.

Asymmetry in the processing of sensory information by the two brain hemispheres is also the topic of the article by Valencia-Alfonso et al. (2009), featuring the pigeon (Columba livia) as a model system of the hemispheric lateralization of visual abilities. In pigeons, as in all birds, the optic nerves almost completely decussate at the level of the chiasm, so the visual input to each eye is processed more or less entirely by the contralateral hemisphere. Moreover, the avian visual system is divided into two main subsystems (the tectofugal and the thalamofugal systems). These anatomical constraints are the basis of an empirical analysis of the functional asymmetries ascribed to the visual system of the pigeon, and it is shown that these asymmetries depend on the interplay of descending and ascending visual information streams (between telencephalic and subtelencephalic structures), whose net balance is the left-hemispheric lateralization observed in many visual discrimination tasks in pigeons.

Daisley et al. (2009) focus on the domestic chick as a model system for the study of hemispheric lateralization of social cognition, echoing some of the phenomena described in the preceding article on human social perception (Brancucci et al. 2009). Both in reviewing the literature and in describing their own research work (that take advantage of the monocular occlusion technique), the authors present solid evidence of right-hemispheric asymmetry of social representations in chicks, modulated by perinatal environmental effects such as light exposure, and social rearing, as already shown in the article by Schafsma et al. (2009).

A pivotal role is assumed by the article of Andrew et al. (2009), for it links the articles based on avian models dealing with visual perception and cognition, to those dealing with the genetics and embryology of brain and behavioural asymmetries of other increasingly important model systems: fishes. Indeed, the research presented in Andrew et al.’s article shows that environmental manipulation (i.e. exposure of the eggs to light or dark) during the pre-hatching development of chicks and zebrafish (Brachydanio rerio), determines strong similarities in lateralized visual behaviour and in ‘personality traits’ of the two species, as assessed by the timing and dynamics at which tasks involving visual exploration and response to releasers are accomplished.

Genetic approaches that provided insights on the asymmetric development of the viscera (Hamada et al. 2002) are recently proving valuable for exploring left–right differences in the fish nervous system, particularly in the zebrafish—which has gained the status of top model organism for the study of developmental biology. Recent work has been carried out on the dorsal diencephalic region of the forebrain, the epithalamus, which in zebrafish is organized asymmetrically and has been correlated with lateralized visual behaviour. The last three articles provide a sort of ‘theme issue in the theme issue’, as they all specifically target epithalamic asymmetries in the zebrafish. Signore et al. (2009) compare the well-known temporal and spatial features of asymmetrical development of epithalamic structures in the zebrafish, with the events that bring the establishment of asymmetries in the equivalent regions of another teleost fish, medaka (Oryzias latipes). Similarities in the developmental events triggered by the Nodal signalling pathway are taken as evidence of shared ancestry and as indicators of a roughly comparable bauplan for symmetry in the two species, although differences emerge when the temporal and spatial details of neurogenesis are compared at a fine level of detail. Together with testing methods for comparing neural development across species, their empirical work provides a convincing demonstration that medaka can be considered as valuable an animal model system of neural lateralization as the more used zebrafish.

Bianco & Wilson (2009) review the asymmetries of the dorsal diencephalic conduction system (comprising the habenulae and related structures), its development, and its multifaceted reflections on the behaviour of vertebrates (from a role in regulating sleep and circadian rhythms to involvement in attention, learning and higher cognitive processes), with special
reference to the zebrafish model. They present a theoretical framework for the design of asymmetrical circuitry describing multiple forms of implementation that apply to known vertebrate cases, from the realization of size asymmetry using identical elements to the realization of microstructural asymmetry based on different element types or their ratios.

Finally, Facchin et al. (2009) concentrate on the behavioural consequences of epithalamic asymmetry reversal in zebrafish (obtained by targeting the southpaw gene), and show that the main effect of reversing the side of parapineal is more a matter of altered motor patterns (i.e. swimming latency and duration) rather than altered lateralized visual behaviour. This is in contrast to previous research work that put epithalamic asymmetries in a direct relationship with asymmetries in eye use, and is to be taken as a sign of the complex link between neural and behavioural lateralization.

The overall message conveyed by this theme issue is that brain asymmetries and behavioural lateralization should be taken as a genuine case of successful interaction among the biological and the cognitive sciences. Bringing into play the knowledge acquired on animal model systems it will become more and more obvious that brain and behavioural asymmetries must be studied at the variety of levels as represented in the articles here presented, and the privileged focus on human brain asymmetry that has characterized the field until very recently should become complementary to a more general picture, taking into account more seriously the evolutionary and developmental dimensions of these fascinating phenomena.

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