



Special Issue “Brain and cognitive asymmetry”: Review

A function for the bicameral mind

Giorgio Vallortigara ^{a,*} and Lesley J. Rogers ^b^a Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy^b School of Science and Technology, University of New England, Armidale, NSW, Australia

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ABSTRACT

Why do the left and right sides of the brain have different functions? Having a lateralized brain, in which each hemisphere processes sensory inputs differently and carries out different functions, is common in vertebrates, and it has now been reported for invertebrates too. Experiments with several animal species have shown that having a lateralized brain can enhance the capacity to perform two tasks at the same time. Thus, the different specializations of the left and right sides of the brain seem to increase brain efficiency. Other advantages may involve control of action that, in Bilateria, may be confounded by separate and independent sensory processing and motor outputs on the left and right sides. Also, the opportunity for increased perceptual training associated with preferential use of only one sensory or motoric organ may result in a time advantage for the dominant side. Although brain efficiency of individuals can be achieved without the need for alignment of lateralization in the population, lateral biases (such as preferences in the use of a laterally-placed eye) usually occur at the population level, with most individuals showing a similar direction of bias. Why is this the case? Not only humans, but also most non-human animals, show a similar pattern of population bias (i.e., directional asymmetry). For instance, in several vertebrate species (from fish to mammals) most individuals react faster when a predator approaches from their left side, although some individuals (a minority usually ranging from 10 to 35%) escape faster from predators arriving from their right side. Invoking individual efficiency (lateralization may increase fitness), evolutionary chance or simply genetic inheritance cannot explain this widespread pattern. Using mathematical theory of games, it has been argued that the population structure of lateralization (with either antisymmetry or directional asymmetry) may result from the type of interactions asymmetric organisms face with each other.

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1. Introduction

In the last thirty years or so (actually, initial discoveries dated back to the early 1970s, see for historical accounts [Bisazza, Rogers, & Vallortigara, 1998](#); [Rogers & Andrew, 2002](#);

[Vallortigara & Bisazza, 2002](#); [Vallortigara, Chiandetti, & Sovrano, 2011](#); [Vallortigara & Versace, 2017](#)) comparative neuroscientists and behavioural biologists have come to realize that left/right asymmetries in brain and behaviour (so-called «lateralization»), long attributed only to the human

* Corresponding author. Center for Mind/Brain Sciences, University of Trento, Piazza Manifattura 1, I-38068, Rovereto, Italy.

E-mail address: giorgio.vallortigara@unitn.it (G. Vallortigara).

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species, are in fact widespread in the animal kingdom (Rogers, Vallortigara, & Andrew, 2013, p. 229). We know nowadays that asymmetries are apparent in all major taxonomic groups in vertebrates and in invertebrates as well. Fig. 1 schematizes the state of the art as to the phylogeny of brain and behavioural asymmetry.

In fact, if lateralization were a uniquely human characteristic, it would be extremely difficult for biologists to figure out (and experimentally prove) what is the advantage of having it. But luckily enough, we have now dozens of examples of asymmetries at different levels of organization in different animal models, and we can start reasoning and testing directly our hypotheses on what may be the benefits (and the costs) for bilaterian organisms of having a certain degree of asymmetry in their nervous systems.

2. Varieties of lateralization and their advantages

Possessing an asymmetrical brain may confer advantages. And this should have been occurring at least from 500 million years before the dawn of humans, in Cambrian times, when *Anomalocaris*, animals with limbs and thought to be closely related to ancestral arthropods, were preying on trilobites with a right-limbed bias (Babcock & Robinson, 1989; review in Ocklenburg & Güntürkün, 2018, p. 368).

It is apparent, however, that possessing a left-right asymmetry in overt behavior maybe a disadvantage. At the macroscopic level, within the range of magnitude of objects with

which biological organisms usually negotiate - food, prey, predators, mates, social partners – left and right should be immaterial (although we know this may be not true at the microscopic level, see e.g., McManus, 2002 p. 120–125). However, and surprisingly, even if a prey, a mate or a predator has identical probability of occurring on either the left or the right side, we know that organisms manifest a variety of consistent biases favouring one or other side for either motoric or sensory activities. For instance, animals with laterally placed eyes (and sometimes also those with large binocular overlaps, e.g., Casperd & Dunbar, 1996; Quaresmini, Forrester, Spiezio, & Vallortigara, 2014) systematically use their left or the right eye in selecting prey (e.g., Alonso, 1998; Andrew, Mench, & Rainey, 1982; Güntürkün & Kesh, 1987; Hori, 1993; Mench & Andrew, 1986; Miklosi & Andrew, 1999; Valenti, Sovrano, Zucca, & Vallortigara, 2003; Vallortigara, Rogers, & Bisazza, 1999; Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998; 1999), emitting agonistic responses (Deckel, 1995; Hews & Worthington, 2001; Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1997, 1998), responding to predators (e.g., Bisazza et al., 1997; Cantalupo, Bisazza, & Vallortigara, 1995; Franklin & Lima, 2001; Lippolis, Bisazza, Rogers, & Vallortigara, 2002), sleeping (Mascetti & Vallortigara, 2001), or responding to social signals (e.g., Bisazza, De Santi, & Vallortigara, 1999, 2002; Vallortigara, 1992; Vallortigara & Andrew, 1991, 1994a; Daisley, Vallortigara, & Regolin, 2010; Deng & Rogers, 2002; Fernandez-Carriba, Loeches, Morcillo, & Hopkins, 2002; Peirce, Leigh, & Kendrick, 2000; Regolin, Daisley, Rosa-Salva, & Vallortigara, 2012; Sovrano, Bisazza, & Vallortigara, 2001, 1999; Vermeire, Hamilton, & Erdmann, 1998; Versace, Morgante,

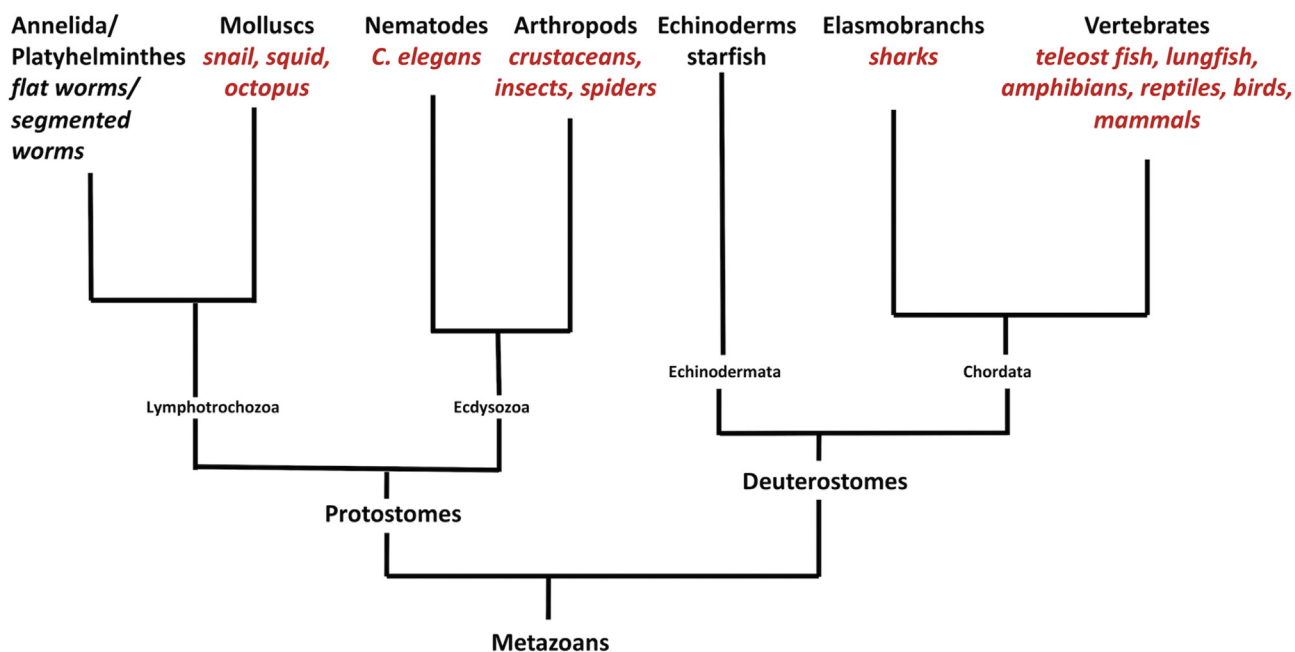


Fig. 1 – A simplified representation of the evolutionary tree of animal species. Phyla have been indicated on the major branches and relevant phyla and subphyla are shown in back type across the top of the figure. Red font shows the classes/orders/species in which population-level, lateralized function of the nervous system has been reported (see also Rogers & Vallortigara, 2015). The focus of this Figure is on extant species (top lines), with their evolutionary relationships indicated.

Pulina, & Vallortigara, 2007; review in; Rosa Salva, Regolin, Mascalzoni, & Vallortigara, 2012). Lateral asymmetries are not confined to vision but extend to other senses as well (e.g., Burne & Rogers, 2002; Burt de Perera & Braithwaite, 2005; LaMendola & Bever, 1997; Vallortigara & Andrew, 1994b). Biases in motor response and tool manufacture and use have been also reported (e.g., Bisazza et al., 1997, 1996; Roth, 2003; Tommasi and Andrew, 2002; Hunt, Corballis, & Gray, 2001; see for a recent review; Stancher, Sovrano, & Vallortigara, 2018).

Animals from molluscs and nematodes to humans show asymmetries of this sort, and thus we should expect that left-right differences provide some important fitness benefits. The case of the nematode worm may offer a way to reveal one such benefit, likely limited to nervous systems with a reduced number of neurons. The nervous system of the nematode worm *Caenorhabditis elegans* consists of just 302 neurons, 198 of which are present as bilaterally symmetrical pairs with similar functions. However, there is a pair of neurons that serve as taste receptors, ASEL and ASER, which are bilaterally symmetrical in several respects (position, axon morphology, dendritic morphology etc.) but in which some of their putative sensory receptors are expressed asymmetrically, and the asymmetry in gene expression correlates with their sensing different classes of water-soluble chemicals: in practice, lateralized responses to salt allow the worm to discriminate between distinct salt ions (review in Vidal & Hobert, 2017). Here we can see that segregation of function in an organism with a limited number of neurons directly increases its processing capacity, in terms of the number/type of stimuli to which it is able to respond. The worm *C. elegans* could represent an extreme case but, in general, making efficient use of brain tissue, which is metabolically very expensive, should underlie strong evolutionary pressure to lateralize as a way of increasing neural capacity, because specializing one side of the brain for a function avoids useless duplication of functions on both sides (Vallortigara, 2000). However, benefits and costs go hand in hand in biology. Benefits here would be counteracted by costs associated with possible unilateral damage of brain tissue, that would not (or scarcely) allow for compensatory mechanisms by the other side of the brain (in human adults, this is apparent in the outcome of left-hemispheric unilateral lesions associated with lateralization of language production, review Corballis, 1998; 2002; 2014).

Before discussing other hypotheses, however, let us first consider whether there is any empirical evidence that lateralization confers some advantage. One way to test this is to look at possible correlations between individual variation in the degree, or strength, of lateralization and performance in a particular task. Animal studies have provided good evidence for such a correlation. For instance, the strength of handedness in chimpanzees correlates positively with success in fishing for termites (McGrew & Marchant, 1999). Also, the stronger the asymmetry in use of an eye in pigeons, the better their ability to discriminate food grains from pebbles (Güntürkün et al., 2000). Similarly, Magat and Brown (2009) have shown that strongly lateralized parrots (in foot and eye use) outperform less strongly lateralized ones in both a pebble-seed discrimination task (that does not require foot manipulation of the food before ingestion) and in a string-

pulling problem (parrots usually use foot and beak movements to pull the string). Furthermore, Dadda, Agrillo, Bisazza, and Brown (2015) has claimed that strongly lateralized guppies, *Poecilia reticulata*, have enhanced numerical abilities compared to non-lateralized guppies.

Of course, as already mentioned, possession of asymmetry must be associated with costs as well as benefits. These costs should not be confined to energetic factors, such as the need for a particular neural overdevelopment in one hemisphere, but should also involve behavioural aspects associated with side biases. An example has been provided by evidence obtained by testing antlion larvae (*Mymeleon formicarius*): greater behavioural asymmetry is accompanied by improved learning abilities. Miler, Kuszewska, and Woyciechowski (2017) found that some antlions showed individual asymmetry in righting from a supine to normal position by turning over one side of their body. These behaviourally asymmetrical individuals showed better learning abilities when tested in a conditioning task in which they had to learn a contingency association between a vibrational cue and the appearance of a prey item (larvae in the training group were presented with a vibrational cue immediately following prey capture and before prey disappearance; larvae in the non-training group were presented with the vibrational cue 5–10 min before or after prey capture, giving them no opportunity to learn the association between the cue and prey removal). One puzzling aspect of these results, however, was the limited number of individuals showing consistent lateralization: given its benefits, one can ask why the asymmetry did not appear in all or most individuals? Miler, Kuszewska, Zuber, & Woyciechowski, 2018 argued that there is a trade-off between learning ability and hunting efficiency. Strongly-lateralized larvae learn better than less-lateralized ones, but the latter seem to be better able to sense vibrational signals used to detect prey and thus capture them more quickly. Given that both traits, learning ability and hunting efficiency, have fitness advantages; the trade-off between the two traits may explain why behavioural asymmetry is relatively rare in individuals of antlion populations.

In general, the literature from human studies confirms the claim that individuals with stronger lateralization have advantages, for example in terms of higher verbal IQ (Everts et al., 2009) and reading skills (Chiarello, Welcome, Halderman, & Leonard, 2009). However, inconsistent findings are reported in the literature, for both non-human and human animals. For instance, in fish that have been selected for a high or low degree of behavioural bias, individuals with stronger lateralization could manifest disadvantages in tasks requiring matching information from both eyes (Dadda, Zandonà, Agrillo, & Bisazza, 2009). In humans, stronger lateralization seems to provide advantages in some but not all tasks (Boles, Barth, & Merrill, 2008, and see also; Somers et al., 2015).

Of course, lateralization is somewhat specific for each different type of function, and advantages in one function may be accompanied by disadvantages in another function. Moreover, it should be considered that advantages could be associated with a certain (usually moderate, see Corballis, 2006) level of asymmetry but not with the naïve idea that the most strongly lateralized individuals have the best performance. Hirnstein, Hugdahl, and Hausmann (2014), for

instance, examined in a large sample ($N = 1839$ participants) language lateralization and performance in a verbal dichotic listening task, discovering a U-shaped relationship between degree of lateralization and overall accuracy. Here, again, it is apparent that the strength of lateralization (at least a certain, optimal degree of lateralization) is a predictor of high performance, while direction—right or left—is not. This leaves us with two open issues. First, what are the mechanisms that confer an advantage of possessing a certain strength of lateralization? Second, if advantages are associated with strength but not with direction of lateralization, then why have directional asymmetries evolved at all? These two issues will be discussed separately in the next two sections.

3. Strength of lateralization: costs and benefits

Several mechanisms can be associated with advantages of individual-level lateralization. They could be specific, at least as to their original appearance during evolutionary times, to particular functions. An example is provided by lateralization of anti-predatory responses such as the C-start reaction of fish. Fish react to a threatening stimulus by bending their bodies into a C-shape with a unilateral contraction of their axial muscle, which then provides a sudden contralateral acceleration away from the stimulus. The response is mediated by a pair of giant reticulospinal neurons, the Mauthner cells, each decussating and innervating contralateral muscles (Eaton, Bombardieri, & Meyer, 1977). Given that predators may make their appearance from either the right or left side (if they are not themselves lateralized, as we shall discuss later) one would expect that the circuitry of Mauthner cells to be symmetrical, and the associated behavioural responses would be symmetrical as well. Quite the opposite, there is evidence in some species of fish that the Mauthner cell in the left brain stem is larger than the one on the right (Moulton & Barron, 1967); besides, there is evidence also for muscular asymmetries (Heuts, 1999) and of behavioural asymmetries (Cantalupo et al., 1995; Lippolis, Joss, & Rogers, 2009) in escape responses. It has been hypothesized (Vallortigara, 2000) that the asymmetry arises because left or right biased individuals can develop higher speeds and accelerations than ambidextrous individuals and can, therefore, escape better from a predator (some empirical evidence for this hypothesis has been provided by Dadda, Koolhaas, & Domenici, 2010).

The fact that, in most tasks in which human subjects have to respond under high time pressure, the dominant side has a significant time advantage (see e.g., Ocklenburg, Güntürkün, & Beste, 2012; Verma, van der Haegen, & Brysbaert, 2013) could be an example of the same kind of general phenomenon.

Note also that these asymmetries in escape responses can form the basis of subsequent asymmetries in eye use (see e.g., De Santi, Sovrano, Bisazza, & Vallortigara, 2001; 2002; Tommasi, Andrew, & Vallortigara, 2000; Facchin, Bisazza, & Vallortigara, 1999; Vallortigara, Regolin, Bortolomiol, & Tommasi, 1996; 2001). After an initial C-start reaction to the sight of a threatening stimulus has occurred, sustained

monitoring of the stimulus with the lateral field of the left or the right eye could in fact arise as a result of the animal's lateral body posture (Vallortigara, 2000).

There is some evidence, though limited to insects, that lateralization at the individual level may improve motor control. In desert locusts, individuals with more strongly lateralized forelimb movements also appear to be less likely to make errors while crossing gaps in the substrate on which they are walking (Bell & Niven, 2014; 2016). The exact mechanism that underlies this advantage is, however, unknown.

Animals with laterally placed eyes (and in general laterally placed sensory organs) may have another reason to develop asymmetry. Receiving different inputs from lateral sense organs makes an organism face the problem of giving rise to a unitary course of action (should I select the prey seen on the left or the right visual field?), which may possibly be solved by making one side of the brain in control of action, for instance by inhibitory interhemispheric connections. In birds there is widespread evidence of this, for instance in aggressive and copulatory responses. Unilateral injection of monosodium glutamate into the left hemisphere of the chick forebrain results in a marked and long-lasting elevation of attack and copulatory behaviour; this was not observed when glutamate was injected into the right hemisphere or both hemispheres, suggesting that these behavioural responses are usually evoked by the right hemisphere but are under inhibitory control by the left hemisphere (Bullock & Rogers, 1986). Another example comes from lateralization of spatial cognition. Chicks trained to ground-scratch on the floor near to a landmark located in the centre of an arena (Tommasi, Vallortigara, & Zanforlin, 1997; 2012; Vallortigara, 2006a), after landmark displacement, searched in the centre when using their left eye only, ignoring the novel position of the landmark, whereas they searched close to the landmark and ignored the global spatial information provided by the environment when using their right eye (Tommasi & Vallortigara, 2001; Vallortigara, 2000; and see also for lesion evidence; Tommasi, Gagliardo, Andrew, & Vallortigara, 2003). The left-eye system (right hemisphere) appeared to have encoded position-specific cues, whereas the right-eye system (left hemisphere) had encoded the object-specific cues. Interestingly, however, in the ordinary, binocular condition, chicks searched in the centre, showing that their responses were completely controlled by the left eye and associated, mostly contralateral, neural structures (see Vallortigara, 2000).

Another important mechanism that may underlie individual-level lateralization is associated with the possibility of parallel and complementary processing of information during task execution. Taking advantage of the fact that light exposure in embryo is a main determinant of visual lateralization in the avian brain (Rogers, 1982, 1990, 1991, 1995, 1997, 1999; Rogers & Deng, 1999; Rogers, Andrew, & Burne, 1998; Rogers & Rajendra, 1993), the ability of strongly-lateralized (light exposed) and weakly-lateralized (dark incubated) chicks to execute dual-tasks could be compared (Rogers, Zucca, & Vallortigara, 2004; Dharmaretnam & Rogers, 2005). Chicks had to tell apart grains of food and pebbles scattered on a floor and the same time monitor overhead for a flying model of an aerial predator. Strongly lateralized chicks performed well in this

dual task, whereas weakly lateralized chicks performed poorly. The lateralized ones could attain this outcome by simultaneously attending to the feeding task with one eye and monitoring the predator with the other eye. Interestingly, weakly lateralized chicks could perform as well as the strongly lateralized chicks when presented with each task as a single or separate one. These results were then replicated in fish (Dadda and Bisazza, 2006).

In animals with laterally placed eyes the hypothesis that hemispheric specialization would increase parallel processing by enabling separate processing of complementary information in the two sides of the brain is relatively easy to test. In animals with partial decussation of visual fibers (such as humans) different methods should be used. Up to now tests with humans have met with mixed results; comparison of single and double task performance of language and visuo-spatial functions in subgroups with distinct lateralization patterns (typical, mirrored and contralateral) found better performance in the dual task of a typical lateralization subgroup in one study (Lust et al., 2011) but not in another (Lust et al., 2011). Further tests with more demanding cognitive tasks seem necessary.

4. Direction of lateralization: costs and benefits

We are thus facing an enigma. If possession of individual-level lateralization has benefits for cognitive functioning, whereas population-level lateralization does not add any further advantage, what could it be the biological function of population-level (i.e., directional) lateralization?

The different specializations of the left and right sides of the brain seems to increase brain efficiency. However, in the animal kingdom left/right biases in the use of an eye and, in some tasks, in the use of a limb frequently occur at the population level (Rogers et al., 2013, p. 229), with most (but not all) individuals showing similar direction of bias. Since individual brain efficiency does not require the alignment of lateralization in the population, there must be another explanation for the latter. We argued some years ago that alignment of the direction of behavioural asymmetries in a population can arise when individually asymmetrical organisms must coordinate their behaviour with that of other asymmetrical organisms (Vallortigara & Rogers, 2005; Vallortigara, 2006b). Specifically, we argued that the alignment of the direction of behavioural asymmetries at the population level or the lack of it arises as an “evolutionarily stable strategy” (ESS) associated with the fact that individually asymmetrical organisms must or must not coordinate their behavior with the behavior of other asymmetrical organisms of the same or different species. This has been supported by mathematical models showing that the usual polymorphism we observe in vertebrate populations can emerge as an ESS with the minority (e.g., left-handedness) maintained by frequency-dependent selection (Ghirlanda & Vallortigara, 2004).

This hypothesis has met with some success in terms of empirical support. For instance, shoaling in fish seems to be consistently accompanied by the presence of asymmetries at the population level (Bisazza, Cantalupo, Capocchiano, &

Vallortigara, 2000) and predatory pressures have been shown to be a main determinant of lateralization determining conformity and conflict in fish schools (Chivers et al., 2016). Asymmetries that are observed at the population level in social honeybees are present only at the individual level in solitary mason bees (Anfora, Frasnelli, Maccagnani, Rogers, & Vallortigara, 2010 and see also; Anfora et al., 2011; Rigosi et al., 2015; Frasnelli et al., 2011, 2014, 2010, Frasnelli and Vallortigara, 2017; Rigosi et al., 2011), apart from occasions on which the mason bees do interact socially, as in agonistic interactions (Rogers, Frasnelli, & Versace, 2016). In general, it seems very well documented that population lateralization is more likely to be observed in social contexts in both vertebrates (Lemaire, Viblanc, & Jozet-Alves, 2019; Prieur, Pika, Barbu, & Blois-Heulin, 2016; Robins, Goma, Quine, & Phillips, 2018; Stor, Rebstock, García Borboroglu, & Boersma, 2019; Williams & Anderson, 2012), and invertebrates (Benelli et al., 2017; Romano et al., 2016, 2015; Schnell, Jozet-Alves, Hall, Radday, & Hanlon, 2019; Frasnelli et al., 2012a, b; Frasnelli, Ponte, Vallortigara, & Fiorito, 2019; though see for a possible exception; Versace, Caffini, Werkhoven, & de Bivort, 2019). However, the hypothesis has also incurred some misunderstanding, such as the idea that the presence of lateralization would depend only on categorizing a species as social or non-social (see for a discussion Frasnelli & Vallortigara, 2017). In fact, the idea of an ESS is more general and effective despite such a naïve categorization. Firstly, it is apparent that even in social species there could be conditions of interaction that would favour the emergence of individual rather than population-level asymmetries. A nice example comes from the group hunting behavior of sailfish that use their saw-like bills to stab or slash at their prey, sardines (Kurvers et al., 2017). Here, sailfish show lateralization (and the stronger they are lateralized, the more successful they are at capturing their prey), but they show individual-level and not population-level lateralization, thereby avoiding predictability in the direction of attack.

Secondly, not only social species, but also so-called “non-social” species of insects can be lateralized at the population level in certain types of behaviour. As mentioned above, this is the case of the mason bees, *Osmia rufa*: they do not show behavioural asymmetry in the recall of short-term olfactory memory, as do honeybees (Anfora et al., 2010), but exhibit population-level lateralization in aggressive displays (Rogers et al., 2013, p. 229; 2016). Thus, it is being engaged in interactions with other asymmetrical individuals, rather than the way in which the species nests (socially or not) that decides whether individual-level or population-level lateralization would be apparent. Conversely, Ong, Bulmer, Groening, and Srinivasan (2017) showed that individual-level lateralization can occur for some patterns of behavior in honeybees (for which there is in general quite a large body of evidence of lateralization at the population-level, see also review in Niven & Frasnelli, 2018).

In an extension of the model Ghirlanda, Frasnelli, and Vallortigara (2009) showed that populations consisting of left- and right-lateralized individuals in unequal numbers can be evolutionarily stable on the basis of strategic factors arising from the balance between antagonistic (competitive) and synergistic (cooperative) interactions. The model predicts that

minority-type individuals are maintained because they are more likely to adopt an unpredictable behaviour during competitive interactions such as fighting, whereas majority-type individuals are maintained because there is a fitness advantage in having their biases synchronized with other conspecifics during interactions that require coordination, such as mating. Schnell et al. (2019) tested these predictions by investigating biases in giant Australian cuttlefish during fighting and mating interactions (see also for further evidence of cuttlefish lateralization: Jozet-Alves et al., 2012; Schnell, Hanlon, Benkada, & Jozet-Alves, 2016; 2018). During fighting, most male cuttlefish showed left eye use and these males also exhibited higher contest escalation. In contrast, minority-type individuals achieved higher fighting success with a right-eye bias. During mating interactions, most male cuttlefish preferentially used the left eye to inspect females. Furthermore, most male cuttlefish approached the female's right side during a mating attempt and these males achieved higher mating success. Overall, these data support the hypothesis that population-level biases are an evolutionary consequence of the fitness advantages involved in intraspecific interactions.

In humans, the issue of the costs and benefits of population-level lateralization has been less explored, with the exception, of course, of handedness (see for a review on comparative studies on limb asymmetries Versace & Vallortigara, 2015). In this regard, there is quite convincing empirical support for the idea that left-handedness would be maintained by frequency-dependent selection, as also predicted by the Evolutionary Stable Strategy, ESS, hypothesis (Ghirlanda & Vallortigara, 2004; see e.g.,; Faurie & Raymond, 2004, 2005; Billiard, Faurie, & Raymond, 2005; Abrams & Panaggio, 2012; Brooks, Bussière, Jennions, & Hunt, 2004; Raymond, Pointer, Dufour, & Moller, 1996).

One interesting hypothesis for humans is the so-called Fighting Hypothesis (Faurie, Raymond, & Uomini, 2016; Faurie & Raymond, 2013; Raymond et al., 1996). Given that handedness is to some degree heritable (Corballis, 2014; McManus, 2002), and the generally low frequency of left-handers suggests some evolutionary costs, we need to account for left-handedness maintenance. Raymond and colleagues have thus suggested that left-handedness could be associated with an important strategic advantage in fighting interactions, and could thus be maintained by negative frequency-dependent selection. Note that in the framework of the ESS theory the issue is to explain the uneven distribution of left- and right-forms, and the frequency-dependent selection emerges spontaneously as a by-product of an ESS strategy. Thus, no *a priori* hypotheses are needed in the ESS theory as to the mechanisms associated with frequency-dependent selection (in fact prey–predator interaction or synergistic interactions could also produce stable polymorphisms in different species, see Ghirlanda et al., 2009). Quite in contrast the Fighting Hypothesis is specific for humans, and explains the persistence of left-handers as associated with situations where fighting abilities are directly linked to success (as in sports) or to Darwinian fitness, as it has hypothesized for past societies or tested in the remaining groups of traditional societies not yet affected by Western habits and market economy (Faurie, Schiefenhövel, le Bomin, Billiard, & Raymond, 2005). For example, Faurie and Raymond (2004) have shown

that the frequency of left-handers is strongly and positively correlated with the rate of homicides across traditional societies: ranging from 3% in the most pacifistic societies to 27% in the most violent and warlike. The interpretation of this finding would be that the advantage of being left-handed should be greater in a more violent context, which should result in a higher frequency of left-handers (see for evidence Richardson & Gilman, 2019). In the absence of any selection pressure, the resulting equilibrium should be a 1:1 ratio of right-/left-handers (which has never been observed in any human population).

There are however both theoretical and empirical problems with the Fighting Hypothesis. Theoretically it is unclear how handedness polymorphism can persist under the new modern conditions of humans (the problem arises obviously under the assumption that handedness is unique of humans and has no roots in other asymmetries shared with non-human animals – an assumption with which we disagree; see e.g., for recent evidence in apes Hopkins, 2018; Hopkins, Mareno, & Schapiro, 2019; Forrester, Quaresmini, Leavens, Spiezio, & Vallortigara, 2012; and for a more general review in non-human species Versace & Vallortigara, 2015). Empirically, some studies have challenged the Fighting Hypothesis (see for a review Groothuis, McManus, Schaafsma, & Geuze, 2013). For example, Schaafsma et al. (2012) measured hand preferences in ten ecologically relevant tasks in a large sample (621 subjects) in the nonindustrial society of the Eipo (Papua, Indonesia), in which homicide rate is very high, without noticing a high frequency of left-handers. They also studied to what extent these measures predict the number of offspring and self-reported illness. They found a positive association between strength of asymmetry of hand skill and the number of children men sired, as well as a positive association for men between strength of hand preference and number of children who died within the first three years of life (for women there were no such effects). These results seem to suggest again that it is the strength of handedness, irrespective of direction, which has fitness advantages, and that the persistence of a stable polymorphism in handedness (with maintaining left-handers presence) may be due to either balancing selection on strength of asymmetry of hand skill versus strength of hand preference, or sexual antagonistic selection (Schaafsma, Geuze, Lust, Schiefenhövel, & Groothuis, 2013).

Other studies using an ethological and evolutionary biology approach to behavioural lateralization in humans are also slowly emerging (see e.g., (Chapelain et al., 2016; Forrester, Crawley, & Palmer, 2014; Güntürkün, 2003; Marzoli & Tommasi, 2009)). For some of them, there seem to be promising links with neurobiological research (e.g., asymmetries of kissing and head turning during embryogenesis in chordates, see Güntürkün, 2005) and with clinical conditions (e.g., cradling biases and atypical development, see (Malatesta et al., 2019).

5. Conclusion

After noting the widespread presence of lateralization across vertebrate and invertebrate species, we have examined the evidence showing the advantages of having a lateralized brain. So far there is evidence that lateralization:

1. Increases the processing capacity of the nervous system,
2. Enhances discrimination performance, success in solving some problems and aids learning.
3. Heightens ability to avoid predators,
4. May improve motor control,
5. Permits parallel and complementary processing of sensory inputs, and
6. Is apparent in (or affected by) interactions between conspecifics.

As to point 2, namely bias detection to one or other side, so that prey on a perceptually nondominant side might escape detection (or complementarily that predators can exploit better detection on a perceptually dominant side) it should be stressed how symmetry can be adaptive too. Martin Gardner, in his 1964 book (Gardner, 1964) “The Ambidextrous Universe”, wrote that “the slightest loss of symmetry, such as the loss of a right eye, would have immediate consequences for the survival of any animal. An enemy could sneak up unobserved on the right!” (p. 70). Thus, there should be specific advantages for breaking symmetry in animal behavior, such as a trade-off between speed of response and direction of response as discussed in Section 3 for lateralization of C-start reaction in fish. Moreover, we would expect that departures from symmetry would be limited in extent or, as argued persuasively by Corballis (2006), that degree of symmetry and asymmetry should be kept in balance.

There is a general trend for most individuals of a species to be lateralized in the same direction depending on the task, which we attribute to social behaviour. The latter is obvious in highly social species but also seen in less social (or ‘asocial’) species during intraspecific interactions. In general, it is apparent that aligning or not aligning the direction of asymmetries at the population level is deeply affected by the nature of interactions between individuals (Frasnelli and Vallortigara, 2017), and that the nature of the resulting asymmetry (directional or anti-symmetric) can be conceptualized and predicted in terms of ESSs. Of course, there is now evidence that the asymmetry of the internal organs in vertebrates is due to a cascade of genetic influences, and there is increasing understanding of the genetic influences on handedness, and to some extent on other cerebral asymmetries (review in Corballis, 2009). There are likely to be environmental and genetic (as well epigenetic, e.g., Ocklenburg et al., 2017) influences on lateralization (a noteworthy example being the role of light stimulation in embryo, see e.g., Rogers, 1982; 1990; Chiandetti & Vallortigara, 2019; Chiandetti, Galliusi, Andrew, & Vallortigara, 2013; 2017). Note, however, that the ESS hypothesis that we have championed here should be not be confused with claims that lateral biases are caused by social pressures; the EES hypothesis rests firmly on the idea that genetic (interacting with environmental, above) mechanisms underlie brain and behavioural asymmetries. The point is that, following the classical tradition of ethology (Tinbergen, 1963), we aim to consider ultimate not just proximal causation. Of course, there should be and there are indeed genes associated with asymmetries (proximal cause) but the point is to explain why (ultimate cause) these genes should produce alignment in the direction of asymmetry,

i.e., why genes exist that specify a direction for asymmetry rather than simply dictating asymmetry and leaving its direction as random (Vallortigara & Rogers, 2005).

The possibility can be also considered, and will require further research and evidence, that at least (some) population asymmetries could be an epiphenomenon of genetic constraints without any obvious function. If a population asymmetry has no evolutionary costs, it is easy to see that early lateralized genetic cascades could result in such patterns. We should expect, however, that these sorts of asymmetries would be very small in quantitative terms (see for an example evidence in *Drosophila* in which population asymmetry is observed, e.g., circling behaviour, but only when extremely large samples are tested, making its biological significance uncertain, Versace et al., 2019).

To summarize, our view about the biological function of the bicameral mind is that it has probably been shaped by two forces, one acting within individuals and the other acting between individuals (echoing in some respect, though without reference to consciousness, the famous breakdown of the bicameral mind by Julian Jaynes (1976). Within the individuals, the nervous systems seem to exploit limited degrees of asymmetries to increase their efficiency. We would be inclined to believe that the early bilaterians in which lateralization first appeared were lateralized at the individual level simply because their overt asymmetries did not affect the behavior of others to any significant degree. This is likely to be true for some modern organisms as well; for instance, it seems that the degree of social interaction found in *Drosophila* is insufficient to drive population-level behavioural asymmetries, even though interestingly it affects individual level asymmetries (Versace et al., 2019). However, when individually-asymmetric animals started to interact with each other in a manner for which their lateral biases (in morphology and/or in behavior) would matter to the morphology and/or behavior of others, then novel selection pressures would have begun to work and could have favoured (or prevented) the alignment of lateralization at the population level.

The study of the function of brain asymmetry thus offers a unique possibility of integration among the different aspects of biological sciences, from neural mechanisms to social interactions, and is likely to provide novel, unexpected insights in the years to come.

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