



Review

Left–right asymmetries of behaviour and nervous system in invertebrates

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ABSTRACT

Evidence of left–right asymmetries in invertebrates has begun to emerge, suggesting that lateralization of the nervous system may be a feature of simpler brains as well as more complex ones. A variety of studies have revealed sensory and motor asymmetries in behaviour, as well as asymmetries in the nervous system, in invertebrates. Asymmetries in behaviour are apparent in olfaction (antennal asymmetries) and in vision (preferential use of the left or right visual hemifield during activities such as foraging or escape from predators) in animals as different as bees, fruitflies, cockroaches, octopuses, locusts, ants, spiders, crabs, snails, water bugs and cuttlefish. Asymmetries of the nervous system include lateralized position of specific brain structures (e.g., in fruitflies and snails) and of specific neurons (e.g., in nematodes). As in vertebrates, lateralization can occur both at the individual and at the population-level in invertebrates. Theoretical models have been developed supporting the hypothesis that the alignment of the direction of behavioural and brain asymmetries at the population-level could have arisen as a result of social selective pressures, when individually asymmetrical organisms had to coordinate with each other. The evidence reviewed suggests that lateralization at the population-level may be more likely to occur in social species among invertebrates, as well as vertebrates.

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Contents

1. Introduction.....	1274
2. Arthropoda: Insecta, Arachnida, Malacostraca.....	1274
2.1. Hymenoptera: Apidae.....	1274
2.1.1. Honeybees.....	1274
2.1.2. Bumblebees.....	1277
2.1.3. Solitary species of bees.....	1277
2.1.4. Stingless bees.....	1277
2.2. Lateralities in ants.....	1278
2.3. Lateralities in spiders.....	1278
2.4. Lateralization in cockroaches.....	1278
2.5. Hand preference in locusts.....	1279
2.6. Wing orientation in crickets.....	1279
2.7. Hearing asymmetry in the Australian bushcrickets.....	1279
2.8. Water bugs.....	1280
2.9. Fruit flies.....	1280
2.10. Earwigs.....	1281
2.11. Escape responses and morphological asymmetry in shrimps and crayfishes.....	1281
2.12. Claw preference in fiddler crabs.....	1281
3. Mollusca: Gastropoda, Cephalopoda.....	1282
3.1. Memory storage in terrestrial slugs.....	1282
3.2. Chirality in pond snails.....	1282
3.3. Asymmetric mesocerebrum in terrestrial snails.....	1282

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3.4.	Asymmetric neuronal activation in molluscs.....	1283
3.5.	Eye and arm preferences in octopuses.....	1283
3.6.	Side-turning preference and asymmetrical optical lobes in cuttlefishes.....	1284
4.	Nematoda: <i>C. elegans</i>	1284
5.	Summary.....	1287
	References.....	1289

1. Introduction

Brain lateralization (i.e. different functional and/or structural specializations of the left and right sides of the brain), once considered to be unique to humans (Corballis, 1989), is now well known to be present in all vertebrate classes (reviewed by Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; MacNeilage et al., 2009; Vallortigara et al., 2011). Recently, evidence of lateralization in invertebrates has begun to emerge, suggesting that lateralization of the nervous system may be a feature of simpler brains as well as more complex ones.

A variety of left–right asymmetries in general morphology has been observed among invertebrates (reviewed by Palmer, 2009) but here we focus on asymmetries in the nervous system and behaviour. Knowledge of invertebrate asymmetries may be crucial to understanding the evolution of brain asymmetry and, given the relative simplicity of some of their brains, invertebrates could provide excellent model systems to investigate molecular, genetic and developmental aspects of lateralization. We address all of these aspects in our review.

The fossil record of animals contains numerous examples of handedness. Babcock (1993) reported examples of morphological or behavioural asymmetry from representatives of the Arthropoda, Annelida, Bryozoa, Echinodermata, Cnidaria, Mollusca, Chordata, and Conodonts. Behavioural asymmetry is seen in predation scars on fossils of trilobites: these scars are more commonly located on the right side than on the left (Babcock, 1993). Sixty specimens (70%) showed injuries only on the right pleural lobe, compared to 23 specimens that had injuries only on the left. Three specimens (3%) had injuries on both sides. This suggests that some predators of trilobites may have attacked the right sides of trilobites, or that the trilobites themselves exhibited an asymmetry in stereotyped escape behaviour. That some of the earliest trilobites or their predators exhibited right–left differences in behaviour suggests that lateralized nervous systems were in existence by the Early Cambrian, i.e. for more than 500 million years.

In this paper we review evidence of asymmetries in extant invertebrate species: Arthropoda (Insecta, Arachnida, Malacostraca), Mollusca (Gastropoda, Cephalopoda) and Nematoda (*Caenorhabditis elegans*).

2. Arthropoda: Insecta, Arachnida, Malacostraca

2.1. Hymenoptera: Apidae

2.1.1. Honeybees

Honeybees (Insecta, Hymenoptera, Apidae, Apinae, Apini) have provided evidence of lateralization in sensory systems, particularly of olfaction. Letzkus et al. (2006) first showed that honeybees (*Apis mellifera*) display laterality in learning to associate an odour with a sugar reward. The researchers used the proboscis extension reflex (PER) paradigm (Bitterman et al., 1983), in which bees are conditioned to extend their proboscis when they perceive a particular odour that has been associated with a food reward. They tested bees in two versions of the PER paradigm: (1) honeybees were conditioned to extend their proboscis to a scented drop of sugar water but not to an unscented drop of salt water, (2) honeybees were

conditioned to extend their proboscis to one odour (dissolved in a sugar solution – reward) but not to another odour (dissolved in a salt solution – punishment). Each version of the learning task was carried out on three groups of bees comprised at least 70 2-week-old bees. The bees in one group had their left antenna covered with a silicone compound, which prevents detection of odour, those in the second group had their right antenna covered, and those in the third group constituted a control in which both antennae were uncovered. Tests were carried out on the morning after the training had been performed. Results revealed that the bees with the right antenna covered learnt less well than the bees with their left antenna covered and bees with both antenna uncovered. In fact, the bees trained with only their right antenna in use performed just as well as the untreated controls.

It is difficult to understand whether this particular lateralization is due to a sensory asymmetry in the antennae or to a difference in learning or memory recall between the right and the left olfactory pathways. Letzkus et al. (2006) compared the number of the olfactory receptor sensory organs, *sensilla placodea*, in the two antennae. Images of 10 right antennae and 10 left antennae (seven of these left–right pairs originated from the same individuals) were obtained using scanning electron microscopy (SEM) and the mean numbers of *sensilla placodea* per flagellum on the two antennae were compared. The number was significantly higher on the right than on the left antenna (mean difference of 10%). This finding should be interpreted with caution, however, since only one type of sensilla was considered, and there are other sensilla, such as *sensilla trichodea* (Dietz and Humphreys, 1971), which play an olfactory role in honeybees. Moreover, in the paper of Letzkus et al. (2006), SEM images did not cover the whole antennal segment surface leaving a hidden, non-characterized area. Finally, only 7 out of 10 left–right pairs of antenna were from the same individuals.

In a recent study, however, Frasnelli et al. (2010b) duplicated the behavioural results of Letzkus et al. (2006) using forager Italian honeybees (*Apis mellifera ligustica* Spin.) and checked for morphological differences in the number of sensilla between the right and the left antenna of 14 honeybees. Both antennae of each bee were imaged from four different perspectives and all of the different types of sensilla were considered. Results showed that putative olfactory sensilla (*placodea*, *trichodea*, *basiconica*) were significantly more abundant on the right antenna surface than on the left antenna surface (mean difference of 3%), whereas sensilla not involved in olfaction (*campaniformia*, *coeloconica*, *chaetica*) were more abundant on the left than on the right antenna surface (mean difference of 7%), apart from on the tenth segment where no difference was observed. In another study, Anfora et al. (2010) recorded the electroantennographic (EAG) responses (that is a measure of the electrical signal over a section of the antenna) of honeybees' antennae stimulated with two different scents. The EAG responses to both a floral volatile compound and to an alarm pheromone were higher in the right than in the left antenna (mean difference of 18% for the floral volatile compound and 20% for the alarm pheromone). Thus, in honeybees, the higher electrophysiological response of the olfactory receptor neurons in the right antenna (Anfora et al., 2010) seems to correspond to a greater number of the olfactory sensilla on the right antenna compared to the left antenna (Letzkus et al., 2006; Frasnelli et al., 2010b).

Nonetheless, it remains questionable whether such a small difference (3–7%) in the number of olfactory sensilla might entirely explain the superior performance of the right antenna in learning or recall and also the one order magnitude (18–20%) greater difference observed in the EAG responses. In fact, there are other factors that might account for lateralization at the peripheral level (i.e. number of ORNs in each sensillum/number and type of olfactory receptor in each ORN). In honeybees, 5–35 ORNs are associated with the *sensilla placodea* (poreplate sensilla) (Schneider and Steinbrecht, 1968). In 13 specimens Kelber et al. (2006) found between 7 and 23 ORNs in the single poreplate sensilla and showed that poreplate sensilla are equipped with different ORN types but that the same ORN types can be found in different poreplate sensilla and they concluded that the equipment of poreplate sensilla with ORNs is overlapping. Unfortunately, this study by Kelber et al. (2006) did not take into account whether the poreplate sensilla analysed were from the right or the left antenna and we are not aware of any other study investigating this issue.

Behavioural data suggest that differences in antennal morphology are only part of the story. Rogers and Vallortigara (2008) investigated recall of olfactory memory at various times after the bees had been trained using both antennae. After PER training with both antennae in use, using lemon plus sucrose solution as the positive stimulus and vanilla plus saturated saline as the negative stimulus, bees were tested for recall 1–2 and 23–24 h later and with the left or right antenna coated with the silicone compound. At 1–2 h after training, bees showed excellent recall when tested using their right antenna, but poor or no recall when tested using their left antenna. By contrast, 23–24 h after training recall was good when the left antenna was in use but not when the right antenna was in use, demonstrating that long-term memory (LTM) is accessed mainly via the left antenna. Thus, retrieval of olfactory learning is a time-dependent process.

It is important to stress the fact that all the bees in the study performed by Rogers and Vallortigara (2008) were trained using both antennae and after the training the left or the right antenna was coated with the silicon compound. In this way bees used both antennae in the learning phase, whereas they used only the right or the left antenna during the recall test. The bees tested by Letzkus et al. (2006) used only one antenna in the learning phase. Considering the results of both studies (Letzkus et al., 2006; Rogers and Vallortigara, 2008), we can deduce that the right antenna is involved in learning and in the recall of short-term olfactory memory (STM). Recall of long-term memory via the left antenna occurs only if both antennae are involved in learning the odour–reward association but not if the bee is forced to use only its right antenna in learning. Hence, the apparent shift of memory recall from right to left antenna depends on competition between the antennae during learning. If the bee is forced to use only its right antenna, it can recall longer-term memory using this antenna and, if it is forced to use only its left antenna, it cannot learn or recall at all. Hence, it seems that both antennae are used in learning but in very different ways that enable either short- or long-term memory traces to be established and then accessed in recall tests.

Rogers and Vallortigara (2008) also checked whether the laterality was manifested as side biases to odours presented to the left or right side of the bee without any covering of the antennae, and hence in a more natural condition than in the paradigm requiring an antenna to be coated with latex. Bees were trained using both antennae and recall was tested at several intervals (1, 3, 6 or 23 h) after training using lateral presentation of the two stimuli and no coating of the antennae. There were significantly more correct PER responses to odours presented to the bee's right than to the left side at 1 h after training; no significant left/right difference occurred at 3 h after training; at both 6 and 23 h after training PER responses were higher on the left side than on the right side. The study by

Rogers and Vallortigara (2008) thus suggests that the asymmetry in number of olfactory sensilla may perhaps account for the asymmetry in short-term memory recall. Compared to short-term memory, long-term memory recall may rely on fewer receptors.

This evidence for a preferred side during olfactory retrievals (right side for shorter-term recall and left side for long-term recall) has been recently confirmed (Frasnelli et al., 2010a). Lateralized recall of olfactory memory in honeybees was tested at 1 or 6 h after training using different odours. After training with lemon(+)/vanilla(-) or cineol(+)/eugenol(-) recall at 1 h was better when the odour was presented to the right side of the bee than when it was presented to the left side. In contrast, recall at 6 h was better when the odour was presented to the left than to the right side. However, when trained with either a familiar appetitive odour (rose) as a negative stimulus, or with a naturally aversive odour (isoamyl acetate, IAA – alarm pheromone) as a positive stimulus, bees showed suppression of the response to odours presented on both the right and the left sides at 1 h after training (likely due to retroactive inhibition – see Cheng and Wignall, 2006) and at 6 h after training proboscis protrusion occurred to both odours on both sides. A possible explanation for this behaviour is that at 6 h, when access to memory has shifted from the left antenna, memory of these familiar odours in the left side of the brain would be present as two mutually exclusive forms. As a result of very long-term memory either biologically encoded or acquired well before testing, the memory would be present as rose positive and IAA negative and, as a result of the long-term memory of training, it would be present as rose negative and IAA positive. This would produce response competition. As a direct test of this hypothesis, bees were first trained with unfamiliar lemon(+)/vanilla(-) and then (16 h later) re-trained with vanilla(+)/lemon(-); as predicted, 6 h after re-training proboscis protrusion occurred to both odours on both the left and right side.

The apparent shift in memory from the left to the right side (i.e. STM encoded on right side and LTM encoded on left side) could be explained by encoding of the memory in different time frames (short- and long-term) on each side of the brain rather than it being transferred from one side to the other (Frasnelli et al., 2010a). Hence there would be asymmetry in the effectiveness of recall at different times. Overall, these results (Frasnelli et al., 2010a) confirm the novel finding (Rogers and Vallortigara, 2008) that in bees there is a difference between the neural circuits accessed via the right antenna and those accessed via the left antenna in exploiting the learnt task. Specifically, bees learn to associate a new odour of a positive stimulus mainly using neural circuits accessed via their right antenna (as was first shown by Letzkus et al., 2006), and that, after a period of a few hours, memory consolidation occurs accompanied by antennal asymmetry, bees now being able to recall the odour mainly when using their left antenna. Moreover, this particular dynamic of memory traces has marked consequences when odours are already known to the bees (either for a biological reason or as a result of previous experience) and are thus already present in the long-term memory store. As a result, response competition arising from multiple memory traces can be observed, with bees showing unexpected lack of specificity in their longer-term olfactory memories. Since the study by Frasnelli et al. (2010a) did not control the previous experience of the bees since the bees were collected while foraging on the flowers, the results have to be interpreted with some caution. Nevertheless, the experiment in which bees were trained with lemon(+)/vanilla(-) and then reverse trained supported the concept of competition between multiple memory traces.

A strong odour dependence of the lateralization of short-term memory recall of odours has been reported in honeybees (Rigosi et al., 2011). A series of behavioural experiments assessed response asymmetry of odour recall following proboscis extension reflex

conditioning at 1 h after training using three different odours (1-octanol, 2-octanone and (–)-linalool). The training and the following test were performed on three groups of bees (the bees in the first group had both antennae in use, the bees belonging to the second and the third groups had respectively only the right or the left antenna in use). Recall of short-term memory at 1 h after training demonstrated a striking odour dependence of the lateralization (Rigosi et al., 2011). After training with 1-octanol and 2-octanone, bees showed no differences in the recall test regardless of whether they had use of only their right antenna, only their left antenna or both antennae. In contrast, bees trained with (–)-linalool showed a significant effect of the antenna in use: bees trained (and tested) with their right antenna in use performed significantly better than individuals with only their left antenna in use, whereas they performed the same as bees with both antennae in use (Rigosi et al., 2011). The behavioural experiments performed by Rigosi et al. (2011) added a new aspect to the previous results (Letzkus et al., 2006; Rogers and Vallortigara, 2008; Anfora et al., 2010; Frasnelli et al., 2010a), showing that in the recall test at 1 h after conditioning, different types of plant odour volatiles manifest asymmetries or not, depending on the biological relevance of the plant compound. The odour (–)-linalool is one of the most common derivatives of floral scents playing a crucial role as cue for pollinators (Knudsen et al., 1993). The odours 1-octanol, and 2-octanone are unspecific and ubiquitous volatiles released from the green organs of the plants and thus of minor importance in pollinator plant interaction. These results, Rigosi et al. (2011) suggest, show that short-term memory induced lateralization in bees may be odour-specific, or that lateral shift (Rogers and Vallortigara, 2008) associated with the transition from short-term memory to long-term memory occurs at different time scales for different types of odours. It has been demonstrated that honeybees are able to learn complex odour mixtures by using a subset of key odours, such as (–)-linalool (Reinhardt et al., 2010) and that, after conditioning bees to a mixture of odours, (–)-linalool elicits higher levels of responding than do other components of the mixture presented singly (Laloi et al., 2000). Since, as this research demonstrates, bees are selective in their responses to odours, the strikingly different biological relevance of the odour compounds used by Rigosi et al. (2011) might be a reason for the observed difference in lateralization.

A shift of recall access from one to the other side of the brain has been noted previously in birds (Cipolla-Neto et al., 1982; Clayton, 1993; Andrew, 1999). This is interesting because it suggests that lateralized events in memory formation may be common in invertebrate and vertebrate species.

What could the functional significance of the transfer of memory information between the two sides of the bee's brain be? Rogers and Vallortigara (2008) suggested that a shift of memory access from the right to the left side of the brain would allow the right antenna to learn about new odours without interference from odour memories in long-term stores. In fact, since bees visit different flowers at different times of the day, as nectar becomes available, the formation of different odour associations during the course of the day would be required, and this is a process that might be aided if recall of older odour memories is avoided on the side of the brain undergoing new learning.

Very recently Biswas et al. (2010) investigated a putative 'synaptic' role in lateralization and brain development associated with sensory input. Honeybee *neuroligin 1–5* (*NLG1–5*) and *neurexin 1* (*Nrx1*) expression levels were examined in bees with the right or the left antennae amputated. *Neuroligin* and *Nrx1* are highly conserved adhesive proteins found on synaptic membranes of neurons, which produce a trans-synaptic bridge that facilitates maturation and specification of synapses. To examine the roles that *neuroligins* and *Nrx1* might play in the previously observed olfactory learning asymmetry (Letzkus et al., 2006; Rogers and Vallortigara, 2008),

Biswas et al. (2010) used three groups of 50 bees: (1) control bees with both antennae intact; (2) bees that had only the right antenna (left antenna amputated); (3) bees that had only the left antenna (right antenna amputated). Antennae were amputated immediately after emergence and the bees were returned to the hive. Brain tissue was examined from bees aged 24 h, 7 days and 14 days, respectively. The expression levels of *Neuroligins 2–5* and *Nrx1* showed no substantial differences among the three groups. Lateralization of sensory input had a significant effect only on expression levels of *NLG1*. At 24 h post-emergence, right-antenna-only bees showed a slight decrease in levels of *NLG1* expression compared to control bees, whereas left-antenna-only bees had a significantly lower expression level of *NLG1*. This result supports previous evidence that learning using the right antenna alone is equivalent to learning using both antennae and that learning performance is significantly poorer when bees use only the left antenna (Letzkus et al., 2006; Anfora et al., 2010; Frasnelli et al., 2010a,b). At 7 days, the control bees and the right-antenna-only bees maintained an equivalent level of *NLG1* expression, whereas left-antenna-only bees showed higher expression of *NLG1* than the other two groups. At 14 days, the left-antenna-only bees and the control bees showed similar *NLG1* expression, whereas the right-antenna-only bees showed a significant increase in *NLG1* expression. The results by Biswas et al. (2010) suggest that lateralized neural trauma is followed by a mechanism that compensates for the loss of sensory input probably by increasing synaptic development and neuronal rewiring in the unaffected side end. Moreover this compensation occurs over time in the adult bee brain and is only evident when the right side is unaffected. Specifically, this compensation mechanism works after loss of either antenna, but possibly represents an urgent response when the right, "dominant" antenna is missing compared to a slower compensation or adjustment in synaptic development at 14 days when the left antennae is removed.

Rigosi et al. (2011) investigated whether an asymmetry can be observed in the volume of the primary olfactory centres of the central nervous system, the antennal lobes (ALs), in honeybees. Precise volume measurements of a subset of the functional units in this structure, the glomeruli, were performed on both sides of the brain, exploiting the advantages of two-photon microscopy. This novel method allowed minimal invasive acquisition of volume images of the ALs, avoiding artefacts from brain extraction and dehydration. However, the measurement accuracy was limited by the decreasing contrast at higher imaging depth, causing problems in defining precisely the border between single glomeruli. Within the newly established accuracy limits, the study by Rigosi et al. (2011) showed that the chosen subset of glomeruli does not differ in volume between the right and left side of the brain. This confirms a previous study (Winnington et al., 1996) in which a single rough comparison between the AL morphology in the two brain hemispheres, based on histological slices at distances of 25 μm , did not show any asymmetry. Note that the study by Rigosi et al. (2011) improved the spatial resolution by almost an order of magnitude with respect to the work by Winnington et al. (1996). It is interesting to underline that the bees used in the volumetric measurements performed by Rigosi et al. (2011) were honeybee foragers without controlled experience and that had not been trained with any odour using the PER paradigm. It has been shown that with changing behavioural tasks and foraging experience antennal lobes and specific glomeruli undergo a significant modification of volume size that is age- and odour-exposure dependent (Winnington et al., 1996; Sigg et al., 1997). Such plasticity of olfactory centres has been also described in other species (Devaud et al., 2001; Harvey and Colley, 1984). For this reason, it is likely that any significant difference in volumes between the ALs in bee foragers with no controlled experience might be masked by volume fluctuations of

specific glomeruli, influenced by both short-term and long-term odour experience.

Recently, Sandoz (2011) reviewed major findings about how the honeybee brain detects, processes, and learns odours, based on behavioural, neuroanatomical, and neurophysiological approaches. The discrimination and generalization ability of the honeybee olfactory system, its capacity to grant special properties to olfactory mixtures as well as to retain individual component information have been described as well as the transformation of the olfactory message from the periphery until higher-order central structures. Moreover, Sandoz (2011) explained how the olfactory processing is subject to plasticity as a function of both age and experience and how this plasticity is manifested by structural and functional changes of olfactory circuits.

Letzkus et al. (2007) also used a PER paradigm to compare visual learning of honeybees using their left or right eye. Bees were tested with their antennae removed because it seems that conditioning to visual stimuli is easier to obtain in bees without antennae (Hori et al., 2006). They were tested with both eyes covered (BEC), both eyes exposed (BEE), their right eye exposed (REE) or their left eye exposed (LEE). The conditioned stimulus (CS) was a large yellow rectangle presented on a computer-controlled display. The bees were conditioned to extend their proboscis in anticipation of a food reward (unconditioned stimulus, US) according to the colour of the CS. Each experiment consisted of two 10-training sessions; the first one was conducted the morning after the eyes had been covered and the second one was conducted the following morning. The two training sessions were subdivided into four five-trial blocks, during which the CS (yellow rectangle on monitor) was presented for 15 s. BEC bees showed no learning throughout the entire training. The BEE bees' performance rose steadily, with a mean response rate of 39% in the last five trials. REE bees also showed an increase in learning performance, but the response rate was slightly (but not significantly) lower than that of BEE bees throughout the training. Only in the last five trials REE bees showed a performance level of 33%. LEE bees reached a mean learning performance of only 13%, which was significantly lower than that of BEE and REE groups. LEE bees were statistically different from BEE and REE bees in trials 6–10 and from BEE bees in trials 11–15. Thus, at least in the last part of the test, bees seem to primarily use their right eye for learning and/or detecting objects (for associating a visual stimulus with a food reward, in this case), and therefore they are better at responding to a visual object when using their right eye than when using their left eye. Since the second 10-training session was performed the day after the first 10-training session, it is unclear whether the lateralization was associated primarily with learning or with memory. Some memory formation must be involved but whether it is long or short-term memory cannot be distinguished.

By comparing these findings with the lateralization found in olfaction, it could be argued that sensory inputs (visual and olfactory) from the right side are used preferentially while foraging or feeding. However, we do not know whether access to long-term memory of visual associations shows the shift to the left side, as in the case of long-term olfactory memory.

2.1.2. Bumblebees

Behavioural asymmetry has also been found in bumblebees. Kells and Goulson (2001) reported that bumblebees *Bombus* spp. (Insecta, Hymenoptera, Apidae, Apinae, Bombini) show preferred directions of circling as they visit florets arranged in circles around a vertical inflorescence. In three (*Bombus lapidarius*, *Bombus lucorum* and *Bombus pascuorum*) out of four species examined the majority of bumble bees circled in the same direction. Interestingly, the researchers did not observe any lateralization in *Bombus terrestris*. Since two species circled anticlockwise and one clockwise, it is

unlikely that the asymmetry is a function of the structure of the florets. Instead, the directionally biased circling might well have something to do with lateralization of antennal responsiveness to odours or lateralized learning and memory recall.

Olfactory lateralization has been investigated in bumblebees *Bombus terrestris* spp. (Anfora et al., 2011). Bumblebees were trained to associate an odour with a reward using the PER paradigm and recall of memory was tested 1 h after. As for honeybees (Letzkus et al., 2006; Frasnelli et al., 2010b), the bumblebees with the left antenna coated performed as well as those with both antennae in use, whereas bumblebees with the right antenna coated performed significantly less well. In contrast to honeybees, no significant differences were observed in electroantennographic responses between the left and right antennae of bumblebees when stimulated by two different compounds (an alarm pheromone and a floral scent). Interestingly, however, one class of bumblebee olfactory sensilla, *trichodea type A*, was shown to be more abundant on the surface of the right antenna than on the left one, and a slight tendency towards asymmetry was shown for a second class, i.e. *sensilla coeloconica*. On the other hand, *sensilla placodea*, the most common olfactory organs in Apoidea species, did not show any consistent asymmetrical distribution in *B. terrestris* (Frasnelli et al., 2010b). Since electroantennographic responses represent the sum of responses of all olfactory receptor neurons housed in the sensilla of a single antenna (Schneider and Kaissling, 1957), the fact that morphological asymmetries were apparent only in a limited class of receptors may explain why, dissimilar to honeybees, no overall asymmetry was observed in EAG responses in bumblebees.

2.1.3. Solitary species of bees

Interestingly, antennal lateralization is not a general characteristic within the Hymenoptera, Apidae. Anfora et al. (2010) compared olfactory lateralization in two species of Hymenoptera, the honeybee (*A. mellifera*, Insecta, Hymenoptera, Apidae, Apinae, Apini), a social species, and the mason bee (*Osmia cornuta*, Insecta, Hymenoptera, Megachilidae, Megachilinae, Osmiini), a solitary species. In the honeybees tested in this study, recall of the olfactory memory 1 h after training to associate an odour with a sugar reward was better in animals trained with their right rather than their left antenna, confirming previous findings (Letzkus et al., 2006; Rogers and Vallortigara, 2008). However, no asymmetry was observed in mason bees. Behavioural results were supported by electrophysiological recordings: whereas honey bees show higher EAG responses in the right than in the left antenna (above), mason bees, as a group, did not show EAG asymmetry. However, mason bees appeared to be lateralized at the individual-level, in the sense that different individuals showed consistently stronger EAG responses in either the left or the right antenna. In fact, only a minority of individuals showed symmetrical responses, and the large majority, 15 out of 21 individual mason bees, showed significantly stronger responses either with the right (seven individuals) or the left (eight individuals) antenna. An analysis of the number of olfactory sensilla present on the mason bees' antennae has not yet been carried out.

Since it has been hypothesized (for vertebrates) that lateralization at the population-level may emerge as a result of social selective pressures (Vallortigara and Rogers, 2005), it could be that the pattern observed in these species of Hymenoptera, Apidae is due to the different degrees of sociality of the two species. As already mentioned, bumblebees, which are also a social species (Goulson, 2003), though different than honeybees, also show lateralization at the population-level (Anfora et al., 2011).

2.1.4. Stingless bees

Frasnelli et al. (2011) studied primitive social bees, stingless bees (Insecta, Hymenoptera, Apidae, Apinae, Meliponini) to shed

light on the possible evolutionary origins of the left–right antennal asymmetry. Three species of Australian native, stingless bees (*Trigona carbonaria*, *Trigona hockingsi* and *Austroplebeia australis*) were trained to discriminate two odours, lemon(+)/vanilla(–), using the PER paradigm. Recall of the olfactory memory at 1 h after training was better when the odour was presented to the right than to the left side of the bees. In contrast, recall at 5 h after training was better when the odour was presented to the left than to the right side of the bees. An additional experiment with *T. hockingsi* bees fed with sugar 1 h before the recall test at 5 h also responded on the left and not the right, indicating that the shift in lateralized recall was due to the lapse of time per se and not to changes in motivation to feed.

Hence, stingless bees (Meliponini) have the same laterality as honeybees (Apini), which may suggest that olfactory lateralization is likely to have evolved prior to the evolutionary divergence of these species. The distributional pattern and fossil records are indicative of greater antiquity for the Meliponini compared to Apidi, Bombini and Euglossini, and suggestive of an independent origin or an early divergence from a proto-other Apidae branch (Camargo and Pedro, 1992). However, the phylogenetic relationships among the four tribes of bees (i.e. corbiculate Apidae: Euglossini, Bombini, Meliponini, and Apini) are controversial and the single origin of eusociality is questionable. Noll (2002) expanded the term “social” from the restricted typological definitions, such as solitary and eusocial to 42 characters and proposed a tree based only on behavioural characters. The reconstructed relationships were similar to those observed in morphological and “total evidence” analyses, i.e., (Euglossini + (Bombini + (Meliponini + Apini))), all of which support a single origin of eusociality. Very recently, Cardinal and Danforth (2011) investigated whether highly eusocial behaviour has evolved once or twice within the corbiculate Apidae, using a model-based approach to reconstruct the evolutionary history of eusociality. They also dated the antiquity of eusocial behaviour in apid bees, using a recent molecular phylogeny of the Apidae. Their study led them to the conclusion that eusociality evolved once in the common ancestor of the corbiculate Apidae, advanced eusociality evolved independently in the honeybee and in stingless bees, and that eusociality was lost in the orchid bees. Fossil-calibrated divergence time estimates reveal that eusociality first evolved at least 87 Mya (78–95 Mya) in the corbiculates, much earlier than in other groups of bees with less complex social behaviour.

Considering all this information, it can be argued that the similarity found between honeybees and the three species of Australian stingless bees in population-level lateralization in recall of olfactory memory is linked with the social feature shared by the two tribes and may have evolved independently in the trajectory that led to honeybees and trajectory that led to stingless bees.

2.2. Lateralities in ants

Evidence of lateral biases in ants (Insecta, Hymenoptera, Formicidae) has been reported (Heuts et al., 2003). Twelve ant species *Lasius* spp. kept mainly to the right side of their foraging “streets”, whereas there was only one species that kept to the left. On streets in trees, 49 *Lasius niger* colonies kept to the right versus 26 to the left. In this ant species a significant majority of couples in the laboratory had the left side of their bodies exposed to their partners when resting. This identical left body side exposure when resting and foraging in streets also correctly predicted that lone foraging *L. niger* would turn to the right significantly more often than to the left (the ratio was 14–2) since the right side of the brain has been shown to be involved in foraging in many species (Vallortigara and Rogers, 2005).

2.3. Lateralities in spiders

Spiders of many species (Arachnida, Araneae) have been shown to possess left–right asymmetries in behaviour (Heuts et al., 2003). A significant majority of spiders captured in the field had mainly left-leg lesions. The greater vulnerability of left legs compared to right legs in spiders in general is indicated by the evidence of 305 left-leg versus 254 right-leg lesions (obtained from 18 families of spiders – Heuts and Lambrechts, 1999). It has been shown that separate spider families and species are also significantly left-biased and never significantly right-biased (Heuts and Lambrechts, 1999). The left-side vulnerability may be due to anatomical factors (joint strength and leg length) and/or a complex of various behavioural factors, such as a propensity to move the legs on one side when alarmed, or left/right attack biases in predators of spiders, as has been documented in some vertebrates species (Vallortigara and Rogers, 2005).

There are some direct observations of leg-use when spiders interact with their prey. Ades and Ramires (2002) demonstrated that the spitting spider *Scytodes globula* (Arachnida, Araneae, Scytodidae) uses its legs in an asymmetric way during prey handling. This species catches its prey by rapidly ejecting a mixture of glue and venom from the chelicerae and, on direct contact during the handling of the prey, it uses legs I and/or II more often than the other legs (we refer to legs' numbers in the rostrocaudal direction). Looking at the missing legs in spiders collected in the field it was found that of 162 field-collected spiders, 36 had one leg missing; among these 36 the frequency of spiders with leg I or II missing was significantly higher than that of spiders with leg III or IV missing. There was a significant difference between those missing the left I leg and those missing the right I (15 missing the left I leg and 4 missing the right I leg) but, even though more spiders lacked left-leg II than right-leg II, there was no significant bias in use of legs II. Ades and Ramires (2002) also looked at touches during predatory encounters of individual *S. globula* with prey from three species of spiders, *Loxosceles intermedia*, *Loxosceles gaucho*, and *Loxosceles laeta* and they observed that touching movements with the left anterior legs were significantly more frequent than with the right anterior legs. The spiders, however, were tested only once, and thus repeated testing of the same individuals is required to determine consistency of use of a preferred leg. Additionally, it would be interesting to investigate the use of the legs in handling non-spider prey and in other behavioural contexts in order to assess the generality of leg preference. The reason and possible adaptive benefits of a preferential use of left-leg I could be discovered by checking whether left-leg I explores by touching after shorter latency than right-leg I or whether the left leg has a higher density of tactile (chemo) receptors than the right leg. In other words, this side bias might reflect a sensory lateralization.

2.4. Lateralization in cockroaches

Behaviour of the common American cockroach, *Periplaneta americana* (Linnaeus) (Insecta, Blattaria, Blattidae) has been investigated to determine whether lateralization is evident in a bias to turn left or right (Cooper et al., 2010). The cockroaches were allowed to run through a Y-tube and make a choice of which direction to take. Vanilla and ethanol were placed randomly at the ends of the Y-tube to entice the cockroaches to reach the end of the tubes. Thirty-eight adult cockroaches were tested on each of the five conditions: both antennae intact, half of the left antenna cut, all of the left antenna cut, half of the right antenna cut, and all of the right antenna cut. Antennal amputation was performed on CO₂ anesthetized individuals to reduce trauma and facilitate handling. Results showed that the odours of vanilla and ethanol play

an insignificant role in the decision-making. Injury of one antenna affected the choice of direction, but not in any consistent way: while the majority of cockroaches with the left antenna amputated chose to go right, the same was not the case if the entire right antenna was removed. In fact, similar injury to either the right or the left antenna revealed an innate bias for turning right. Similar results were obtained when either antenna was cut in half. More evident was the skew towards the right path when both antennae were intact. The antennae of these gregarious insects are very long and, in addition to their role in detecting chemicals, they are very important as tactile organs (Okada and Toh, 2004). The study by Cooper et al. (2010) thus suggests that *P. americana* has a motor bias towards the right and not that this species is right-side dominant in their tactile and odour senses. The cockroaches turn right when there is no sensory input from the antennae, showing that they have a motor bias and input from the antennae modifies this motor bias, often to reduce its strength.

2.5. Hand preference in locusts

A pronounced “handedness” in response to stimulation of the legs has been documented in adult desert locusts *Schistocerca gregaria* (Insecta, Orthoptera, Acrididae) (Rowell, 1964). In this species a reflex cleaning or grooming movement by the front leg is evoked by stimulation of the sensilla of the prothoracic sternum (Rowell, 1961a). This response can be seen only rarely, but it can be obtained if the neurones connecting the prothoracic ganglion to the rest of the central nervous system (CNS) are cut. The inhibition of the prothoracic cleaning reflex was studied by progressively isolating the prothoracic ganglion from the rest of the CNS using lesion techniques and measuring the responsiveness of the reflex at each stage (Rowell, 1964). The number of leg movements made by the left and right legs was recorded and these measures showed that most of the insects had a pronounced “handedness”, a preference for response by either the left or the right leg. Scores were reported for a single animal tested in 20 trials after an experimental lesion: left 12 and right 19. The L/R ratio (the ratio of the score of the left leg to the score of the right leg in a series of tests) was therefore 0.63 and the locust was distinctly right-handed. The aim of the study (Rowell, 1964) was to compare the effects of asymmetric lesions on leg-use in the locust and not to study the leg preference itself. It was difficult to compare the effects of asymmetric lesions on leg preference because each individual started with a different preference. A possible common reference point in all experiments would be the natural “handedness” of the animal before the lesions were made but unfortunately the responsiveness of the intact animal was so slow that this “handedness” (expressed by L/R ratio) could not be determined. Thus, the reference L/R ratio was taken to be that obtained from the prothoracic ganglion alone, at the end of lesion series, when it was completely separated from the rest of the nervous system and the animal was, in consequence, highly responsive. The L/R ratios obtained from three different locusts after each had suffered the same series lesions were: 0.77 (slightly right-handed); 6.0 (markedly left-handed) and 13.3 (extremely left-handed). Clearly, the sample size of animals used in the study was too small to allow determination of the level of this asymmetry in the leg-use. Interestingly unilateral section of the cervical connections was found to have no effect on the L/R ratio of the prothoracic ganglion (Rowell, 1964). This means that each side of the suboesophageal ganglion influences both sides of the prothoracic ganglion equally, which is opposite to that found for the two posterior thoracic ganglia (Rowell, 1964). Thus the detail of the neural connections is different not only from species to species, but also from ganglion to ganglion and almost certainly from reflex to reflex.

2.6. Wing orientation in crickets

Male field crickets, *Gryllus campestris* (Insecta, Orthoptera, Gryllidae), show physiological asymmetry in wing orientation during singing: they use the right forewing more commonly than the left (Elliott and Koch, 1983). If this wing orientation is inverted (i.e. the left wing lies over the right), during stridulation, almost no sound is produced (the sound intensity is 100 times less – Elliott and Koch, 1983) although the wings are morphologically identical (Stärk, 1958). Moreover, a special wing-spreading behaviour is used by the insect to restore the normal right over left orientation and thus to ensure an effective acoustical communication. The physiological basis of this asymmetry and of the mechanism used by male crickets to restore the effective wing orientation has been investigated (Elliott and Koch, 1983). A set of hair plates in the sub-costal region of the wings seems to play an important role in preventing the inversion of the wings during stridulation. In their study, Elliott and Koch (1983) showed that a set of two hair fields on each wing have a stabilizing effect on wing orientation. After removal of the inner hair plates, that is the lower on the right forewing and the upper on the left forewing, the wing opening increased by 13% and the jitter in the opening position increased by 100%. Since the wings are then fully separated in 2% of the calling song syllables observed, the chance of accidental wing inversion rose dramatically as result of removal of the inner hair plates. Results thus showed that sensory feedback from these hair fields stabilizes the wing movement amplitude, preventing wing inversion during calling, which ensures the high intensity sound production necessary to attract females.

2.7. Hearing asymmetry in the Australian bushcrickets

The degree of left–right natural asymmetry in the hearing system of the ensifera orthoptera *Requena verticalis* (Insecta, Orthoptera) was examined by measuring the size of the auditory spiracle of females (Bailey and Yang, 2002). Naturally occurring asymmetry was investigated by measuring the aperture of the prothoracic auditory spiracle of both right and left sides using the digital scanning process of OptimusTM, which provided an area based on a defined perimeter. Bailey and Yang (2002) measured to what extent are females asymmetrical in regard to spiracle area, and what is the largest detectable left–right difference. Differences ranged from 0 to 8%, which translates to maximum area differences right–left of 0.03 mm². This was related to expected right–left difference in threshold as dB loss (or gain) per unit of area, using the regression of threshold on spiracle area for *R. verticalis*. Right–left differences of 0.03 mm² would approximate 0.8 dB differences.

Bailey and Yang (2002) reduced the sensitivity of one ear to a level that may be considered two standard deviations outside the natural range of variation, by packing cotton wool into either the right or left auditory spiracle. With this asymmetry, they measured hearing loss using neurophysiological recording from the ascending auditory T-fibre in the neck connective. The sound was delivered to the operated side of the insect from a speaker placed at either 90° or 30° to the long-body axis. Results showed that the left–right bias created by this operation approximated 5 dB; this is greater than that found in nature. Moreover, to evaluate the influence of this induced auditory bias, the unrestrained animal’s ability to orient to conspecific calls in an open arena was tested. Free-moving females were allowed to orient towards a speaker emitting male calls at near-natural call intensities of 51 and 82 dB (SPL), 80 cm from the speaker on a flat arena. There was no variation in angle or vector between experimental and control insects, and there was no difference in acuity between call intensities. In conclusion the study by Bailey and Yang (2002) showed that the natural bilateral asymmetry of one of the controlling traits of sound input (i.e.

the size of the auditory spiracle) is so small that it has a negligible effect on a female's ability to find a sound source. Furthermore, when the approximately 1 dB maximum left–right difference was experimentally increased to 5 dB by unilaterally blocking the spiracle with cotton wool, females showed no diminution in their ability to find the target. The hypothesis that sensory asymmetry may have an effect on adult reproductive fitness implied that asymmetrical females would have less likelihood of finding a mate than symmetrical animals. The experiments performed by Bailey and Yang (2002) did not produce evidence in support of this hypothesis.

2.8. Water bugs

Asymmetrical hearing in the water bug *Corixa punctata* (Insecta, Hemiptera, Corixidae) has been observed (Prager and Larsen, 1981). In this insect, the two ears are physiologically asymmetrical. This physiological asymmetry is correlated with bilaterally asymmetric rocking movements of the clubbed process. Prager and Larsen (1981) examined these rocking movements and in particular the bilateral asymmetry with laser vibrometry at physiological sound pressure levels. The intensity characteristics showed that the vibration velocities and displacement of the clubbed process of the left tympanic organ were larger than those of the right organ at the two examined frequencies (1.73 and 2.35 kHz) and over the intensity range 84–112 dB. Specifically, in the right tympanic organ the vibrations were larger at 1.73 kHz than at 2.35 kHz, whereas in the left organ the vibrations were larger at 2.35 kHz than at 1.73 kHz. Furthermore, Prager and Larsen (1981) observed that at a given peak sound pressure the vibration amplitude of the left organ was about three times larger than that of the right organ. The higher velocity of the clubbed process of the left tympanum at 2.35 kHz correlates well with the greater sensitivity of the left receptor cell A1 at this frequency. In a further study, Prager and Streng (1982) determined the resonance properties of the physical gill and the variability determined by changes in volume of the air bubble during breathing with respect to the bilateral asymmetry of the mesothoracic tympanic organ. Because the oscillatory behaviour of the mesothoracic tympanic organ on the right side differs somewhat from that on the left, there are bilateral differences in the characteristic frequencies of the two receptor cells A1 (Prager and Larsen, 1981). This bilateral asymmetry has been shown to extend the frequency band of high sound sensitivity to cover the frequency range containing the resonant frequencies of the respiratory air bubble at the different temperatures. Overall, the finding by Prager and Streng (1982) underlined the significance of the bilateral asymmetry of the receptor cells A1, for this asymmetry ensures high sensitivity over the entire range of stridulation-sound carrier frequencies.

Evidence of a population-level lateralized behaviour has been found in the giant water bugs, *Belostoma flumineum* Say (Insecta, Hemiptera, Belostomatidae; Kight et al., 2008). Giant water bugs are large aquatic insects, predators of other aquatic invertebrates and small fishes. The initial idea of the study performed by Kight et al. (2008) was to train bugs to swim left or right in a T-maze. Surprisingly, a significant preference of the water bugs to turn left, even when not reinforced, was observed, revealing a naïve bias in this species. To control for environmental cues that might bias the turning direction of water bugs in the maze, the authors ran two separate experiments on independent groups of 20 water bugs. Both experiments were identical with the exception that, after the first group of 20 water bugs had been tested, the maze apparatus was rotated 180°, thereby reversing the polarity of all directional environmental cues such as lighting or electromagnetic fields. Again the same left turn tendency was observed. Hence, the explanation of the presence of this bias could be the existence of asymmetries in the nervous system or asymmetric exoskeletal morphology (i.e. leg length) that could cause biased swimming behaviour.

2.9. Fruit flies

Evidence of olfactory lateralization in invertebrates has been reported also in the fruitfly *Drosophila melanogaster* (Insecta, Diptera, Drosophilidae, Drosophilini; Duistermars et al., 2009). The use of bilateral olfactory cues to track odours in flight has been investigated using a modified flight simulator that enables manoeuvres in the yaw axis. Results showed that flies readily steer directly toward a laterally positioned odour plume and do so by orienting saccades directly up an odour gradient. This ability is abolished when the sensory input to one antenna is occluded, precluding odour detection in one antenna and thus eliminating bilateral spatial comparison. Flies with a single intact antenna performed frequent yaw deviations but these paired saccades frequently occurred outside of the plume. Moreover, odour presentation resulted in a significant bias in flight oriented toward the intact antenna and, most relevant here, occluding the left antenna had a stronger effect than occluding the right antenna. Hence, sensory signals from the left antenna contribute disproportionately more to odour tracking than do signals from the right antenna. Input to the left antenna has been shown to be sufficient to elicit a significant odour-mediated decrease in saccade frequency and to be able to generate a higher proportion of left turns in response to odour than does input to the right antenna. These results reveal a consistent asymmetry in antenna-mediated flight control, suggesting that asymmetrical cross-modal olfactory and mechanosensory signals facilitate stable odour tracking in complex multisensory environments and likely also increase the efficiency of search behaviour.

Chemotaxis behaviour in *D. melanogaster* larvae with a single functional olfactory sensory neuron (OSN) on either the left or right side of the head has been studied to examine unilateral or bilateral olfactory input (Louis et al., 2008). The larval olfactory system is composed of 21 pairs of OSNs housed in two bilaterally symmetric dorsal organs at the tip of the head. Each OSN expresses one, or occasionally two, specific odorant receptors together with *Or83b*, a ubiquitously expressed co-receptor. Using genetic and transgenic approaches, the expression of odorant receptor genes were manipulated to generate animals with only a single functional OSN in either the left or the right side of the head, and these animals were tested in multi-source odorant gradients. Animals with a right-functional OSN displayed significantly better chemotaxis than the corresponding left-functional animals, and bilateral animals performed better than either of the unilateral ones. In the study by Louis et al. (2008), the mechanisms allowing *Drosophila* larvae to orient in an airborne odorant gradient were investigated and they showed that *Drosophila* larvae adopt a direct orientation strategy that is based on sequential detection of odour concentration along the path of motion. Unilateral input from a single OSN suffices for orientation in a gradient field and unilateral right animals showed significantly better chemotaxis than unilateral left animals in both *Or42a*- and *Or1a*-functional animals (two different genotypes). The side-specific hypersensitivity was explained by the authors as resulting from differential levels of gene expression in the left and right neurons, suggesting that the right bias is an inherent feature of the larval olfactory system.

In the fruitfly *D. melanogaster* a structure located near the fan-shaped body connects the right and the left hemispheres (Heisenberg, 1994). This structure is an asymmetrical round body (called AB) with a diameter of about 10 µm and is not characteristic of all flies since some flies have symmetry in this region. In a sample of 2550 wild-type flies, 92.4% of individuals were found to have the AB in the right side of the brain (Pascual et al., 2004). Wild-type flies presenting symmetric structures were trained to associate an odour with an electric shock: a single training cycle was used for short-term memory testing and five individual training sessions

(15-min rest intervals) for long-term memory testing. Pascual et al. (2004) observed no evidence of 4-day long-term memory in wild-type flies with a symmetrical structure, although their short-term memory was intact. Long-term memory was formed by flies with the asymmetrical structure. Thus, brain asymmetry is not necessary for the *Drosophila* to establish short-term memory but it is important in the formation or retrieval of long-term memory.

It is difficult to make direct comparisons between the findings in fruitflies (Pascual et al., 2004) and honeybees (Letzkus et al., 2006; Rogers and Vallortigara, 2008; Frasnelli et al., 2010a,b; Rigosi et al., 2011), although lateralization is important for memory formation in both species. In fruitflies brain morphological asymmetry has been shown (Pascual et al., 2004) and this affected the ability to form memories but so far there has been no demonstration of functional asymmetry in behaviour itself. In honeybees the time-dependent recall of odour memories is lateralized (Rogers and Vallortigara, 2008) but no asymmetry of a structure in the CNS has been found.

2.10. Earwigs

Behavioural asymmetries in mating behaviour have been reported in some invertebrate species. In a study conducted on the earwig *Labidura riparia* (Insecta, Dermaptera) by Kamimura (2006) and, in particular, on the males of this species, which have two penises, nearly 90% of field-collected and laboratory-reared males hold their intromittent organs in the 'right-ready' state when not mating as well as when mating. However, not all earwig taxa have two penises, warranting more study of the earwig species. Looking at the phylogenetic relationships in this species, Kamimura (2006) suggested an intriguing evolutionary scenario: viz., male earwigs may have evolved from a primitive state in which both penises are held in the 'not-ready' orientation when they are not mating, firstly to a stage in which they always held one penis (either the right or left at random) in the 'ready' orientation. Males that still possessed two morphologically indistinguishable penises, but which preferentially held the right in the 'ready' orientation represented the next evolutionary step. Finally, the less-preferred (left) penis disappeared altogether, leaving only traces of a closed, non-functional ejaculatory duct. Thus, a purely behavioural asymmetry might have facilitated the evolution of a complete morphological asymmetry.

This is a good example of a phenotype-precedes-genotype mode of evolution because the right-ready and left-ready penis variants, which are equally common in evolutionary intermediates, and therefore probably not heritable (Palmer, 2004), clearly existed before the genetically captured right-ready phenotype appeared.

2.11. Escape responses and morphological asymmetry in shrimps and crayfishes

Takeuchi et al. (2008) conducted morphological measurements, analysed escape responses, and performed crossing experiments on lateral asymmetry in atyid shrimps. They demonstrated asymmetry in the curvature of the abdomen and laterality of the evasive responses of two atyid shrimps, *Limnocaridina latipes* and *Neocaridina denticulata* (Malacostraca, Decapoda, Atyidae). The frequency distributions of the angle of the abdominal curvature in both species were bimodal, suggesting that the two populations are composed of both left- and right-type individuals. In *N. denticulata*, behavioural analysis illustrated that the escape direction taken by each individual, when evoked by a sudden non-lateralized stimulus, was correlated with the abdominal curvature: left- (right-) type shrimps jumped backwards to the left (right) significantly more than often than expected by chance. A crossing experiment with *N. denticulata* indicated that the trait frequency in the F1 generation from two left-type parents differed significantly from that of

the F1 generation from two right-type parents, and that the trait frequency for the F1 generation from parents of different laterality types did not deviate from random. That is, offspring laterality type is affected by the lateralities of the parents, indicating that abdominal dimorphism in shrimps is genetically derived. These results suggest that shrimps have an innate laterality that controls their escape direction, which in turn may affect prey–predator interactions in the aquatic community. However, in the escape experiment conducted by these authors (Takeuchi et al., 2008), each shrimp was tested only once. It therefore remains to be determined whether the lateralized direction of an escape jump shows a consistent side bias within an individual. Replication of individual trials is necessary.

Tobo et al. (2011) investigated morphological asymmetry and behavioural laterality of a wild crayfish *Procambarus clarkia* (Malacostraca, Decapoda, Cambaridae). The morphological asymmetry was determined in 411 crayfish based on the difference in the length (specifically, the length from the orbital cavity to the posterior end of the dorsal sagittal line in the carapace) between the left and right sides of the cephalothorax. Results indicated the presence of a bimodal distribution, which is not fluctuating asymmetry but antisymmetry and suggests that the population is composed of two distinct types of individuals. In one, the right side of the carapace was larger than the left side, whereas in the other type, the left side was larger. A bimodal distribution in the direction of escape behaviours induced by a tactile stimulus was also observed in 10 individuals. Experimental crayfish were definitively divided into two groups: individuals that frequently jumped leftward (right type) and those that jumped rightward (left type). Carapace asymmetry and lateralized escape responses were significantly correlated. The results obtained by Tobo et al. (2011) suggest that crayfish exhibit left–right dimorphism in natural populations.

2.12. Claw preference in fiddler crabs

Govind (1989) noted right-claw anatomical and behavioural dominance in a crab species, suggesting stronger right than left appendage muscles similar to that in ants (an assumption based on their sharp and fast left turns). A more recent study (Backwell et al., 2007) conducted on male fiddler crab *Uca vocans vomeris* (Malacostraca, Decapoda, Ocypodidae) – a species that can be recognized by the distinctively asymmetric claws – investigated the consequences of being left-clawed in this species composed of predominantly right-clawed individuals (less than 1.4% of males are left-clawed). Left-clawed males usually fight opposite-clawed opponents. Thus, the prediction, in line with the theoretical models on the evolution of population-level asymmetries (Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009) and with the evidence in humans of the advantage conferred by being left-handed in interactive sports such as tennis or boxing (Raymond et al., 1996; Brooks et al., 2004), is that left-clawed males would be better fighters due to their relatively greater experience in fighting opposite-clawed opponents. However, the expectation did not match the results, which showed that a left-clawed male retains a burrow for a period that is significantly shorter than a size-matched right-clawed male. Moreover, when experimentally displaced from their burrow, even though no difference was found in the tactics used by left- and right-clawed individuals to obtain a new burrow, right-clawed males were significantly more likely than left-clawed males to initiate fights with resident males. In the same way, right-clawed residents engaged in significantly more fights than left-clawed residents. This occurred as a consequence of a previous observation that a significantly greater proportion of left-clawed males retreated into their burrow to observe and avoid fights. However, when a fight occurs, no significant difference in the proportion won by left- and right-clawed residents was observed. Overall left-clawed males appeared to be less likely to fight and, when they did fight, they were less

likely to win than right-clawed males. An explanation for that may be that the left-clawedness is causally related to reduced ability to fight, i.e. it is associated with developmental pathway that affects general performance. Lastly, left-clawed males might be generally inclined to avoid fights, as they are more likely to escalate an encounter with a larger opponent, which they are unlikely to defeat. The underlining strategy could be that it is easier to assess an opponent's strength when it has the same direction of clawedness (Hyatt and Salmon, 1978).

3. Mollusca: Gastropoda, Cephalopoda

3.1. Memory storage in terrestrial slugs

Studies on memory of odours have been conducted on the terrestrial slug *Limax* (Gastropoda, Limacidae, Limacinae; Matsuo et al., 2010). In this species olfaction is the most important sensory modality and this slug is capable of acquiring odour-aversion memories; i.e. when presented with the odour of food (e.g. carrot juice) in combination with an aversive odour (e.g. the bitterness of a quinidine sulphate solution), it avoids that food. Bilateral ablation of the procerebrum (PC), a secondary olfactory centre of terrestrial molluscs, is necessary for this type of learning (Kasai et al., 2006) and the PC is the site of memory storage. It has also been shown (Matsuo et al., 2010) that, when the PC is surgically ablated only unilaterally before or after conditioning, approximately half of the slugs are unable to form an odour-aversion association, whereas the other half retain unimpaired memory performance. These findings support the hypothesis that the PC only on one side, randomly determined, is used for the storage of odour-aversion memory in *Limax*. Thus, terrestrial slugs do not show lateralization at the population-level for the storage memory side, as do honeybees (Rogers and Vallortigara, 2008).

Interestingly, no transfer of the unilaterally stored memory from one PC to the other, after up to 7 days post-conditioning, has been observed. The study by Matsuo et al. (2010) shows clearly that either the left or right PC is used at random for olfactory learning. Evidence is different from that found in honeybees (Sandoz and Menzel, 2001; Rogers and Vallortigara, 2008) showing that access to unilaterally acquired memory for odours is transferred to the other side of the brain, specifically from the right to the left side (Rogers and Vallortigara, 2008). Even though no transfer has been observed in the terrestrial slugs, it is possible that odour-aversion memory in this species is transferred gradually on a longer time scale.

3.2. Chirality in pond snails

A similar behavioural asymmetry in mating behaviour, due to an anatomical asymmetry controlled by a maternal effect locus (i.e. the sinistral or dextral shell coil, or chirality, of the snail) has been observed in the pond snails *Lymnaea stagnalis* (Gastropoda, Lymnaeidae, Lymnaeinae; Asami et al., 2008; Davison et al., 2009). The pond snail *L. stagnalis* is a self-fertilising hermaphrodite; in any single mating an individual takes the male role or the female role. Breeding experiments have shown in four phylogenetically independent families of pulmonates (Wade et al., 2006) that either sinistral or dextral form is dominant in maternal inheritance (Toyama, 1913) at a single nuclear locus (Sturtevant, 1923). In other words, the coil of the shell is determined by the chirality of the maternal genotype (Boycott and Diver, 1923; Sturtevant, 1923).

Asami et al. (2008) used crossing experiments to demonstrate that the primary asymmetry of *L. stagnalis* is determined by the maternal genotype at a single nuclear locus where the dextral allele is dominant over the sinistral allele.

Davison et al. (2009) investigated the occurrence and the inheritance of a potential laterality trait in the pond snail and tried to understand whether laterality traits are associated with both body chirality and nervous system asymmetry. Dextral is dominant in *Lymnaea* (by convention D = dextral allele; S = sinistral allele). The dextral and sinistral stocks are genetically DD or SS, respectively. Mating virgin sinistral and dextral types produces offspring (F1 generation) that are genetically dextral (genotype = DS) but with a shell coil that is either sinistral (sinistral mother) or dextral (dextral mother). By allowing the sinistral F1 mother to self-fertilise, the offspring produced have a dextral coil, but are genetically DD, DS or SS (F2 generation). Dextral SS individuals were identified by virtue of their producing sinistral young.

The coiling direction of the shell of the snail playing the male role is a predictor of the direction of circling behaviour during mating and is independent of the chirality of the female. Davison et al. (2009) found that all dextral "male" snails circled in a counter-clockwise manner, no matter whether they were paired with another dextral or a sinistral snail. Similarly, all the sinistral snails, both those paired with dextral and those paired with sinistral, circled in a clockwise manner. The circling direction of the sinistral male was independent of the chirality of the female. The circling behaviour was entirely dependent on the maternal genotype, rather than the individual's own genotype. All sinistral snails (genotype DS) and dextral snails (also genotype DS) circled either clockwise or anticlockwise, respectively; all dextral snails (genotype SS) circled anticlockwise, implying that the behaviour is maternally inherited.

Chirality in mating behaviour is matched by an asymmetry in the brain. *L. stagnalis* has a ring of nine ganglia that form a central nervous system (CNS) around the oesophagus, with two more distant buccal ganglia on the buccal mass. In all dextral individuals, the right parietal ganglion is fused with the visceral ganglion and the left visceral ganglion is unpaired. By contrast, in all sinistral individuals, the reverse is observed; the left parietal ganglion is formed by fusion with a visceral ganglion. The CNS in sinistral pond snails, therefore, has an asymmetry that is the reverse of that of dextral snails. As the coil of the shell is determined by the maternal chirality genotype and the asymmetry of the behaviour is in accordance with this, it is likely that the same genetic locus, or a closely linked gene, determines the behaviour. These findings suggest that the lateralized behaviour of the snails is established early in development and is a direct consequence of the asymmetry of the body. Interestingly enough, in their study Davison et al. (2009) discovered a dextral individual with a typical "sinistral" brain. Although they were, unfortunately, not able to determine the asymmetry in the mating behaviour of this individual, the result is in line with studies in other animals, including humans, where it has been found that a variable proportion of individuals have a brain asymmetry that is not in the direction that might be expected based on their behaviour (McManus, 2002).

3.3. Asymmetric mesocerebrum in terrestrial snails

Another case of asymmetry in the nervous system is that of the snail *Helix aspersa* (Gastropoda, Helicidae; Chase, 1986). In this species, Chase (1986) showed morphological and physiological results demonstrating a right-sided bias in the mesocerebrum, which has a major role in the control of sexual behaviour. The right lobe has 23% more neurons than the left lobe, and the neurons are 24% larger. It has been observed that excitatory synaptic inputs derive predominately from neurons on the right side (Chase, 1986). Furthermore, the axons of right-side mesocerebral neurons and even those of left-side neurons travel mostly in right-side connecting nerves. Direct evidence for a role of the mesocerebrum in controlling sexual behaviour has been provided by experiments

with electrical stimulation. Thus, the asymmetry in the mesocerebrum is consistent with the fact that sexual behaviour is executed almost entirely on the animal's right side.

H. aspersa is a simultaneous reciprocal hermaphrodite. Most of the reproductive organs are located on the right side of the animal, which is reflected in the bilateral size asymmetry of the mesocerebral lobes (Chase, 1986). Koene et al. (2000) investigated the role of the right mesocerebrum in the expression of mating behaviour in this species. *In vivo* stimulation and recording techniques were used to provide evidence for both sensory and motor functions in the mesocerebral neuronal population. Results showed that electrical stimulation of the right mesocerebrum evoked genital eversion and, in combination with tactile stimulation, dart-shooting and penial eversion, suggesting that neurones of the right mesocerebrum play a key role in controlling the mating behaviour of *H. aspersa*. Moreover, the study by Koene et al. (2000) demonstrated that the peptide Ala-Pro-Gly-Trp-NH₂ (APGWamide) can mediate genital eversion in *H. aspersa*. The immunohistochemical localization of APGWamide in several additional species of gastropod mollusks suggests that the homology is robust within the class Gastropoda. The evidence provided by Koene et al. (2000) together with previous studies of mating behaviour in related gastropod mollusks (De Lange and Van Minnen, 1998) leads us to conclude that the right anteromedial region of the cerebral ganglion is an evolutionarily conserved region of the gastropod brain specialized for the control of male mating behaviour. It is striking to find such functional conservation in the CNS of phylogenetically distant gastropods given the large differences in behaviour during mating.

3.4. Asymmetric neuronal activation in molluscs

Kharchenko et al. (2010) showed that learning involves synchronous and asymmetric serotonin-dependent mitogen-activated protein kinase/extracellular signal-regulated kinase (MAPK/ERK) activation in identified neurons of the food-aversion network in the mollusc, *Helix lucorum* (Gastropoda, Helicidae). The signal transduction pathway MAPK/ERK plays an important role in the regulation of gene expression during memory formation both in vertebrates and invertebrates. In the mollusc *H. lucorum*, serotonin induces activation of MAPK/ERK in the CNS during food-aversion learning. Such learning depends on a neuronal network in which specialized neurons play distinct roles. Kharchenko et al. (2010) used serotonin application to the CNS in order to mimic learning and analysed the MAPK/ERK activation in single neurons of the food-aversion network, focusing both on command neurons, which mediate withdrawal behaviour and process information pertaining to the unconditioned stimulus, and on neurons of the pro-cerebrum, the mollusc's olfactory centre, which process information from the conditioned stimulus. Results showed that after food-aversion learning phospho-ERK levels increased significantly in RPa(2/3) command neurons of the right parietal ganglia and in the pro-cerebrum. In contrast, no activation of MAPK/ERK was detected in similar conditions in the corresponding neurons of the left parietal ganglia LPa(2/3). This finding that learning involves synchronous and asymmetric serotonin-dependent MAPK/ERK activation may correspond to a lateralization of memory processes in the mollusc brain. It may be argued that, as in nematodes (Hobert et al., 2002), in *Helix* the left and right neurons controlling avoidance behaviour may be asymmetric in the expression of some receptors connected to the intracellular MAPK/ERK cascade and thus the asymmetry is associated with the ability of molluscs to discriminate small differences in odour concentration and taste information. One more possible explanation of why the memory trace should be asymmetrical in these animals might be related to the developmental processes in gastropods, which are characterized by a visceral mass that undergoes an 180° rotation during development. A result of

such torsion is the fact that snails develop structural asymmetry with the majority of growth occurring on the left or right side.

3.5. Eye and arm preferences in octopuses

Asymmetries in eye use have been studied also in cephalopods. Byrne et al. (2002, 2004) measured preferential eye use in octopus *Octopus vulgaris* (Cephalopoda, Octopoda, Octopodidae) by recording the time animals spent watching a stimulus presented to them outside their tanks while they were holding on to the front glass of the tank. The stimulus used was a life-sized plastic model of a crab (resembling the crabs usually fed to the octopuses) mounted on a transparent stick. This was presented at five equidistant positions along the length of the tank and was held at each position for 3 min according to a random sequence, so that the time at each of the five positions was the same in order to avoid directional bias. Individuals displayed lateral preferences for either the left or right eye (Byrne et al., 2002, 2004) but the asymmetry in octopuses followed an antisymmetrical distribution, with no systematic bias towards left or right at the population-level. It is interesting to note that *O. vulgaris* is a solitary species (Hanlon and Messenger, 1998) and, therefore, an antisymmetrical distribution of preferential eye use would be not unexpected according to the reasoning outlined above for social and solitary species of Hymenoptera.

Behavioural asymmetries (left–right, anterior–posterior) in arm use have been observed in octopuses, *O. vulgaris* (Byrne et al., 2006a). Preferential use of posterior arms for walking was reported (Mather, 1998) and, in their study, Byrne et al. (2006a) tested the limb use of eight animals, seven of which had been involved in the eye preference study described above (see Byrne et al., 2004). A T-maze containing a food reward was placed in the tank so that the octopus could explore and retrieve the food from the T-maze by inserting only one arm at a time. Within each trial, the researchers scored (1) the contact arm used to first touch the T-maze, (2) the arm used in the first choice (i.e. that used to make a choice into the left or the right) and (3) the arm used in the second choice (used to search for additional food). The results showed a preference to make contact using the frontal arms (five octopuses used their frontal arms and three used their frontal arms first and then their posterior ones). Only four octopuses showed a significant preference on the first contact (two left and two right); two right-eyed animals preferred the anterior right-most arm (conventionally indicated as R1); two left-eyed preferred L2 arm. Thus, arm preference in octopuses is present at the individual-level. However, in comparison to lateral bias in eye use (Byrne et al., 2004), in which 92% of the population showed a preference to view with either the left or right eye, lateral bias in arm use was not as strong. Five subjects were tested for both eye and arm preferences: four of them exhibited a preference for the arms on the same side of the body as the preferred eye. Byrne et al. (2004) argued that lateralized eye use might depend on the task being performed because the two hemispheres of the octopus brain may control different behaviour. The experimental setup in the former study triggered an exploratory response to a prey-like object. In the latter study, the food item was visible to the octopuses through a transparent T-maze; thus the arm choice could have been influenced by the eye preference. This gives rise to the question of how strongly eye and arm choice influence each other. Byrne et al. (2006b) considered the visual–motor connections between eye and arm. They suggested that motor asymmetry may influence the choice of eye use or that lateralized eye use may influence arm preference.

To investigate these alternative possible explanations plastic objects were positioned at three different levels in a water column and the octopuses were observed during approach, contact initiation and exploration of objects. None of the seven subjects showed a left/right bias for approaching the objects, irrespective

of the position of the objects in the water column. A strong association was found between the direction of approach and the first arm used to touch the objects. The most commonly used arm was the one in a direct line between the eye being used to look at the object and the object itself. In 99% of all cases, if the object was in front of or above the octopus, the octopus used an anterior arm and, if the object was behind or below the octopus, a posterior arm was used. If the object was to the right (or left) of the octopus, a right (or left) arm was used. The results of this study indicate that octopuses most commonly use an arm to initiate contact with an object that is in a direct line between the eye used and the object. Anatomically this is a logical solution, because it would be more complicated for an octopus to use an arm that is on the other side of its body to grab an object during monocular visual exploration. However, the researchers did not investigate whether the same eye and arm coordination occurred in a more demanding task.

3.6. Side-turning preference and asymmetrical optical lobes in cuttlefishes

An asymmetry in T-maze behaviour has been reported in the cuttlefish *Sepia officinalis* (Cephalopoda, Sepiida, Sepiidae) trained to learn how to enter a dark, sandy compartment at the end of one arm of the maze (Alves et al., 2007). Fifteen cuttlefish (six adults and nine sub adults) were tested in the T-maze configuration of the cross-shaped maze. Each cuttlefish was placed individually in the start box and allowed to move freely out of the start box and into either arm of the maze. The arm choice for each of the 20 trials was recorded. Side-turning preference was determined using a criterion of 15 or more choices of the same arm (significant side-turning preference at 5% level of significance with a binomial test). The study revealed that 11 out of 15 cuttlefish displayed a pervasive side-turning preference. Interestingly, the side bias could be detected reliably in a single probe trial, i.e. during the preliminary test aimed to confirm the possible existence of a spontaneous side-turning preference in cuttlefish that could influence learning performances in a T-maze.

It is unclear at present whether the asymmetry is motor or sensory (preferential eye use) in origin. This study, and previous ones (Karson, 2003; Karson et al., 2003), used a sample size too small to establish whether lateralization was at the individual or population-level. More recent work by Alves et al. (2009) on a large sample ($N = 107$) has, however, confirmed the existence of a population-level bias; moreover, to find out whether or not visual perception plays a role in determining the direction of turning, cuttlefish were tested either inside the empty apparatus or with attractive visual stimuli (sand and shadow) on either sides of the T-maze. Alves et al. (2009) found that in both cases there was a preference to escape leftwards and this increased from three to 45 days post-hatching.

In cuttlefish, the development of side-turning preference could be linked to asymmetrical postembryonic maturation of the brain. The optic lobes are paired structures of the central nervous system in cuttlefish (Nixon and Young, 2003). It is within the outer cortex of these optic lobes that the major processing of visual information is believed to occur (Williamson and Chrachri, 2004). Axons run from the outer cortex towards a central medulla (Young, 1974), considered a visual-motor region. Electrical stimulation of the medulla evokes responses from many effectors of the body (Boycott, 1961; Sanders and Young, 1940), and induces ipsilateral rotation (Chichery and Chanelet, 1976). Alves et al. (2009) reported a correlation between side-turning bias and the size of the left and right optic lobes (OL) of cuttlefish. The authors reported a strong correlation at 30 days post-hatching between the laterality index (LI) and the ratio (volume of the right optic lobe)/(volume of the left optic lobe); the ratio decreased as the LI increased (Alves et al.,

2009). Cuttlefish with a right turning preference possess a larger left OL, and cuttlefish with a left turning preference possess a larger right OL.

A similar asymmetry has been previously observed in the squid *Histioteuthis* (Cephalopoda, Teuthida, Histioteuthidae; Wentworth and Muntz, 2009). The left eye and left optic lobes have been shown to be larger than the right ones. At the histological level, the rhabdomes of the retinas of both eyes have been shown to present the usual rectilinear pattern typical of cephalopods, but unlike other species described, the orientation of the pattern is not uniform over the retina. Wentworth and Muntz (2009) measured the optic lobes and showed that the plexiform and inner granular layers are thicker on the left side. In life it is likely that the animals orient at an oblique angle with the arms downward, and the left eye pointing upwards (possibly to detect predators) and the right eye downwards (perhaps for prey), and the asymmetries of the visual system are probably related to this posture (Wentworth and Muntz, 2009). Interestingly, no corresponding asymmetries in the statocysts or other parts of the central nervous system have been detected in the study performed by Wentworth and Muntz (2009).

4. Nematoda: *C. elegans*

The nematode *C. elegans* (Secernentea, Rhabditida, Rhabditidae) offers a unique opportunity to address the manner in which symmetrical neuronal assemblies deviate to create functional lateralization. Hobert et al. (2002) have provided a detailed cellular and molecular description of left-right (L-R) asymmetry in the nervous system of *C. elegans* (Fig. 1). In this species, 2/3 of the neurons (198 out of a total of 302) are present as bilaterally symmetrical pairs. Most of the remaining neurons, including 75 ventral nerve cord (VNC) neurons, are located on or very close to the midline, and have no contralateral analogue. Particularly intriguing components of L-R asymmetry in the *C. elegans* nervous systems are neuron pairs (or neuroblasts) that are bilaterally symmetrical in terms of their post-morphogenetic position, morphology and lineage, but at some point during embryogenesis, after bilaterality has been established, undergo L-R-specific sub-differentiation programmes.

Such a case of L-R asymmetry in *C. elegans* deriving from previously symmetrical cells is the antisymmetry in odour sensory neurons. The Amphid Wing “C” (AWC) neuron class consists of two neurons, AWCL (left) and AWCR (right), which are bilaterally symmetrical according to several distinct criteria (cell position, axon morphology, outgrowth and placement, dendritic morphology and pattern of synaptic connectivity) and are functionally symmetrical in that they express similar sets of genes and are both required for chemotaxis to specific odorants (Fig. 1). Surprisingly, Hobert et al. (2002) found that these two neurons show an asymmetrical pattern of expression of a putative G-protein coupled olfactory receptor, encoded by the *str-2* gene. The expression of *str-2* is turned on in one of the two bilateral homologues during late embryogenesis and the induction of this gene occurs stochastically in either the left or the right cell. This is a case of individual asymmetry in which the sidedness is random in a population and, thus, is classified as ‘antisymmetry’. The antisymmetry of calcium-dependent odour receptor expression in a bilaterally symmetrical *C. elegans* odour sensory neuron class is the best understood case of antisymmetry in the nervous system, in terms of functional relevance and genetic mechanisms.

In contrast, the taste receptor neurons in *C. elegans* are an example of ‘directional asymmetry’, i.e. biased forms of asymmetry. The amphid single-ciliated endings, ASEL (left)/ASER (right) neurons are the main taste receptors of *C. elegans*. ASEL and ASER are bilaterally symmetrical with regard to cell position, axon morphology,

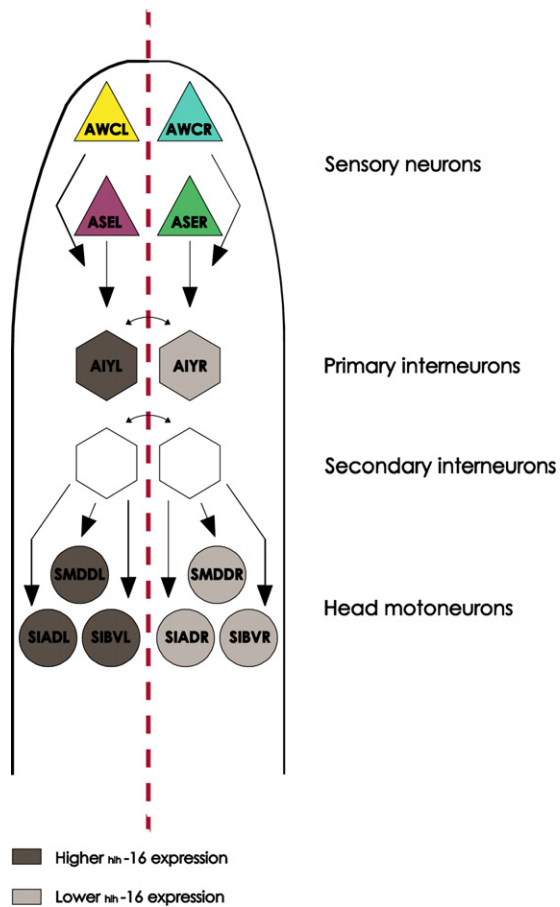


Fig. 1. Asymmetries in the nematode *C. elegans*. ASE neurons are asymmetric based on the expression of many genes, including chemoreceptors. AWC is another sensory neuron that inputs into this circuit and is L/R asymmetric (this asymmetry is, however, stochastic). *hhl-16* is asymmetrically expressed. Colour code: Dark grey = higher *hhl-16* expression; light grey = lower *hhl-16* expression.

outgrowth and placement, dendritic morphology and qualitative aspects of synaptic connectivity patterns (Fig. 1). However, three putative sensory receptors of the guanylyl cyclase class, *gcy-5*, *gcy-6* and *gcy-7*, are expressed asymmetrically in ASEL (*gcy-6*, *gcy-7*) and ASER (*gcy-5*), two to left and one to the right (Yu et al., 1997). This asymmetry of gene expression correlates with a significant functional asymmetry of the two neurons: laser-ablation studies revealed that each of the individual neurons is responsible for sensing a distinct class of water-soluble chemicals (Pierce-Shimomura et al., 2001).

A genome-wide analysis of all *gcy* genes has been undertaken (Ortiz et al., 2006) to examine the extent of lateralization of *gcy* gene expression patterns in the ASE neurons. The existence of a total of 27 *gcy* genes encoding receptor-type guanylyl cyclases and of 7 *gcy* genes encoding soluble guanylyl cyclases in the complete genome sequence of *C. elegans* has been reported. The receptor-type guanylyl cyclases have been found to be highly biased but not exclusively restricted to the nervous system: 41% (11/27) of all receptor-type guanylyl cyclases are expressed in the ASE gustatory neurons and one-third of all *gcy* genes (9/27) are expressed in a lateral, left/right asymmetric manner in the ASE neurons (Ortiz et al., 2006).

A comparative study in the related nematode *C. briggsae* (Ortiz et al., 2006) has shown that the complement of *gcy* genes in *C. briggsae* differs from *C. elegans* in chromosomal localization, number of *gcy* genes, and expression patterns. Specifically, differences in *gcy* expression patterns in the ASE neurons of *C. briggsae* arise from a difference in cis-regulatory elements and trans-acting factors

that control ASE laterality. Results (Ortiz et al., 2006) indicate the existence of a surprising number of putative chemoreceptors in the gustatory ASE neurons and suggest the existence of a substantial degree of laterality in gustatory signalling mechanisms in nematodes.

An additional asymmetry has been demonstrated in ASE chemosensory neurons (ASEL and ASER) of *C. elegans* (Suzuki et al., 2008). Optical recordings of calcium concentration in ASE neurons in intact animals have shown that ASEL is an ON-cell, stimulated by increases in NaCl concentration, whereas ASER is an OFF-cell, stimulated by decreases in NaCl concentration, with both ASE neurons reporting changes in concentration rather than absolute levels. Moreover, the ON-OFF difference is the result of intrinsic differences between ASE neurons and it extends to the level of behavioural output. Specifically, ASEL lengthens bouts of forward locomotion (runs), whereas ASER promotes direction changes (turns). The asymmetry of ASE neurons at the sensory level (ON-cell versus OFF-cell) and the behavioural level (runs versus turns) are precisely those of a simple, yet novel, neuronal motif for computing the time derivative of chemosensory information. This means that the net effect of ASE activation is a behavioural signal that approximates the time derivative of salt concentration. It is probable that the functional asymmetries of ASE neurons have emerged as a means of computing a quantity that is essential to chemotaxis in this organism. ASE asymmetry is established and maintained by a complex gene regulator network, the complexity of which could be justified by the critical role of chemotaxis in the search of food and habitat.

Ortiz et al. (2009) investigated the extent of functional lateralization of the ASE neurons and genes responsible for the left/right asymmetric activity of ASEL and ASER. They showed that a substantial number of salt ions are sensed in a left/right asymmetric manner and that lateralized responses to salt allow the worm to discriminate between distinct salt ions. Examining the chemotaxis behaviour of animals harbouring mutations in eight different receptor-type, transmembrane guanylyl cyclases (encoded by *gcy* genes), which are expressed in either ASEL (*gcy-6*, *gcy-7*, *gcy-14*), ASER (*gcy-1*, *gcy-4*, *gcy-5*, *gcy-22*), or ASEL and ASER (*gcy-19*), the authors identified the molecules involved in sensing salt ions and/or transmitting such sensory information. Disruption of a particular ASER-expressed *gcy* gene, *gcy-22*, results in a broad chemotaxis defect to nearly all salts sensed by ASER, as well as to a left/right asymmetrically sensed amino acid. In contrast, disruption of other *gcy* genes resulted in highly salt ion-specific chemosensory defects.

Recently the cellular and molecular mechanisms that lead to neuronal asymmetries in the nematode *C. elegans* have been investigated and compared to the mechanisms involved in asymmetrical neural development in the zebrafish *Danio rerio* (Taylor et al., 2010). The specification of the left and right AWC neurons of the worm olfactory system and the asymmetry in the fish epithalamus has been analysed. It has been shown that both *C. elegans* and *D. rerio* use iterative cell-cell communication, i.e. reciprocal interactions rather than a simple linear pathway, to establish left-right neuronal identity and reinforce this left-right asymmetry but with different outcomes and molecular details. The functional differences in morphologically identical neurons in the olfactory system of *C. elegans* are the result of gap-junctional communication and calcium influxes; whereas the neuroanatomical left-right differences in the epithalamus of *D. rerio* are the result of morphogenic changes regulated by secreted signalling molecules. Although it is remarkable that the two species considered share some common aspects – the interaction of neurons across the midline during formation of the asymmetrical nervous system and the inherently stochastic nature of some developmental pathway – results need to be interpreted with caution since the evolutionary gap between the

Table 1
List of the invertebrate species studied in the 51 research papers cited in the review, with a brief summary of each example of lateralization. As in the text, the species are grouped by the type of asymmetry: sensory asymmetries, motor asymmetries and asymmetries in the nervous system. For each species the level of the lateralization is reported: lateralization at the individual-level (IL) and lateralization at the population-level (PL) and a brief description of the sociality degree: eusocial (EUSOC), social (SOC), sub-social (SUBSOC), solitary (SOL).

Species	Evidence	Level	Sociality	References
Trilobites fossil record	Asymmetric distribution of predation scars	PL		
Honeybee <i>A. mellifera</i>	Asymmetry in olfactory responses, electrophysiology and morphology of antennae Shift of recall of olfactory memory Asymmetry in visual responses Asymmetry in the <i>neuroligin 1</i> expression	PL	EUSOC	Letzkus et al. (2006, 2007) Rogers and Vallortigara (2008) Frasnelli et al. (2010a,b) Rigosi et al. (2011) Anfora et al. (2010) Biswas et al. (2010)
Bumble bee <i>Bombus spp</i>	Asymmetry in circling around a vertical inflorescence Asymmetry in olfactory response and in the number of olfactory sensilla	PL	SOC	Kells and Goulson (2001)
	Asymmetry in the electrophysiology of the antennae	IL		Anfora et al. (2011)
Mason bee <i>O. cornuta</i>	Asymmetry in the electrophysiology of antennae	IL	SOL	Anfora et al. (2010)
Australian stingless bee <i>T. carbonaria</i>	Asymmetry in olfactory responses	PL	Primitive SOC	Frasnelli et al. (2011)
Australian stingless bee <i>T. hockingsi</i>	Asymmetry in olfactory responses	PL	Primitive SOC	Frasnelli et al. (2011)
Australian stingless bee <i>A. australis</i>	Asymmetry in olfactory responses	PL	Primitive SOC	Frasnelli et al. (2011)
Ants <i>L. niger</i> (Formicidae)	Asymmetry in the choice of a preferential path in foraging and in alarm situations	PL	EUSOC	Heuts et al. (2003)
Spiders (Araneae)	Asymmetry in the leg-use in predation	PL	SOL	Heuts and Lambrechts (1999)
Splitting spider <i>S. globula</i>	Asymmetry in the leg-use in prey handling and in touches during predatory encounters	PL	SOL	Ades and Ramires (2002)
American cockroach <i>Periplaneta americana</i>	Motor bias	PL	SUBSOC	Cooper et al. (2010)
Desert locusts <i>S. gregaria</i>	Asymmetry in the preference for response by leg after lesion	Not investigated (Not significant sample size)	SOLGregarious	Rowell (1964)
Cricket <i>G. campestris</i>	Asymmetry in the wing orientation during calling songs	PL	SUBSOC	Elliott and Koch (1983)
Australian bushcricket <i>R. verticalis</i>	Asymmetry in the hearing system	PL	SUBSOC	Bailey and Yang (2002)
Water bug <i>C. punctata</i>	Physiologically asymmetrical ears Asymmetry of the receptor cells A1	PL	SOL	Prager and Larsen (1981) Prager and Streng (1982)
Giant water bug <i>B. flumineum</i> Say	Asymmetry in the preferential direction of turning	PL	SOL	Kight et al. (2008)
Fruitfly <i>D. melanogaster</i>	Asymmetry in the olfaction during flight	PL	SOL	Duistermars et al. (2009) Louis et al. (2008) Pascual et al. (2004)
	Asymmetry in the larval olfactory system Asymmetry in the position of the round body Correlation with ability to form long-term memory			
Earwig <i>L. riparia</i>	Asymmetry in penis-use	PL	SUBSOC	Kamimura (2006)
Atyid shrimp <i>L. latipes</i> and <i>N. denticulata</i>	Lateralized escape response Corresponding morphological asymmetry of the abdomen	IL	SOL	Takeuchi et al. (2008)
Crayfish <i>Procambarus clarkii</i>	Lateralized escape response Corresponding morphological asymmetry of the carapace	IL	SOL	Tobo et al. (2011)
Fiddler crab <i>U. vocans vomeris</i>	Asymmetry in claw size	PL	SOL	Govind (1989) Backwell et al. (2007) Matsuo et al. (2010)
Terrestrial slug <i>Limax</i>	Asymmetry in the storage memory side Correlation with the long-term memory	IL	SOL	
Pond snail <i>L. stagnalis</i>	Asymmetry in the chirality and mating behaviour	PL	SOL	Asami et al. (2008) Davison et al. (2009)
Snail <i>H. aspersa</i>	Corresponding brain asymmetry Asymmetry in the mesocerebrum Correlation with the side of the sexual behaviour Role of the asymmetry in the control of mating behaviour	PL	SOL	Chase (1986) Koene et al. (2000)
Mollusc <i>H. lucorum</i>	Asymmetric serotonin-dependent MAPK/ERK activation involved in learning process Possible lateralization of memory processes		SOL	Kharchenko et al. (2010)
Octopus <i>O. vulgaris</i>	Asymmetry in the eye-use Asymmetry in arm-use Asymmetry in the connection between arm and eye-use	IL	SOL	Byrne et al. (2002, 2004) Byrne et al. (2006a,b), Mather (1998)

Table 1 (Continued)

Species	Evidence	Level	Sociality	References
Cuttlefish <i>S. officinalis</i>	Asymmetry in the side-turning preference Correlation with the size of the optical lobe	PL	SOL Aggregations	Alves et al. (2007, 2009)
Squid <i>Histioteuthis</i>	Asymmetry in the size of the eye and optical lobe	PL	SOL Schooling	Wentworth and Muntz (2009)
Nematode <i>C. elegans</i>	Asymmetry in odour sensory neurons AWC Asymmetry in taste receptor neurons ASE Lateralized responses to salt allow the worm to discriminate between different salt ions L/R asymmetrically expressed Beta3/Olig-type bHLH transcription factor <i>hlh-16</i> Asymmetry in the soma size of ASE neurons	IL PL	SOC/SOL	Hobert et al. (2002) Hobert et al. (2002) Ortiz et al. (2006, 2009) Suzuki et al. (2008) Bertrand et al. (2011) Goldsmith et al. (2010)
Bilateria	Ancestral feature of involvement of the Nodal pathway in the left–right asymmetries			Grande and Patel (2009)

302 neurons of the worm and the estimated 78,000 neurons of the larval fish (Hill et al., 2003) is considerable. However, even if the striking differences in the genetic and cellular pathways underline the improbability that nematode and zebrafish lateralization arose from the same ancestral event, because of the advantages conferred by asymmetrical neural systems it is possible to assume that the left–right differences in the two species have evolved convergently.

Very recently, Bertrand et al. (2011) investigated the extent of neuronal asymmetry in the *C. elegans* nervous system, beyond the ASE and AWC neurons. Bertrand et al. (2011) reported that the Beta3/Olig-type bHLH transcription factor *hlh-16* is L/R asymmetrically expressed in several distinct, otherwise bilaterally symmetric interneuron and motor neuron pairs that are part of a known navigation circuit (Fig. 1). Specifically *hlh-16* asymmetry is generated during gastrulation by an asymmetric LAG-2/Delta signal originating from the mesoderm that promotes *hlh-16* expression in neurons on the left side through direct binding of the Notch effector LAG-1/Su(H)/CBF to a *cis*-regulatory element in the *hlh-16* locus. Removal of *hlh-16* revealed an unanticipated asymmetry in the ability of the axons of the AIY interneurons to extend into the nerve ring, with the left AIY axon requiring elevated *hlh-16* expression for correct extension. The study by Bertrand et al. (2011) suggests that the extent of molecular L/R asymmetry in the *C. elegans* nervous system is broader than previously anticipated, establishes a novel signalling mechanism that crosses germ layers to diversify bilaterally symmetric neuronal lineages, and reveals L/R asymmetric control of axonal outgrowth of bilaterally symmetric neurons.

The reported studies (Hobert et al., 2002; Ortiz et al., 2006, 2009; Suzuki et al., 2008; Bertrand et al., 2011) showed that *C. elegans* serves as a good model to investigate the problem of neuronal left/right asymmetry. However, even though the neuronal anatomy has been described in detail, neuronal size has not been studied in any great depth in *C. elegans*. Goldsmith et al. (2010) investigated whether a pair of functionally lateralized chemosensory neurons, the ASE neurons, display some size differences. ASE and ASER have been found to differ substantially in size: the volume of the soma of the ASER neuron is more than 30% larger than that of ASE. Interestingly, Goldsmith et al. (2010) also examined the AWCL/R olfactory neuron pair, that is known to be functionally lateralized (Hobert et al., 2002), and they found that none of these neurons showed, on average, any indication of a consistent laterality in soma size. Note that AWCL/R asymmetry is an 'antisymmetry' (i.e. stochastic), whereas ASE/R is a 'directional asymmetry' (i.e. deterministic). A lack of directional asymmetry in AWCL/R neurons means that it is not simply the case that one side of the nematode is larger than the other, but rather that neuron size is regulated in a neuron-type-specific manner. The difference in size between ASE and ASER has been found to be independent of activity (i.e. it does not depend on sensory input), but developmentally controlled. A pathway of gene regulatory factors controls both size laterality and

left/right asymmetric chemoreceptor expression of the ASE/R neurons. The transcriptional regulator that controls size laterality has been identified in the Zn finger transcription factor *die-1*. Moreover, Goldsmith et al. (2010) linked genetic mechanisms that control functional lateralization to lateralized size control. The functionally fibrillar gene *fib-1* gene has been shown to be a gene required for ASE/R size laterality, providing the first direct implication of fibrillar in cell size control.

To conclude this section about the nematode, it is important to mention the constraints present in *C. elegans* due to the very small number of cells: left/right differences may be needed to generate enough different cell types (e.g. chemoreceptors). However, we would like to point out that the same constraint could be present and operate in larger brains too.

5. Summary

All the evidence of the 51 research papers cited in this review reporting brain and behavioural asymmetries in invertebrates is summarized briefly in Table 1.

It seems that invertebrates not only share the characteristic of lateralization with many vertebrates but may also show some similarities in its appearance.

This raises the question of whether lateralization is determined by homologous genes in invertebrates and vertebrates (Vallortigara and Rogers, 2005) or whether there has been analogous evolution of lateralized function in the two subphyla. We think it is most likely that the latter occurred, but presently we are not aware of evidence in favour or against this idea, although new insights into the evolution of body plans and left–right specification in Bilateria have been recently provided (Grande and Patel, 2009). The signalling molecule Nodal, a member of the transforming growth factor- β superfamily, is involved in the molecular pathway that leads to left–right asymmetry in vertebrates and in other deuterostomes, but no nodal orthologue had been reported previously in the two main clades of Bilateria: Ecdysozoa (including flies and nematodes) and Lophotrochozoa (including snails and annelids). Grande and Patel (2009) reported the first evidence for the presence of a nodal orthologue in a non-deuterostome group, indicating that the involvement of the Nodal pathway in left–right asymmetry might have been an ancestral feature of the Bilateria. Furthermore, this study suggests that nodal was present in the common ancestor of bilaterians and it too may have been expressed asymmetrically.

As mentioned before, theoretical models based on Game Theory have been developed to account for the evolution of population-level asymmetry in vertebrates (Vallortigara and Rogers, 2005; Vallortigara, 2006; Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009). The basic idea is that, whereas asymmetry may confer an advantage at the individual-level (associated with the computation carried out by the brain, e.g. Rogers et al., 2004), the alignment of asymmetries at the population-level could be the

outcome of selective pressures associated with social behaviour (even in its simplest forms), i.e. pressures associated with the need for individuals to align with the direction of asymmetries of the group or species. These models could explain the presence of stable polymorphisms in the populations, with a minority of individuals showing lateralization in the opposite direction than in the majority (as in the case of left-handed humans), maintained by frequency-dependent selection (Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009). In principle, the hypothesis would hold true irrespective of whether asymmetries in vertebrates and invertebrates are homologous or analogous phenomena. Thus, it is interesting to discuss whether lateralization is more likely to be found in social than in solitary species of invertebrates.

The evidence of behavioural and brain asymmetries reported here includes several phyla of invertebrates: Arthropoda (subphylum Chelicerata, class Arachnida; subphylum Hexapoda, class Insecta; subphylum Crustacea, class Malacostraca), Mollusca (classes: Cephalopoda, Gastropoda), Nematoda. A direct link between the level of the lateralization (individual-level versus population-level) and the level of sociality has been argued for the order Hymenoptera.

The fruitfly *D. melanogaster* shows population-level asymmetry although the fruitfly does not behave as a gregarious species. It is more likely to be considered a solitary species. However, aggregation tendency in small groups of *D. melanogaster* has been documented (del Solar Osses, 1998). In particular, the most widely studied expression of this gregarious behaviour is selection of an oviposition site. Moreover, many species of fruitfly also aggregate on mating sites (Starmar et al., 2000). It has been hypothesized that these gregarious distributions could contribute to local genetic differentiation (del Solar Osses, 1998). Hence, a case can be made for social behaviour in *Drosophila* being linked to the population-level lateralization.

Cockroaches, also showing population-level lateralization, are gregarious sub-social insects (Choe and Crespi, 1997). The octopus, in contrast, exhibits individual-level asymmetry and it is a solitary species.

The locust *S. gregaria* shows pronounced handedness but the sample size used did not allow evaluation of the level of the asymmetry. This species should be considered, however, for future studies on the connection between sociality and level of lateralization since it is a species that changes its degree of sociality (from solitary species to gregarious species) on the basis of ecological factors (Simpson et al., 2002). The cricket *G. campestris* exhibits a population-level asymmetry in the wing orientation during calling songs. This species is considered sub-social (Choe and Crespi, 1997). The same speculation can be made concerning the sub-social related species, the Australian bushcricket *R. verticalis* that shows a population-level asymmetry in the hearing system.

The ant *L. niger* presents a population-level bias in the choice of a preferential path (right-biased) in foraging and an opposite bias (left-biased) in alarm situations. As in bees, ants are highly social insects belonging to the order Hymenoptera and, also as in honeybees and Australian stingless bees, they are lateralized at the population-level. On the other hand, spiders (*Araneae*), which are solitary species, show a population-level asymmetry in the leg-use in predation, as also splitting spiders *S. globula* show population-level asymmetry in the leg-use in prey handling and in touching during predatory encounters. This evidence does not support the hypothesis unless the aggressive interactions that occur between spiders provide sufficient social pressure to align the direction of lateralization.

The fiddler crab *U. vocans vomeris* is a species in which 98.6% of the individuals are right-clawed. They live in solitary burrows and their social interactions are limited to fights between males. As in spiders, this appears to be the kind of social interaction that may

require an alignment of the asymmetry in the population. On the contrary, the atyid shrimp *L. latipes* and *Neocaridina denticulate* and the crayfish *P. clarkia* display an individual-level lateralized escape response, corresponding to a morphological asymmetry. Both these Decapoda species are solitary. However, eight apparently innate components of social interactions have been described for the primary burrowing crayfish, *Procambarus gracilis* by Hayes (1975): alert, approach, threat, combat, submission, avoidance, escape and courtship.

The earwig *L. riparia* shows a preference in the penis used in mating. Interestingly not all the earwig species have two penises; it seems that a purely behavioural asymmetry (the preferential use of one penis) might have facilitated the evolution of the morphological asymmetry. Earwigs are among the few non-social insect species that show maternal care (Gullan and Cranston, 2005) and because of this they are considered a sub-social species (Choe and Crespi, 1997). However, the lateralized behaviour described here is related to mating by earwig males and not to females. For this reason it can be hypothesized that this lateralization at population-level is connected to the social aspect of this specific lateralized behaviour.

Likewise, the pond snail *L. stagnalis* has population-level asymmetry in chirality and mating behaviour and has a corresponding brain asymmetry. As in all snails, this species is considered to be non-social. Interestingly, it has been shown that snails are capable of social enhancement since they are attracted to feeding conspecifics, to under-grazed areas, and are capable of long-term retention of food cues towards preferred feeding substances (Suboski, 1994; Suboski et al., 1993). Perhaps, as for the earwig, it could be that the population-level asymmetry of this species is connected with mating.

The water bug *C. punctata* possesses physiologic asymmetrical ears, a lateralized trait which is consistent in the population. The giant water bug *Belostoma flumineum* Say, an evolutionary linked species, is a solitary species of the Insecta class but it shows paternal care (Choe and Crespi, 1997). This species is lateralized at the population-level in the preferential direction of turning. Such a turning preference is also the case in the cuttlefish *S. officinalis*. Cuttlefishes are solitary most of their lives with aggregations typically found only at the time of spawning; recognition ability appears to be limited to sex, i.e. male versus female, and perhaps social dominance, i.e. dominant versus subordinate (Boal, 2006). Similarly the squid *Histioteuthis*, that shows a population-level asymmetry in the size of the eye and the optical lobe, is a solitary species that schools when young before becoming solitary later in life (Pitcher and Parrish, 1993). Thus in water bugs, cuttlefishes and squids the population-level asymmetry observed may be related to some social aspects of their behaviour.

On the other hand the solitary terrestrial slug *Limax* has individual-level asymmetry in the side of memory storage. The solitary hermaphrodite snail *H. aspersa* exhibits a population-level asymmetry in the mesocerebrum, asymmetry that is linked to the side of sexual (social) behaviour. Another solitary species of Gastropoda, the mollusc *H. lucorum* shows asymmetric serotonin-dependent MAPK/ERK activation involved in a learning process that is likely to be connected to a possible lateralization of memory processes.

The nematode *C. elegans* offers a unique example of both individual-level and population-level asymmetries. In fact, this worm exhibits individual-level asymmetry in the odour sensory neurons AWC and a population-level asymmetry in the taste receptors neurons ASE. Moreover, lateralized responses to salt allow the worm to discriminate between distinct salt ions. Natural *C. elegans* isolates exhibit either social or solitary feeding on bacteria (De Bono et al., 2002). It has been shown that social feeding is induced by nociceptive neurons that detect adverse or stressful

conditions; ablation of these neurons (ASH and ADL) transforms social animals into solitary feeders (De Bono et al., 2002). We are not aware about possible asymmetry in the ASH and ADL neurons that may be related to the role of these neurons in social behaviour. In the *C. elegans* nervous system diversification of sensory function has been possible thanks to diversification across the L–R axis. This underlines the importance of the evolution of lateralization since a symmetrical body axis could result in redundancy of L–R structures and may not have led to the resulting benefit of the establishment of novel functions (as in the diversification of sensory function in the case of the nematode). Moreover, the findings of Ortiz et al. (2009) broaden our understanding of lateralities in neural function, providing insights into how this laterality is encoded at the molecular level, and revealing an unusual range of molecules involved in gustatory signal transduction.

We have mentioned several examples that support the idea predicted by the theoretical model on the evolution of asymmetries, namely that lateralization at the population-level is more likely to evolve in social species, whereas lateralization at the individual-level is more likely to evolve in solitary species. Specifically, bees, ants, cockroaches, crickets, earwigs are social species (gregarious behaviour) showing a population-level lateral bias, whereas octopuses, terrestrial slugs, shrimps and crayfishes are solitary species showing individual-level asymmetries. However, there are a few not predicted examples of solitary species showing population-level asymmetries: spiders, water bugs, fruitflies, crabs, snails, cuttlefishes and squids. As already argued, the population-level asymmetries exhibited by these species are connected with mating or social aspects (such as schooling, recognition ability of conspecifics and social feeding) or aggressive interactions (such as fighting and escape behaviour) and thus they may be explained by the interactions these solitary species have with conspecifics or predators.

Moreover, regarding the solitary individuals that show population-level asymmetry, it is interesting to consider a different point of view: sociality may be a common feature in the ancestor (see Vallortigara and Rogers, 2005). In general, evaluating the role of sociality in generating consistent asymmetry makes too much of possible special reasons why in some cases solitary species show population-level asymmetry. Thus, it seems more plausible that sociality may be an important feature in some specific groups such as Hymenoptera.

In conclusion, lateralization of both function and structure, at the individual and population-level, is commonly observed among invertebrates. The relative simplicity of the nervous systems and behavioural patterns of these organisms could make them ideal experimental subjects to elucidate basic neurobiological and ecological mechanisms of brain asymmetries.

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