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Laterality in vertebrates and invertebrates: linked or different?

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QUESTION

Is there a link between lateralized behaviour in vertebrates and invertebrates?

ABSTRACT

This paper compares lateralized behaviour in invertebrates and vertebrates and considers whether any similar patterns indicate homology or are examples of convergent evolution. It covers evidence for left-right asymmetries of memory consolidation, approach and withdrawal in social, predatory and predation situations, aggressive behaviour and sexual behaviour. Although the pattern of these asymmetries in the brains of vertebrate species is the mirror image of the pattern in invertebrates, the direction of behavioural asymmetry matches since sensory inputs cross the midline in vertebrates (for vision) but not in invertebrates (for olfaction and vision). Similarities in the lateralization pattern in vertebrate and invertebrate species suggest that a basic plan of lateralized brain function may have been conserved during the transition from invertebrates to vertebrates.

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INTRODUCTION

Over the last five decades, asymmetry of brain function and behaviour has been found in a wide range of vertebrate species and, in recent years, it has been reported also in invertebrate species [1]. Quite unexpectedly, even invertebrates that are considered to be radially symmetrical in body structure express asymmetry of behaviour, as in spiders that prefer to use their left legs for predatory responses [2] and, as in eye preferences of octopuses at the individual but not population level [3,4]. Eye preferences are also present in other invertebrate species, as reported recently in species of crab [5]. The question that now arises is whether some of the lateral asymmetries known in vertebrate species have originated from lateralities already present in invertebrates or, alternatively, whether the two expressions of asymmetry represent homoplasy (convergent evolution) and not homology (evolved from a common ancestor).

The transition from invertebrates to vertebrates involved radical changes in the nervous system's organisation [6,7], as well as the shift from an exoskeleton to an internal skeleton with a notochord or vertebral column. This evolutionary step required reshaping of the genome, which included two-fold duplication of the whole genome coupled with changes in protein coding [8] and a change from mosaic, or no, methylation of the genome in invertebrates to genome-wide methylation in vertebrates [9]. Despite these pervasive changes that took place in the transition from invertebrates to vertebrates, does asymmetry in invertebrates and vertebrates share some commonalities in gene expression and/or in structural and functional manifestations of laterality? Although some investigators consider that vertebrate and invertebrate nervous systems evolved independently, others see similarities in expression of genes controlling development and inducing neural patterning, and hence neural circuity, in vertebrates and invertebrates [10-12].

Signore et al. [13] have proposed that signalling by the transforming growth factor, Nodal, plays a vital role in the development of asymmetry of the nervous system in both invertebrates and vertebrates. Other researchers describe similar expression of specific genes associated with particular types of behaviour in both invertebrates and vertebrates. An example is the report of common molecular mechanisms associated with “autism-like behaviour” in bees and humans [14], although, at this stage of knowledge, it is uncertain whether the behaviour of the bees in this study has any genuine similarity to autistic behaviour in humans. Nevertheless, there is considerable interest to find models of human behaviour in lower vertebrates and invertebrates since this might provide simpler systems to investigate and simpler methods of doing so. Does the same apply to the study of lateralized brain mechanisms and behaviour?

Our knowledge of the genes expressed in specific types of lateralized behaviour is, at this stage, insufficient to answer with any certainty the question of similarity or difference in the molecular mechanisms associated with lateralization of brain and behaviour in vertebrates versus invertebrates. We can, however, examine the differences and similarities in expression of lateralized behaviour in vertebrates and invertebrates. The following categories of behaviour permit us to explore this question; they are hemispheric differences in memory storage, side differences in approach versus withdrawal behaviour and side biases in agonistic and sexual behaviour.

SHORT-TERM AND LONG-TERM MEMORY

Vertebrates

The first evidence that long-term memory (LTM) and shorter-term memory (STM) are located in different regions of the brain came from research on imprinting memory in chicks (*Gallus gallus domesticus*) conducted by Gabriel Horn and colleagues at Cambridge University (summarised in [15,16]). A body of studies showed that a region in both sides of the chick forebrain, the

intermediate and medial mesopallium (IMM), formerly known as the intermediate and medial hyperstriatum ventral (IMHV), is essential for the acquisition of imprinting and for recall of imprinting memory for up to 6 hours after exposure to the imprinting stimulus: during this period, chicks with lesions of both the left and right IMM regions are unable to recall the imprinting memory. However, the role of the right IMM in recall of the memory is only for a relatively short-term and, after 6 hours, a LTM is established in a site located elsewhere in the forebrain, most probably in the right hemisphere. Consequently, memory recall following a delay of more than 6 hours after training is unaffected by lesions of both the left and right IMM regions.

These left-right differences in imprinting memory storage were subsequently supported by studies of subcellular changes following imprinting. For example, the area of post-synaptic density in excitatory synapses was shown to increase in the left IMM, but not the right IMM, where the post-synaptic density decreases [17,18]. This change in synaptic density is paralleled by increased density of the excitatory neurotransmitter, N-methyl aspartate, in the left IMM only [19]. To summarise, these and other subcellular changes [20] are evidence that imprinting and STM recall of imprinting are functions of the left hemisphere, whereas the right hemisphere is the site of LTM of imprinting (Figure 1).

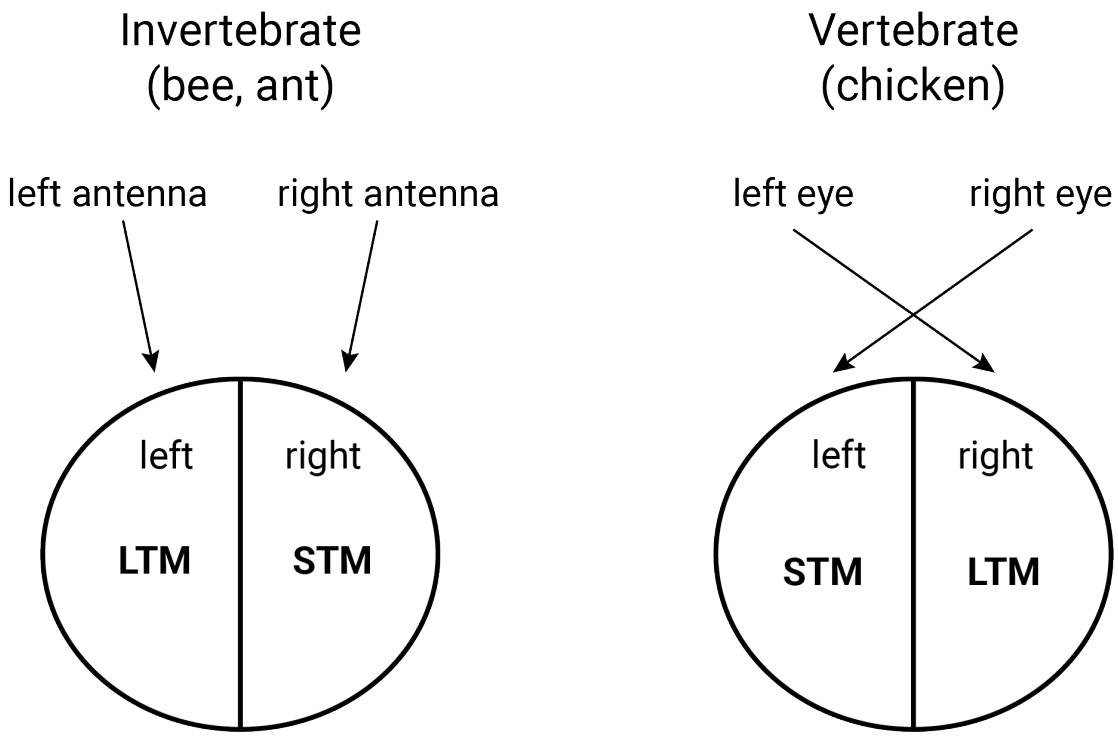

Figure 1 - The general pattern of asymmetry for short-term (STM) and long-term memory (LTM). The bisected ellipses represent the left and right sides of the brain (hemispheres in the case of vertebrates). The arrows represent the sensory inputs to the brain: note that they do not cross the midline in invertebrates (for olfaction) but do cross it in vertebrates (for vision). In both invertebrates and vertebrates the right side of the animal has access to STM, and the left side has access to LTM.

Similar lateralization of memory has been shown for another task, passive avoidance learning. In this task, a chick is presented with a bitter-tasting bead which has a specific colour

(usually red) and the chick shows memory of this aversive experience by subsequently failing to peck at a clean bead of the same colour, whereas it will peck at a bead of a different colour. [Note that this task relies on visual information and visual input from each eye crosses the midline to go to the hemisphere on the opposite side, as shown in Figure 1, on the right side.] For up to one hour following training, structural and molecular changes associated with memory formation of this task occur in the left IMM but not in the right IMM [21] (reviewed in [22]). When the delay between training and recall is several hours longer, changes in synapse structure and in the levels of particular neurotransmitters occur in the right IMM, and not in the left IMM [23-25]. Thus, similar to imprinting memory, following passive avoidance learning STM is located in the left hemisphere and LTM in the right hemisphere. It needs to be said that the terms shorter-term memory (STM) and long-term memory (LTM) are used in this paper in reference to timing of one versus the other, not as absolutes related to specific cellular and subcellular processes of memory formation.

The next question to consider is how the left-right asymmetry in memory distribution might affect recall in chicks using both eyes and hence with potential access to memory traces located in both hemispheres. Andrew [26] examined interactions between memory traces in the left and right hemispheres at various times after training, and showed the existence of cycles of good and poor retrieval. To simplify the evidence, such cycles occur across time after training first with events in the left hemisphere and later with events in the right hemisphere (for details see [26,27]). This translates into preferred use of the right eye (left hemisphere) to view a training stimulus, such as the red bead used in passive avoidance learning, in the initial phase of memory formation (STM), followed by preferred use of the left eye (right hemisphere) when the LTM store has to be accessed. Without going into detail of differing cycles in the left and right hemispheres or interhemispheric transfer, here it is noted that the research by Andrew illustrates the way in which behaviour of the whole animal is influenced by the different roles of the left and right hemispheres in STM and LTM, respectively.

Not only is time after training a factor contributing to laterality of memory formation and retrieval but, as shown by a body of research, the left and right hemispheres attend to different aspects of a stimulus and process this information differently [28,29]. Thus, the hemispheres differ in how they process sensory inputs and also in their different abilities to access memory. Such lateralization has also been shown for song learning and recall in certain species of songbird (summarised in [30]).

In rats, however, there is evidence that the hippocampal region of the left hemisphere is essential for recall of LTM, whereas the hippocampal regions in both hemispheres are involved in STM [31,32]. Although this demonstrates lateralization of memory formation in a mammalian

species, the direction of laterality is opposite that in the chick. Clearly, further research on different species and on different types of memory is needed.

Invertebrates

The first study revealing asymmetry of memory recall in an invertebrate was conducted on the fruitfly, *Drosophila melanogaster*. Pascual et al. [33] found the LTM recall of a task requiring the association of an odour with and electric shock was possible only by fruitflies that had a particular structure located asymmetrically in the right hemisphere of the brain, close to the pathway connecting the left and right hemispheres. The structure is called the 'asymmetrical body'. Fruitflies without this structure can recall STM (at 3 hours after training) but not LTM (4 days after training). The researchers concluded that brain asymmetry was required for retrieval of LTM but not STM. The study did not determine whether the left or right side of the brain is essential for recall of LTM but indicated that the 'asymmetrical body' might have a role in communication between the hemispheres.

Lateralization of memory formation and recall has more recently been investigated in the honeybee, *Apis mellifera*. This species shows lateralization of STM and LTM, each accessed via a different antenna and from a different side of the brain. Rogers and Vallortigara [34] trained honeybees to associate a specific odour (e.g., vanilla) with a sugar reward and then tested recall of the memory at different times after training. The bees were trained using both antennae and then tested for recall via only one antenna (the other antenna being rendered unable to detect odours by coating it with a silica gum). Recall was scored as the extension of the proboscis, indicating the bee's expectation to ingest the sugar liquid. Provided they were using their right antenna (left antenna coated) they could recall STM at 1 hour after training. LTM tested at 6 and 23 hours after training could be recalled only via the left antenna (right antenna coated). In other words, the right antenna and its neural connections in the brain can recall only STM and the left antenna and its neural connections can recall only LTM (Figure 1).

This lateral asymmetry depends on competition between inputs from the left and right antennae since Letzkus et al. [35] found that honeybees trained and tested for recall with only the right antenna (the left coated with the silica gum) were able to recall the association between an odour and a sugar reward after an interval of 23-24 hours (i.e., LTM) but not when they were trained using only their left antenna. Hence, it is possible for LTM to be established on the right side provided that the bee is forced to use only its right antenna in training. In this case, the untrained left antenna has no access to this LTM. Only when both the left and right antennae are used in training does the left antenna gain the ability to recall LTM and it does so at the expense of the right antenna being able to do likewise [34]. The left side of the brain must compete with the right side for storage and recall of LTM.

These asymmetries of olfactory memory in honeybees are matched by asymmetry of olfactory coding in the antennal lobes [36] and left-right differences in the expression of genes [37]. In addition, the right antenna is more responsive to presentation of sucrose and it is also more resistant to habituation than is the left antenna [38]. All of these studies provide support for the asymmetry of memory recall by honeybees.

Stingless bees, which are social but more primitive than honeybees, have the same laterality for recall of olfactory memory. Frasnelli et al. [39] tested three species of stingless bees (*Trigona carbonaria*, *T. hockingsi* and *Austroplebeia australis*) and in all three species recall of STM was possible only via the right antenna, whereas LTM could be recalled only via the left antenna.

Furthermore, in wood ants, *Formica rufa*, memory of a visual stimulus associated with a sugar reward is lateralized, similarly to the lateralization of olfactory memory in bees. Fernandes and Niven [40] found that the right antenna has access to STM, up to an hour after training in which both eyes saw the visual stimulus but only the right antenna received the sugar reward. Rewarding the left antenna allows the left antenna to have access to LTM (present at 24 hours) even though it has no access to STM. This, therefore, is another example of STM on the right side of the central nervous system and LTM on the left side.

Comparison of invertebrate and vertebrate direction of laterality

Here only the research on lateralized memory in the chick will be compared to the five species of invertebrate discussed above. It is, of course, recognised that the location of STM and LTM in more vertebrate species needs to be investigated.

The direction of the asymmetry for STM recall versus LTM recall found in invertebrate species trained on an odour-association task appears, at least initially, to be in the opposite direction to that found in chicks. On face value, this would suggest separate paths of evolution in invertebrates and vertebrates (homoplasy), both achieving left-right asymmetry for encoding STM and LTM. However, something extra evolved in primates and that was the midline crossing of all sensory inputs, except for olfactory inputs. In vertebrate species with their eyes positioned on the sides of their head, as in chicks and many other vertebrate species, visual inputs from the left eye go to the right side of the brain and vice versa.

Considering the cross-over of visual inputs in the chick, the link between right eye access to STM in the left hemisphere versus left eye access to LTM in the right hemisphere is equivalent to right-side sensory access to STM and left side sensory access to LTM in invertebrates (Figure 1). Hence, in both invertebrates and vertebrates, sensory receptors on the right side of the animal

can access STM, whereas sensory receptors on the left side can access LTM. Given this similarity between invertebrates and vertebrates, a case for homology may be a possibility.

SOCIAL APPROACH OR WITHDRAWAL

Vertebrates

In vertebrate species, withdrawal from a threatening stimulus is elicited by visual input to the right hemisphere. This has been demonstrated in three species of toad [41] and a marsupial, the dunnart [42]. Both species were tested with a model snake that moved towards the animal being tested on its left or right side. Escape responses occurred sooner and more strongly when the model predator approached on the test animal's left side, indicating that the right side of the brain controls avoidance of predators [41,42]. The same left eye and right hemisphere laterality is found in domestic chicks, in this case tested by "flying" a model predator overhead at a time when the chick was searching for food: the chick was more likely to detect the predator when it entered the visual field of its left eye than when it entered the visual field of the right eye [43].

Other species also are more reactive to a threatening stimulus on the left side, as found in magpies [44,45], lizards [46], cattle [47] and horses [48]. Also, the zebra finch has a preference to view a predator using the left eye and right hemisphere [49]. In all these examples, use of the left eye means that the right hemisphere is detecting and controlling response to the model predator.

In contrast, the right eye and left hemisphere of the vertebrate brain is specialised for approach and pursuit of potential food. This has been shown in chicks [50], the zebra finch [51], the zebrafish [52], toads [53,54] and lizards [55]. For example, chicks using their right eye and left hemisphere, but not those using their left eye and right hemisphere, can distinguish food grains from inedible pebbles [50,56]. Likewise, toads strike at prey that have moved into their right hemifield but not at prey in their left hemifield [57].

The right hemisphere is also specialised for social behaviour as revealed by a preference of maternal animals, in many mammalian species, to keep their offspring on their left side [58,59]. Fish also prefer to keep conspecifics on their left side [60-62]. The processing of social information (e.g., recognition of companions and of faces) has been investigated in chicks and they too carry out these functions using their right hemisphere, hence with a left-eye preference [63,64].

In summary, the complementary specializations of the hemispheres of the vertebrate brain are left hemisphere for approach (as in seeking food or a companion) and right hemisphere for withdrawal (as in escape from a predator).

Invertebrates

Laterality of approach versus withdrawal has also been studied in invertebrates. Honeybees presented with the odour of their alarm-pheromone (iso-amyl acetate) turn away when they detect it with their left antenna and towards it when they detect it with their right antenna [65]. This has been interpreted as avoidance of an agonistic situation on the left side and approach for attack on the right side. Approach on the right side could also mean approach to inspect the situation before making a decision to respond (by attacking or not). This could be tested using different concentrations of iso-amyl acetate.

Iso-amyl acetate is a component of the sting pheromone, which recruits bees from the hive to either flee [66] or attack [67]. Indeed, iso-amyl acetate primes worker bees to either take flight or attack [68]. As shown by electroantennographic recording, the right antenna responds more strongly than the left to iso-amyl acetate [69], which might be consistent with the right, and not the left, antenna being stimulated above a threshold for eliciting attack. Consistent with this, although not tested for laterality, other research has provided evidence that stimulation by iso-amyl acetate up-regulates the levels of serotonin and dopamine in the brain and modulates the internal threshold for attacking behaviour [70]. It is possible, if not very likely, that the threshold for stimulating attack is lower for the right antenna than it is for the left antenna.

A study which examined the interaction between honeybees in pairs showed that use of the right antenna leads to shorter latency of the bees to approach and contact each other [71]. Also, provided both bees are from the same colony and, hence, interact in a positive manner, using the right antenna leads to more proboscis extension responses, which involves exchange of odoriferous information [71]. Overall, therefore, in honeybees, the right antenna and the right side of the brain control approach and social behaviour involving positive interactions. A similar side bias occurs in ants, *Formica rufa*, during exchange of food (i.e., trophallaxis): the ant receiving the food has a preference to use its right antenna to contact the donor [72].

In the stingless bee species, *Tetragonula carbonaria*, tested in pairs, higher levels of physical contacts, involving one bee touching the other bee with an antenna, occur between bees using only their right antennae compared to pairs of bees using only their left antennae [73]. This result matches that found in honeybees.

In summary, social interaction involving approach of one bee to another is supported by consistent evidence of control by sensory inputs to the right antenna. These approaches can be triggered by pheromones eliciting positive interactions leading to proboscis extension, as found in honeybees.

Laterality of withdrawal from a predator has been studied in a species of locust, *Locusta migratoria* [74,75]. Although the locusts showed a preference to use the right eye to view a model predator, it was those using their left eye that withdrew, or escaped, sooner.

As another example, the European common cuttlefish, *Sepia officinalis* [76] has a preference to scan for predators using the left visual field and to pursue prey using the right visual field [76] (Figure 2).

Comparison of invertebrate and vertebrate laterality for approach versus withdrawal

The invertebrate/vertebrate comparison of lateralized approach/withdrawal is a case similar to that discussed for memory (LTM versus STM). The brain sides used for each of these opposing responses (to approach or withdraw) in invertebrates and vertebrates are mirror images of each other (Figure 2). In both vertebrates and invertebrates, stimulation of receptors on the left side of the animal leads to escape or withdrawal, whereas stimulation of receptors on the right side leads to approach. In vertebrates that right-side elicited approach is seen in pursuit of food, whereas approach in invertebrates is expressed as making social contact, which can be agonistic or positive. Therefore, the patterns of lateralization in vertebrates and invertebrates match if one takes into account the crossing over of sensory inputs in vertebrates and this is a further piece of evidence suggesting possible homology.

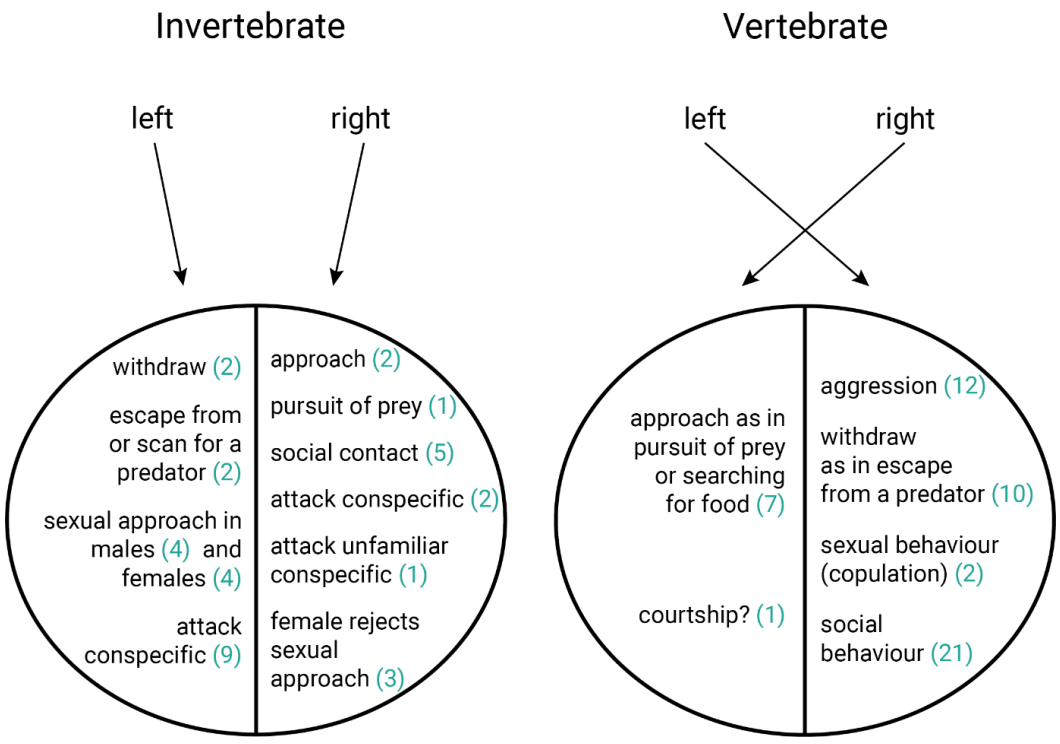

Figure 2 - Lateral functions in vertebrates and invertebrates represented in a way similar to Figure 1. The numbers in parenthesis indicate the number of species in which laterality of a particular function has been reported, all of which are discussed in this paper. The arrows represent the sensory inputs, not crossing in invertebrates and crossing for vision in vertebrates.

AGGRESSIVE BEHAVIOUR

Vertebrates

The left eye and right hemisphere are specialised to control aggressive behaviour in vertebrate species, as first shown in gelada baboons [77] and in chicks [50,78] and then in toads [53,79], a frog species [80], a lizard species [81] and the horse [82]. In all of these species, agonistic behaviour is directed most often to conspecifics detected in the left, monocular field of vision.

Two recent studies have recorded lateralized agonistic behaviour in penguins and found a similar asymmetry to use the left eye, and right hemisphere. Stor et al. [83] reported that wild Magellanic penguins, *Spheniscus magellanicus*, have a significant preference to use the left eye when they attack a conspecific and, as a consequence, they inflict more wounds on the recipient's right side, especially evident when attacks are more intense. A similar bias to attack conspecifics located in the left monocular lateral visual field has been recorded in male king penguins, *Aptenodytes patagonicus* [84]. However, females displayed laterality in the opposite direction: they directed more attacks at conspecifics located in their right monocular visual field.

Zebrafish also display a leftwards bias in aggressive behaviour (left eye, right side of brain) and this asymmetry is stronger in males than females [85].

In summary, and setting aside consideration of possible sex differences because more evidence needs to be collected on this aspect, aggression expressed when using the left eye and right hemisphere has been demonstrated in a broad range of vertebrate species (Figure 2).

Invertebrates

When honeybees from different colonies are paired, those forced to use only their right antenna show higher levels of C-responses (arching of the body into a pose adopted for stinging, and hence aggressive behaviour) than do pairs forced to use only their left antenna [71]. Hence, the right antenna responds to the odours of an unfamiliar bee and the right side of the nervous system, in this case, controls aggression. Fewer C-responses occurred when two bees of the same colony were paired but, in these pairs of bees from the same-colony, more C-responses were recorded in bees using only the left antenna than in pairs using the right antenna [71]. Similar bias for aggression when using the left antenna has been found in the stingless bee, *T. carbonaria*. In pairs of conspecifics with one bee using its left antenna and the other using its right antenna, agonistic encounters were reported to be more frequently initiated by the bee using its left antenna [73]. Similar to this result, the so-called asocial mason bee, *Osmia bicornis*, displays

higher aggressive behaviour when bees using the left antenna are paired, compared to pairs in which both bees are using their right antenna [86]. Thus, in the three species of bee tested so far, the left antenna and left side of the brain initiates aggressive behaviour towards conspecifics.

To consider the asymmetry of aggressive behaviour in other invertebrate species, the giant Australian cuttlefish, *Sepia apama*, tested in both natural populations and in the laboratory, displays a left-eye preference to view a rival male [87]. Also, a species of fruitfly, *Ceratitis capitata*, has laterality of aggressive displays and the direction of the bias is to the left side [88]: fruitflies have a preference to box and perform wing-strikes using their left-side body parts and left-biased fights are more successful than right-biased fights. A left-side bias of performance of and success in aggressive interactions is also found in olive fruit flies, *Bactrocera oleae* [89]. In spiders too, the left-side bias is expressed in predatory behaviour, as reported for three species [2,90]. Therefore, a total of nine invertebrate species display a left-side bias for agonistic behaviour (Figure 2).

The opposite is the case for fighting behaviour in the blowfly, *Calliphora vomitoria*: in this species, males have a preference to box with their right legs and using the right legs leads to more success in the outcome of fights than does using the left legs [91]. In fiddler crabs, *Uca vocanus*, there is a strong bias for the right claw to be larger than the left and crabs with a larger right claw engage in more agonistic encounters than do those with a larger left claw [92]. As Barnatan et al. [5] have found, the visual optomotor response is greater when driven by inputs to the eye on the side of the larger claw. Hence, crabs of this species have a right-side bias for visual responsiveness and aggressive behaviour.

Comparing laterality of aggressive behaviour in invertebrates and vertebrates

Dissimilar to the previous examples, and despite the findings in vertebrate species of consistent preference to attack conspecifics detected in the left visual field, and with the right hemisphere, the side bias of attack in invertebrate species seems to vary between species. Nevertheless, in nine invertebrate species tested so far, there is a preference to attack conspecifics detected on their left side, using the left eye, left legs or left antenna, whereas only two invertebrate species attack conspecifics on their right side.

This evidence generally fits the paradigm outlined above and presented in Figure 2 (i.e., similar direction of sensory side-bias in vertebrates and invertebrates). Further experimental work is needed to determine whether the exceptions to this direction of bias in invertebrate species are, in fact, cases of reversed direction of asymmetry or whether they represent different degrees of aggression or types of aggressive behaviour.

SEXUAL BEHAVIOUR

Vertebrates

Limited information is available on laterality in sexual behaviour of vertebrates. In chicks, copulation responses are elevated following pharmacological treatment of the left hemisphere [50]. Seemingly, in young chicks, the treatment prevents an ability of the left hemisphere to suppress the right hemisphere's activation of copulation behaviour. In testosterone-treated chicks, copulation behaviour is elevated when they are tested using their left eye, and not at all when they are tested using their right eye [93]. Both of these procedures implicate the right hemisphere in activation and control of copulation behaviour. Such a role of the left eye and right hemisphere has also been found in stilts, *Himantopus himantopus*, scored in natural conditions [94]. Copulation behaviour is expressed more frequently when a male stilt can see a female in his left monocular visual field.

Research in this field is complicated by the need to distinguish between courtship displays and copulation behaviour since actual performance of courtship requires at least temporary suppression of copulation [49]. Courtship and copulation may, therefore, depend on neural pathways in opposite hemispheres. For example, zebra finches show a preference to view females using the right eye during courtship [95,96] and when performing courtship singing [97]. It is likely that performance of these courtship displays requires use of the left hemisphere to suppress the actual performance of copulation, controlled by the right hemisphere, while the courtship behaviour is being performed.

Therefore, based on the limited evidence available, performance of copulation in vertebrate species appears to be controlled by the right hemisphere and performance of the behaviour can be suppressed by the left hemisphere.

Invertebrates

During mating behaviour, male giant cuttlefish, *Sepia apama*, show a preference to use their left eye to view the female [76]. This left-side preference is consistent with the left-side bias found in vertebrate species, although the hemisphere controlling the behaviour is opposite since crossing the midline by sensory inputs occurs only in vertebrate species, as already discussed (Figure 2).

Lateralization of copulation attempts have been scored in two species of beetle, *Sitophilis oryzae* and *Tribolium confusum*. In both species, approaching of females was performed with a significant preference for males to do so on their (the male's) left side [98,99]. Furthermore, males that approached from their left side were more successful in achieving success in mating, as also found to be the case in mealworms, *Tenebrio molitor* [100]. Male olive flies, *Bactrocera oleae*, have

a preference to approach on the female's left side but, in this species, the side bias has no relationship to mating success [89]. The flower beetle, *Tribolium castaneum*, has greater success in mating when the male approaches the female on her left side [101]: see the figures in [101] showing that, in this species, the first contact between the male and female is frontal, both beetles using their antennae, and then the male moves to one side of the female before mounting. Although not a measure of approach, after mounting the female, the majority of male parasitic wasps, *Leptomastidea abnormis*, commence tapping the female with their right antenna and these males have more success in mating than do males tapping with the left antenna [102]. All of these are examples of left-side preference for sexual behaviour.

Females reject sexual approaches more often on their right side. The mosquito, *Culex pipiens*, females are more successful in rejecting courting males by kicking them with their right hind legs [103]. A similar right-side preference of females to reject male advances by kicking has also been found in another species of mosquito, *Aedes albopictus* [104]. Likewise, in the mating behaviour of the larger grain borer, *Prostephanus truncate*, females were found to be more aggressive when approached by a male on their right side, and likely using her right antenna for sexual recognition, although other experiments are needed to confirm this [105]. In this species, and also found in the neem bug *Halys dentatus*, mating success is higher when the male approaches the female on her left [106].

To summarise, males are more likely to achieve copulation when they approach the female on their (males') left side and females are more likely to reject males approaching on their (females') right side. Hence, copulation is more successful if the contact between males and females is on the left side.

Comparing laterality of sexual behaviour in invertebrates and vertebrates

Lateralized courtship and copulation have been examined in far too few species of vertebrate. Thus far, however, the evidence implicates use of sensory inputs to the right hemisphere in the activation of sexual behaviour, whereas the left hemisphere inhibits the right hemisphere during courtship (Figure 2).

Asymmetry of sexual behaviour, or courtship, has been reported in four species of invertebrate so far. The male approaches on his left side using sensory inputs received on his left side and this approach is more successful in achieving copulation. In another four species, the female shows a preference to be approached on her left side by the male. In these examples, the left side of the brain is used in both males and females (Figure 2). It is the opposite direction of lateralization in the central nervous system found so far in vertebrate species. However, the side bias of behaviour in the whole animal (left) is the same for both vertebrates and invertebrates.

CONCLUSION

At the sensory-input level, side-bias for access to STM and LTM is the same in invertebrates and invertebrates: in general, in the species tested so far, sensory receptors on the right side of the animal are able to gain access to STM, whereas LTM memory is accessed via receptors on the left side of the animal. As mentioned earlier in this paper, the terms STM and LTM are used only relatively speaking and, given the time course of the STM discussed, STM could include certain aspects of memory consolidation that can be accessed only initially while another engram is being consolidated at a slower rate in the opposite hemisphere or side of the brain. Once the latter process of memory consolidation has been completed, the shorter-term memory becomes inaccessible. Asymmetry of access to memory may depend on the new engram being consolidated rapidly into some existing memory schema on one side of the brain followed by gradual consolidation of the memory on the other side of the brain [107].

Also, in both invertebrates and vertebrates, stimulation of receptors on the right side of the animal elicits approach, whereas stimulation of equivalent receptors on the left side of the animal elicits withdrawal. These similarities of directional laterality could, of course, be coincidental or they may suggest the possibility of homologous evolution. In the very least, it would be worth investigating the latter idea by using genome wide analysis or exploring other aspects of molecular expression. Indeed, Boutet [108] has examined the evidence for asymmetrical and cephalic expression of the Nodal signalling pathway in vertebrates and invertebrates and concluded that it has a more widespread role in generating asymmetry of the neural structures than thought previously. Extending this research to include genes expressed in asymmetry of behaviour in invertebrate and vertebrate species would now be of interest.

This paper has argued that similar matching side biases of sensory responses, as performed by the whole animal, are present in both invertebrates and vertebrates. But how did this matching of the direction of lateralized behaviour occur? If we look inside the animal, we find that the direction of laterality in the brains of invertebrates is opposite to that in vertebrates. In parallel with the evolution of sensory decussation in vertebrates, the brain functions swapped sides. How did that occur? It does seem that the allocation of separate functions to one and the other side of the brain evolved already in invertebrate species and that this functional division was retained by vertebrates, albeit with sideways flipping. Now we can ask whether it was the flipping of the brain that led to decussation of the sensory input pathways or was the sensory decussation instrumental in flipping of brain laterality? It is argued here that the general pattern and direction of lateralization of sensory inputs to the brain persisted across the transition from invertebrates to vertebrates, whereas the directional bias of lateralized functions in the brain reversed.

Although laterality is often discussed as a unitary characteristic, the examples of behavioural laterality covered in this paper emphasise the need to consider each behavioural expression of laterality as a separate entity. This is important not only when studying lateralized behaviour itself but when considering molecular and cellular asymmetries. Furthermore, the different modalities of sensory inputs eliciting behaviour should be examined separately. Due to lack of sufficient data across species, this distinction has not been made in this paper. Future research comparing inputs that cross the midline (visual, auditory and tactile) in vertebrates with inputs that do not cross the midline (olfaction), and then comparing the transition of these systems from invertebrates to vertebrates, should be enlightening. In fact, olfactory lateralization has been studied in dogs, finding that the right nostril (and right hemisphere) is used to sniff novel odours that elicit heightened arousal, whereas the left nostril (and left hemisphere) is used to sniff familiar odours [109]. As the authors of the paper explain [109], this result showing brain asymmetry matches the prediction for inputs of a sensory system not crossing the midline and hence fits with the pattern illustrated in Figure 2.

This paper has been concerned with the pattern of asymmetry for sensory inputs and central nervous system processing. This general pattern is sometimes, but not always, expressed in motor preferences. In fact, limb preferences may depend on the species ecological niche, as concluded by Ströckens et al. [110] in a wide-ranging study of limb preferences in vertebrate species [111], and limb preference for simple reaching may vary independently of the direction of sensory and/or brain lateralization, as has been found in some primate species [112, 113, 114]. For example, left-handed marmosets are less likely than are right-handed marmosets to interact with novel stimuli [115], show stronger fear responses to predators [114] and express negative cognitive bias [116]. These findings could be explained if both left- and right-handers have the same direction of lateralization in the brain and for processing sensory inputs, as supported by studies showing no association between eye preference and hand preference in primate species [117, 118], and hand preference reflects which hemisphere is used preferentially.

The pattern of asymmetry in the whole animal has been conserved across the transition of invertebrates to vertebrates, and so represents evolutionary constraints over the design of neural connections (cf., [119]). Since each side of the brain carries out different processes of stimulus response, it is possible that, once incompatible responses separated to different sides of the brain, the basic pattern was retained in vertebrate and invertebrate nervous systems. For example, once one side became specialised, let us say, for shorter-term memory storage, the other side specialised for a complementary function, LTM. Later evolved functional lateralities may be linked to a basic pattern. There are bound to be species, and individuals, which break this pattern of asymmetry and these cases could result from active selection against a basic pattern (e.g., reversed laterality), rather than being examples of *de novo* evolution.

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