

Laterality in vertebrates and invertebrates: linked or different?

Lesley J. Rogers¹

¹ School of Life Science, University of New England, Australia

Correspondence: lrogers@une.edu.au

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.

Keywords: lateralized behaviour, evolution, memory, approach-withdrawal, escape, aggression, sexual behaviour, social behaviour, comparison, invertebrates, vertebrates

29 **INTRODUCTION**

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

42 The transition from invertebrates to vertebrates involved radical changes in the
43 nervous system's organisation [6,7], as well as the shift from an exoskeleton to an
44 internal skeleton with a notochord or vertebral column. This evolutionary step required
45 reshaping of the genome, which included two-fold duplication of the whole genome
46 coupled with changes in protein coding [8] and a change from mosaic, or no,
47 methylation of the genome in invertebrates to genome-wide methylation in vertebrates
48 [9]. Despite these pervasive changes that took place in the transition from
49 invertebrates to vertebrates, does asymmetry in invertebrates and vertebrates share
50 some commonalities in gene expression and/or in structural and functional
51 manifestations of laterality? Although some investigators consider that vertebrate and
52 invertebrate nervous systems evolved independently, others see similarities in
53 expression of genes controlling development and inducing neural patterning, and
54 hence neural circuitry, in vertebrates and invertebrates [10-12].

55 Signore et al. [13] have proposed that signalling by the transforming growth
56 factor, Nodal, plays a vital role in the development of asymmetry of the nervous system
57 in both invertebrates and vertebrates. Other researchers describe similar expression
58 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 short-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 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).

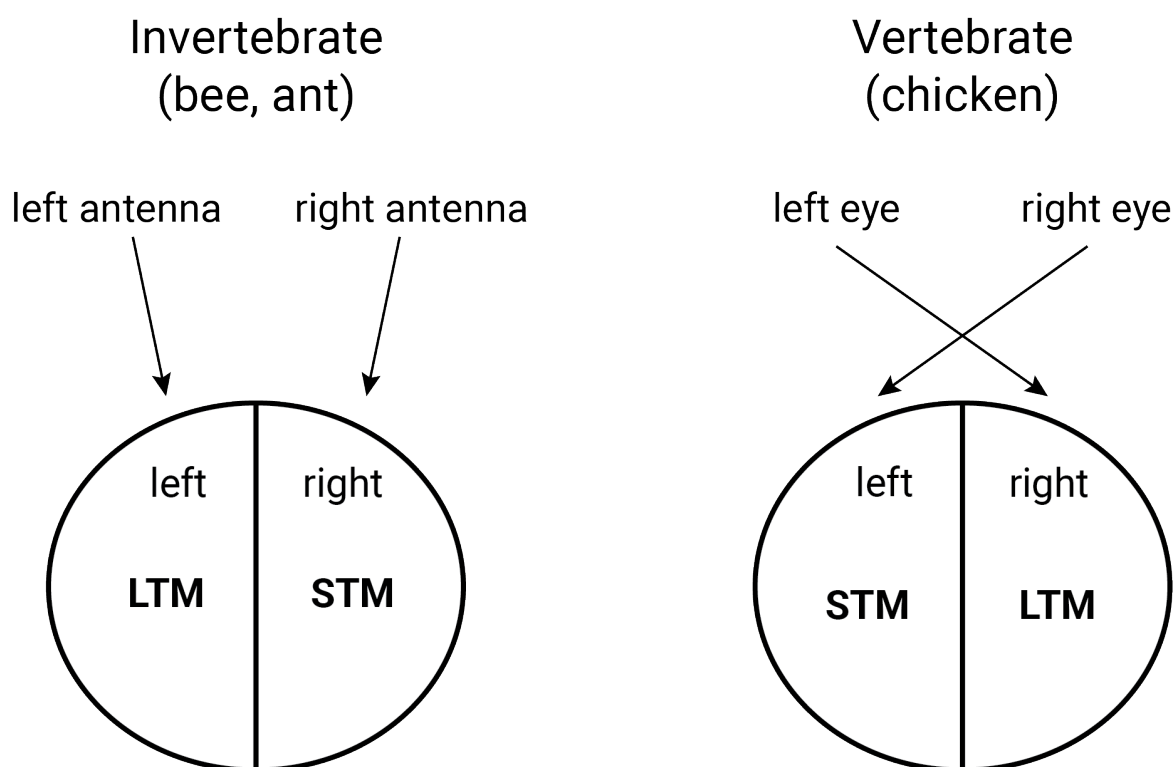


Figure 1 - The general pattern of asymmetry for short-term (STM) and long-term memory (LTM). The bisected ellipses represent the left and right sides of the brain (hemispheres in the case of vertebrates). The arrows represent the sensory inputs to the brain: note that they do not cross the midline in 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.

107 Similar lateralization of memory has been shown for another task, passive
108 avoidance learning. In this task, a chick is presented with a bitter-tasting bead which
109 has a specific colour (usually red) and the chick shows memory of this aversive
110 experience by subsequently failing to peck at a clean bead of the same colour, whereas
111 it will peck at a bead of a different colour. For up to one hour following training,
112 structural and molecular changes associated with memory formation of this task
113 occur in the left IMM but not in the right IMM [21] (reviewed in [22]). When the delay
114 between training and recall is several hours longer, changes in synapse structure and
115 in the levels of particular neurotransmitters occur in the right IMM, and not in the left
116 IMM [23-25]. Thus, similar to imprinting memory, following passive avoidance learning
117 STM is located in the left hemisphere and LTM in the right hemisphere.

118 The next question to consider is how the left-right asymmetry in memory
119 distribution might affect recall in chicks using both eyes and hence with potential
120 access to memory traces located in both hemispheres. Andrew [26] examined
121 interactions between memory traces in the left and right hemispheres at various times
122 after training, and showed the existence of cycles of good and poor retrieval. To
123 simplify the evidence, such cycles occur across time after training first with events in
124 the left hemisphere and later with events in the right hemisphere (for details see
125 [26,27]). This translates into preferred use of the right eye (left hemisphere) to view a
126 training stimulus, such as the red bead used in passive avoidance learning, in the initial
127 phase of memory formation (STM), followed by preferred use of the left eye (right
128 hemisphere) when the LTM store has to be accessed. Without going into detail of
129 differing cycles in the left and right hemispheres or interhemispheric transfer, here it is
130 noted that the research by Andrew illustrates the way in which behaviour of the whole
131 animal is influenced by the different roles of the left and right hemispheres in STM and
132 LTM, respectively.

133 Not only is time after training a factor contributing to laterality of memory
134 formation and retrieval but, as shown by a body of research, the left and right
135 hemispheres attend to different aspects of a stimulus and process this information
136 differently [28,29]. Thus, the hemispheres differ in how they process sensory inputs

137 and also in their different abilities to access memory. Such lateralization has also been
138 shown for song learning and recall in certain species of songbird (summarised in [30]).

139 In rats, however, there is evidence that the hippocampal region of the left
140 hemisphere is essential for recall of LTM, whereas the hippocampal regions in both
141 hemispheres are involved in STM [31,32]. Although this demonstrates lateralization of
142 memory formation in a mammalian species, the direction of laterality is opposite of
143 that in the chick. Clearly, further research on different species and on different types
144 of memory is needed.

145

146 Invertebrates

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

158 Lateralization of memory formation and recall has more recently been
159 investigated in the honeybee, *Apis mellifera*. This species shows lateralization STM
160 and LTM, each accessed via a different antenna and from a different side of the brain.
161 Rogers and Vallortigara [34] trained honeybees to associate a specific odour (e.g.,
162 vanilla) with a sugar reward and then tested recall of the memory at different times
163 after training. The bees were trained using both antennae and then tested for recall via
164 only one antenna (the other antenna being rendered unable to detect odours by coating
165 it with a silica gum). Recall was scored as the extension of the proboscis, indicating

166 the bee's expectation to ingest the sugar liquid. Provided they were using their right
167 antenna (left antenna coated) they could recall STM at 1 hour after training. LTM tested
168 at 6 and 23 hours after training could be recalled only via the left antenna (right antenna
169 coated). In other words, the right antenna and its neural connections in the brain can
170 recall only STM and the left antenna and its neural connections can recall only LTM
171 (Figure 1).

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

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

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

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

202

203 **Comparison of invertebrate and vertebrate direction of laterality**

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

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

216 Considering the cross-over of visual inputs in the chick, the link between right
217 eye access to STM in the left hemisphere versus left eye access to LTM in the right
218 hemisphere is equivalent to right-side sensory access to STM and left side sensory
219 access to LTM in invertebrates (Figure 1). Hence, in both invertebrates and vertebrates,
220 sensory receptors on the right side of the animal can access STM, whereas sensory
221 receptors on the left side can access LTM. Given this similarity between invertebrates
222 and vertebrates, a case for homology may be a possibility.

223

224 **SOCIAL APPROACH OR WITHDRAWAL**225 **Vertebrates**

226 In vertebrate species, withdrawal from a threatening stimulus is elicited by visual input
227 to the right hemisphere. This has been demonstrated in three species of toad [41] and
228 a marsupial, the dunnart [42]. Both species were tested with a model snake that moved
229 towards the animal being tested on its left or right side. Escape responses occurred
230 sooner and more strongly when the model predator approached on the test animal's
231 left side, indicating that the right side of the brain controls avoidance of predators
232 [41,42]. The same left eye and right hemisphere laterality is found in domestic chicks,
233 in this case tested by "flying" a model predator overhead at a time when the chick was
234 searching for food: the chick was more likely to detect the predator when it entered the
235 visual field of its left eye than when it entered the visual field of the right eye [43].

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

241 In contrast, the right eye and left hemisphere of the vertebrate brain is
242 specialised for approach and pursuit of potential food. This has been shown in chicks
243 [50], the zebra finch [51], the zebrafish [52], toads [53,54] and lizards [55]. For example,
244 chicks using their right eye and left hemisphere, but not those using their left eye and
245 right hemisphere, can distinguish food grains from inedible pebbles [50,56]. Likewise,
246 toads strike at prey that have moved into their right hemifield but not at prey in their
247 left hemifield [57].

248 The right hemisphere is also specialised for social behaviour as revealed by a
249 preference of maternal animals, in many mammalian species, to keep their offspring
250 on their left side [58,59]. Fish also prefer to keep conspecifics on their left side [60-62].

251 The processing of social information (e.g., recognition of companions and of faces)
252 has been investigated in chicks and they too carry out these functions using their right
253 hemisphere, hence with a left-eye preference [63,64].

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

257

258 **Invertebrates**

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

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

277 A study which examined the interaction between honeybees in pairs showed
278 that use of the right antenna leads to shorter latency of the bees to approach and

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

286 In the stingless bee species, *Tetragonula carbonaria*, tested in pairs, higher
287 levels of physical contacts occur between those bees using only their right antennae
288 compared to pairs of bees using only their left antennae [73]. This result matches that
289 found in honeybees.

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

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

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

301

302 **Comparison of invertebrate and vertebrate laterality for approach versus withdrawal**

303 The invertebrate/vertebrate comparison of lateralized approach/withdrawal is a case
304 similar to that discussed for memory (LTM versus STM). The brain sides used for each
305 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.

314

315 AGGRESSIVE BEHAVIOUR

316 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].

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

337

338 Invertebrates

339 When honeybees from different colonies are paired, those forced to use only their right
340 antenna show higher levels of C-responses (arching of the body into a pose adopted
341 for stinging, and hence aggressive behaviour) than do pairs forced to use only their left
342 antenna [71]. Hence, the right antenna responds to the odours of an unfamiliar bee and
343 the right side of the nervous system, in this case, controls aggression. Fewer C-
344 responses occurred when two bees of the same colony were paired but, in these pairs
345 of bees from the same-colony, more C-responses were recorded in bees using only the
346 left antenna than in pairs using the right antenna [71]. Similar bias for aggression when
347 using the left antenna has been found in the stingless bee, *T. carbonaria*. In pairs of
348 conspecifics with one bee using its left antenna and the other using its right antenna,
349 agonistic encounters were reported to be more frequently initiated by the bee using its
350 left antenna [73]. Similar to this result, the so-called asocial mason bee, *Osmia bicornis*,
351 displays higher aggressive behaviour when bees using the left antenna are paired,
352 compared to pairs in which both bees are using their right antenna [86]. Thus, in the
353 three species of bee tested so far, the left antenna and left side of the brain initiates
354 aggressive behaviour towards conspecifics.

355 To consider the asymmetry of aggressive behaviour in other invertebrate
356 species, the giant Australian cuttlefish, *Sepia apama*, tested in both natural populations
357 and in the laboratory, displays a left-eye preference to view a rival male [87]. Also, a
358 species of fruitfly, *Ceratitis capitata*, has laterality of aggressive displays and the
359 direction of the bias is to the left side [88]: fruitflies have a preference to box and
360 perform wing-strikes using their left-side body parts and left-biased fights are more
361 successful than right-biased fights. A left-side bias of performance of and success in

362 aggressive interactions is also found in olive fruit flies, *Bactrocera oleae* [89]. In spiders
363 too, the left-side bias is expressed in predatory behaviour, as reported for three species
364 [2,90]. Therefore, a total of nine invertebrate species display a left-side bias for
365 agonistic behaviour (Figure 2).

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

375

376 Comparing laterality of aggressive behaviour in invertebrates and vertebrates

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

384 This evidence generally fits the paradigm outlined above and presented in
385 Figure 1 (i.e., similar direction of whole-body side-bias in vertebrates and
386 invertebrates). Further experimental work is needed to determine whether the
387 exceptions to this direction of bias in invertebrate species are, in fact, cases of
388 reversed direction of asymmetry or whether they represent different degrees of
389 aggression or types of aggressive behaviour.

390

391 **SEXUAL BEHAVIOUR**392 **Vertebrates**

393 Limited information is available on laterality in sexual behaviour of vertebrates. In
394 chicks, copulation responses are elevated following pharmacological treatment of the
395 left hemisphere [50]. Seemingly, in young chicks, the treatment prevents an ability of
396 the left hemisphere to suppress the right hemisphere's activation of copulation
397 behaviour. In testosterone-treated chicks, copulation behaviour is elevated when they
398 are tested using their left eye, and not at all when they are tested using their right eye
399 [93]. Both of these procedures implicate the right hemisphere in activation and control
400 of copulation behaviour. Such a role of the left eye and right hemisphere has also been
401 found in stilts, *Himantopus himantopus*, scored in natural conditions [94]. Copulation
402 behaviour is expressed more frequently when a male stilt can see a female in his left
403 monocular visual field.

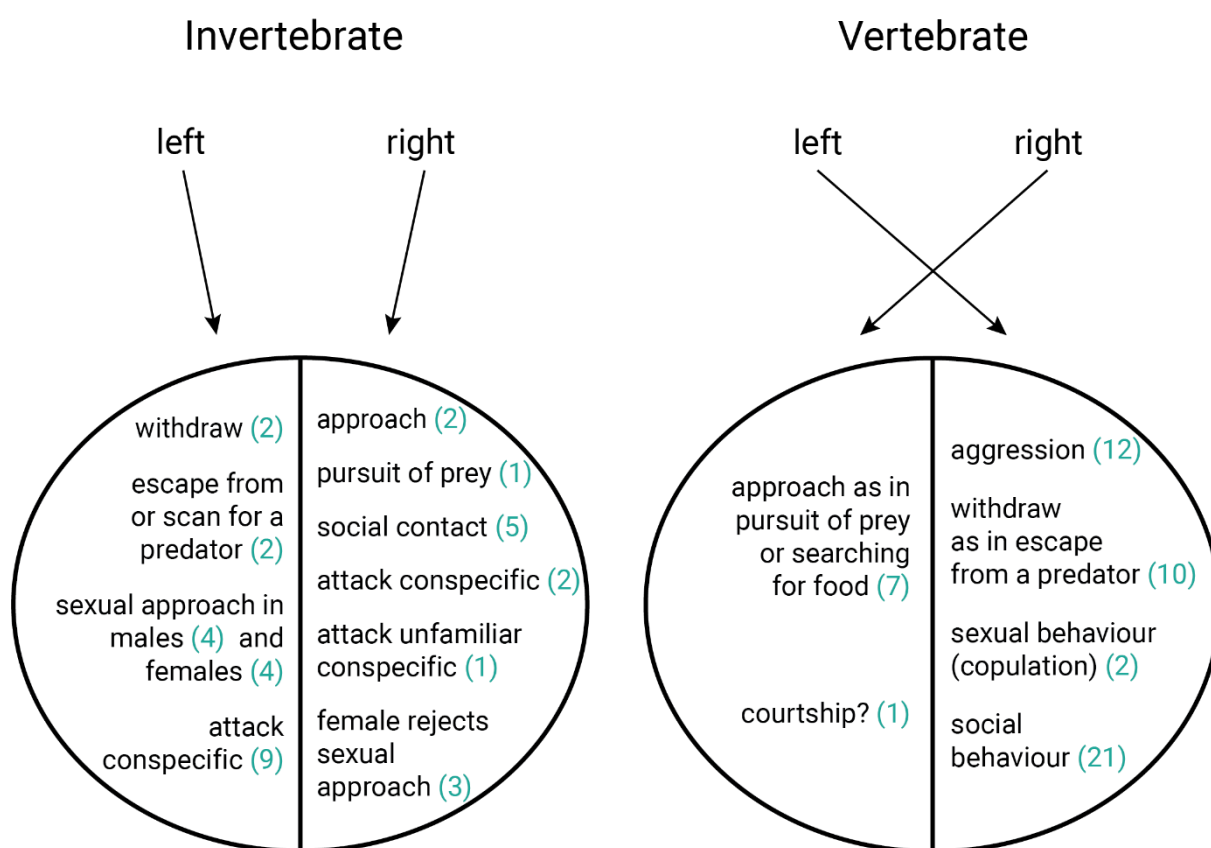
404 Research in this field is complicated by the need to distinguish between
405 courtship displays and copulation behaviour since actual performance of courtship
406 requires at least temporary suppression of copulation [49]. Courtship and copulation
407 may, therefore, depend on neural pathways in opposite hemispheres. For example,
408 zebra finches show a preference to view females using the right eye during courtship
409 [95,96] and when performing courtship singing [97]. It is likely that performance of
410 these courtship displays requires use of the left hemisphere to suppress the actual
411 performance of copulation, controlled by the right hemisphere, while the courtship
412 behaviour is being performed.

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

416

417 Invertebrates

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



423
424 Figure 2 - Lateral functions in vertebrates and invertebrates represented in a way similar to Figure 1. The numbers in
425 parenthesis indicate the number of species in which laterality of a particular function has been reported, all of which
426 are discussed in this paper. The arrows represent the sensory inputs, not crossing in invertebrates and crossing for
427 vision in vertebrates.

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

434 approach on the female's left side but, in this species, the side bias has no relationship
435 to mating success [89]. The flower beetle, *Tribolium castaneum*, has greater success
436 in mating when the male approaches the female on her left side [101]. Although not a
437 measure of approach, after mounting the female, the majority of male parasitic wasps,
438 *Leptomastidea abnormis*, commence tapping the female with their right antenna and
439 these males have more success in mating than do males tapping with the left antenna
440 [102]. All of these are examples of left-side preference for sexual behaviour.

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

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

455

456 Comparing laterality of sexual behaviour in invertebrates and vertebrates

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

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

469

470 CONCLUSION

471 At the whole-body level, side-bias for access to STM and LTM is the same in
472 invertebrates and invertebrates: in general, in the species tested so far, sensory
473 receptors on the right side of the animal are able to gain access to STM, whereas LTM
474 memory is accessed via receptors on the left side of the animal. Also, in both
475 invertebrates and vertebrates, stimulation of receptors on the right side of the animal
476 elicits approach, whereas stimulation of equivalent receptors on the left side of the
477 animal elicits withdrawal. These similarities of directional laterality could, of course,
478 be coincidental or they may suggest the possibility of homologous evolution. In the
479 very least, it would be worth investigating the latter idea by using genome wide analysis
480 or exploring other aspects of molecular expression. Indeed, Boutet [107] has examined
481 the evidence for asymmetrical and cephalic expression of the Nodal signalling
482 pathway in vertebrates and invertebrates and concluded that it has a more widespread
483 role in generating asymmetry of the neural structures than thought previously.
484 Extending this research to include genes expressed in asymmetry of behaviour in
485 invertebrate and vertebrate species would now be of interest.

486 This paper has argued that similar matching side biases of behaviour, as
487 performed by the whole animal, are present in both invertebrates and vertebrates. But
488 how did this matching of the direction of lateralized behaviour occur? If we look inside
489 the animal, we find that the direction of laterality in the brains of invertebrates is

490 opposite to that in vertebrates. In parallel with the evolution of sensory decussation in
491 vertebrates, the brain functions swapped sides. How did that occur? It does seem that
492 the allocation of separate functions to one and the other side of the brain evolved
493 already in invertebrate species and that this functional division was retained by
494 vertebrates, albeit with sideways flipping. Now we can ask whether it was the flipping
495 of the brain that led to decussation of the sensory input pathways or was the sensory
496 decussation instrumental in flipping of brain laterality?

497

498 Although laterality is often discussed as a unitary characteristic, the examples
499 of behavioural laterality covered in this paper emphasise the need to consider each
500 behavioural expression of laterality as a separate entity. This is important not only
501 when studying lateralized behaviour itself but when considering molecular and cellular
502 asymmetries. Furthermore, the different sensory inputs eliciting behaviour should be
503 examined separately. Due to lack of sufficient data across species, this distinction has
504 not been made in this paper. Future research comparing inputs that cross the midline
505 (visual, auditory and tactile) in vertebrates with inputs that do not cross the midline
506 (olfaction), and then comparing the transition of these systems from invertebrates to
507 vertebrates, should be enlightening.

508 The pattern of asymmetry in the whole animal has been conserved across the
509 transition of invertebrates to vertebrates, and so represents evolutionary constraints
510 over the design of neural connections (cf., [108]). Since each side of the brain carries
511 out different processes of stimulus response, it is possible that, once incompatible
512 responses separated to different sides of the brain, the basic pattern was retained in
513 vertebrate and invertebrate nervous systems. For example, once one side became
514 specialised, let us say, for short-term memory storage, the other side specialised for a
515 complementary function, LTM. Later evolved functional lateralities may be linked to a
516 basic pattern. There are bound to be species, or individuals, which break this pattern
517 of asymmetry and these cases could result from active selection against a basic
518 pattern (e.g., reversed laterality), rather than being examples of *de novo* evolution.

519

520 REFERENCES

- 521 1. Frasnelli E, Vallortigara G, Rogers LJ (2012) Left-right asymmetries of behaviour and
522 nervous system in invertebrates. *Neuroscience and Biobehavioral Reviews* 36; 1273-
523 1291
- 524 2. Ades C, Ramires EN (2002) Asymmetry of leg use during prey handling in the spider
525 *Scytodes globula* (Scytodidae). *Journal of Insect Behavior*, 15:563–570
- 526 3. Byrne RA, Kuba MJ, Meisel D (2004) Lateralized eye use in *Octopus vulgaris* shows
527 antisymmetrical distribution. *Animal Behaviour*, 68:1107-1114
- 528 4. Frasnelli E, Ponte G, Vallortigara G, Fiorito G (2019) Visual lateralization in the
529 cephalopod mollusk *Octopus vulgaris*. *Symmetry*, 11:1121
- 530 5. Barnatan Y, Tomsic D, Sztarker J (2019) Unidirectional optomotor responses and
531 eye dominance in two species of crabs. *Frontiers in Physiology*, 10:586
- 532 6. Holland ND (2016) Nervous systems and scenarios for the invertebrate-to-vertebrate
533 transition. *Philosophical Transactions R. Soc. B* 371:20150047
- 534 7. Hudson C, Yasuo H (2021) Neuromesodermal lineage contribution to CNS
535 development in invertebrate and vertebrate chordates. *Genes*, 12:592
- 536 8. Marlétaz F, Firbas P, Maeso I, Tena JJ, Bogdanovic O, et al. (2018) *Amphioxus*
537 functional genomics and the origins of vertebrate gene regulation. *Nature*, 564, 64-70
- 538 9. Xu X, Li G, Li C, Zhang J et al. (2019) Evolutionary transition between invertebrates
539 and vertebrates via methylation reprogramming in embryogenesis. *National Science*
540 *Review*, 6:993-1003
- 541 10. Holland LZ, Holland ND (1999) Chordate origins of the vertebrate central nervous
542 system. *Current Opinion in Neurobiology*, 9:596-602

- 543 11. Reichert H (2009) Evolutionary conservation of mechanisms for neural
544 regionalization, proliferation and interconnection in brain development. *Biology Letters*
545 5:112-116
- 546 12. Holland LZ (2020) Invertebrate origins of vertebrate nervous system. In
547 *Evolutionary Neuroscience*, Academic Press, Second Edition, Chapter 4, pp. 51-73
- 548 13. Signore IA, Palma K, Concha ML (2016) Nodal signalling and asymmetry of the
549 nervous system. *Philosophical Transactions of the Royal Society B*, 371: 20150401
- 550 14. Shpigler HY, Saul MC, Corona F, Block L, Ahmed AC, Zhao SD, Robinson GE (2017)
551 Deep evolutionary conservation of autism-related genes. *Proceedings of the National*
552 *Academy of Science*, 114:9653-9658
- 553 15. Horn G (1985) *Memory, Imprinting, and the Brain*. Oxford University Press, Oxford
- 554 16. McCabe, B. (2017) Pharmacological agents and electrophysiological techniques.
555 In Rogers LJ, Vallortigara G eds, *Lateralized Brain Functions*. Humana Press, Springer
556 *Nature*, pp. 251-276
- 557 17. Bradley P, Horn G, Bateson P (1981) Imprinting : an electron microscopic study of
558 chick hyperstriatum ventral. *Experimental Brain Research*, 41:115-120
- 559 18. Horn G, Bradley P, McCabe BJ (1985) changes in the structure of synapses
560 associated with learning. *Journal of Neuroscience* 5:3161-3168
- 561 19. McCabe B, Horn G (1988) Learning and memory: regional changes in N-methyl-d-
562 aspartate receptors in the chick brain after imprinting. *Proceedings of the National*
563 *Academy of Science USA*, 85:2849-2853.
- 564 20. Moorman S, Nicol AU (2015) Memory-related brain lateralisation in birds and
565 humans. *Neuroscience and Biobehavioral Reviews* 50: 86-102
- 566 21. Stewart MG, Rose SPR, King TS, Gabbott PLA, Bourne R (1984) Hemispheric
567 asymmetry of synapses in chick medial hyperstriatum ventral following passive

568 avoidance training: a stereological investigation. Developmental Brain Research,
569 12:261-269

570 22. Johnston ANB, Rose SPR (2000) Memory and lateralized recall. In Rogers, L.J. and
571 Andrew, R.J. Comparative Vertebrate Lateralization. Cambridge University Press,
572 Cambridge, pp.533-581

573 23. Gigg J, Patterson TA, Rose SPR (1993) Training-induced increases in neuronal
574 activity recorded from the forebrain of the day-old chick are time dependent.
575 Neuroscience, 56:771-776

576 24. Daisley JN, Rose SPR. (2002) Amino acid release from the intermediate medial
577 hyperstriatum ventral (IMHV) of day-old chicks following a one-trial passive avoidance
578 task. Neurobiology, Learning and Memory, 77:185-201

579 25. Bullock S, Rose SPR, Zamani R (1992) Characterisation and regional localisation of
580 pre- and postsynaptic glycoproteins of the chick forebrain showing changed fucose
581 incorporation following passive avoidance training. Journal of Neurochemistry,
582 58:2145-2154

583 26. Andrew RJ (1997) Left and right hemisphere memory traces: their formation and
584 fate. Evidence from events during memory formation in the chick. Laterality, 2:179-198

585 27. Andrew RJ (2002) Memory formation and brain lateralization In Rogers LJ, Andrew
586 RJ eds Comparative Vertebrate Lateralization. Cambridge University Press,
587 Cambridge, pp. 582-633

588 28. Vallortigara G, Rogers LJ (2005) Survival with an asymmetrical brain: advantages
589 and disadvantages of cerebral lateralization. Behavioral and Brain Sciences, 28:575-
590 633

591 29. Vallortigara G, Rogers LJ (2020) A function for the bicameral mind. Cortex,
592 124:274-285

- 593 30. Moorman S, Nicol AU (2015) Memory-related brain lateralisation in birds and
594 humans. *Neuroscience and Biobehavioral Reviews* 50: 86-102
- 595 31. Shipton OA, El-Gaby M, Apergis-Schoute J, Deisseroth K, Bannerman DM, Paulsen
596 O, Kohl MM (2014) Left-right dissociation of hippocampal memory processes in mice.
597 *Proceedings of the National Academy of Science*, 111: 15238-15243
- 598 32. Sakaguchi Y, Sakurai Y (2021) Disconnection between rat's left and right
599 hemisphere impairs short-term memory but not long-term memory. *Symmetry*, 13:
600 1872
- 601 33. Pascual A, Huang K-L, Nevue J, Pr  at T (2004) Brain asymmetry and long-term
602 memory. *Nature*, 427:605-606
- 603 34. Rogers LJ, Vallortigara G (2008) From antenna to antenna. *PLoS One*, 3:e2340
- 604 35. Letzkus P, Ribi WA, Wood JT, Zhu H, Zhang S-W, Srinivasan S (2006) Lateralization
605 of olfaction in the honeybee *Apis mellifera*. *Current Biology*, 16:1471-1476
- 606 36. Rigosi E, Haase A, Rath L, Anfora G, Vallortigara G, Szyszka P (2015). Asymmetric
607 neural coding revealed by in vivo calcium imaging in the honey bee brain. *Proceedings*
608 *of the Royal Society B* 282:20142571. doi: 10.1098/rspb.2014.2571
- 609 37. Guo Y, Wang Z, Li Y, Wie G, Yuan J, Sun Y et al. (2016) Lateralization of gene
610 expression in the honeybee brain during olfactory learning. *Scientific Reports*, 6:34727.
611 doi: 10.1038/srep34727
- 612 38. Baracchi D, Rigosi E, de Brito Sanchez G, Giurfa M (2018). Lateralization of sucrose
613 responsiveness and non-associative learning in honeybees. *Frontiers in Psychology*,
614 9:425. doi: 10.3389/fpsyg.2018.00425
- 615 39. Frasnelli E, Vallortigara G, Rogers LJ (2011) Origins of brain asymmetry:
616 Lateralization of odour memory recall in primitive Australian stingless bees.
617 *Behavioural Brain Research*, 224:121-127

- 618 40. Fernandes ASD, Niven JE (2020) Lateralization of short- and long-term visual
619 memories in an insect. *Proceedings of the Royal Society B* 287, 20200677
- 620 41. Lippolis G, Bisazza A, Rogers LJ, Vallortigara G (2002) Lateralization of predator
621 avoidance responses in three species of toads. *Laterality*, 7:163-183
- 622 42. Lippolis G, Westman W, McAllan BM, Rogers LJ (2005) Lateralization of escape
623 responses in the striped-faced dunnart, *Sminthopsis macroura* (Dasyuridae:
624 Marsupalia). *Laterality*, 10:457-470
- 625 43. Rogers LJ (2000) Evolution of hemispheric specialisation: Advantages and
626 disadvantages. *Brain and Language*, 73:236-253
- 627 44. Hoffman AM, Robakiewicz PE, Tuttle EM Rogers LJ (2006) Behavioural
628 lateralization in the Australian magpie (*Gymnorhina tibicen*). *Laterality*, 11:110-121
- 629 45. Rogers LJ, Kaplan G (2006) An eye for a predator: Lateralization in birds, with
630 particular reference to the Australian magpie. In *Behavioral and Morphological*
631 *Asymmetries in Vertebrates* edited by Yegor Malashichev and Wallace Deckel and
632 published by Landes Bioscience, pp. 47-57
- 633 46. Bonati B, Csermely D, López P, Martín J (2010) Lateralization in the escape
634 behaviour of the common wall lizard (*Podarcis muralis*) *Behavioural Brain Research*,
635 207:1-6
- 636 47. Robins A, Goma AA, Ouine L, Phillips CJC (2018) The eyes have it: lateralized
637 coping strategies in cattle herds responding to human approach. *Animal Cognition*,
638 21:685-70
- 639 48. Austin NP, Rogers LJ (2007) Asymmetry of flight and escape turning responses in
640 horses. *Laterality*, 12:464-474
- 641 49. Rogers LJ, Koboroff A, Kaplan G (2018) Lateral asymmetry of brain and behaviour
642 in the zebra finch, *Taeniopygia guttata*. *Symmetry*, 10:679. doi:10.3390/sym10120679

- 643 50. Rogers LJ (1982) Light experience and asymmetry of brain function in chickens.
644 Nature, 297:223-225
- 645 51. Alonso Y (1998) Lateralization of visual guided behavior during feeding in zebra
646 finches (*Taeniopygia guttata*). Behavioural Processes, 43:257-263
- 647 52. Miklósi A, Andrew RJ (1999) Right eye use associated with decision to bite in
648 zebrafish. Behavioural Brain Research 109:199-205
- 649 53. Vallortigara G, Rogers LJ, Bisazza A, Lippolis G, Robins A. (1998) Complementary
650 right and left hemifield use for predatory and agonistic behavior. Neuroreport, 9:3341-
651 3344
- 652 54. Robins A, Rogers LJ (2006) Complementary and lateralized forms of processing
653 in *Bufo marinus* for novel and familiar prey. Neurobiology of Learning and Memory,
654 86:214-227
- 655 55. Robins A, Chen P, Beazley L, Dunlop SA (2005) Lateralized predatory responses in
656 the ornate dragon lizard (*Ctenophorus ornatus*). Neuroreport, 16:849-852
- 657 56. Rogers LJ, Anson JM (1979) Lateralisation of function in the chicken fore-brain.
658 Pharmacology, Biochemistry and Behavior, 10:679-686
- 659 57. Robins A, Rogers LJ (2004) Lateralised prey catching responses in the toad (*Bufo*
660 *marinus*): Analysis of complex visual stimuli. Animal Behaviour, 68:567-575
- 661 58. Karenina K, Giljov A, Ingram J, Rowntree VJ, Malashichev Y (2017) Lateralization
662 of mother–infant interactions in a diverse range of mammal species. Nature Ecology
663 and Evolution 1(2):0030. <https://doi.org/10.1038/s41559-016-0030>
- 664 59. Karenina K, Giljov A, de Silva S, Malashichev y (2018) Social lateralization in wild
665 Asian elephants: Visual preferences of mothers and offspring. Behavioral Ecology and
666 Sociobiology, 72:21

- 667 60. Bisazza A, de Santi A, Vallortigara G (1999) Laterality and cooperation: mosquito
668 fish move closer to a predator when the companion is on their side. *Animal Behaviour*,
669 57: 1145-1149
- 670 61. Sovrano VA, Rainoldi C, Bisazza A, Vallortigara G (1999) Roots of brain
671 specializations: preferential left-eye use during mirror-image inspection in six species
672 of teleost fish. *Behavioural Brain Research*, 106:175–180
- 673 62. Sovrano, VA, Bisazza A, Vallortigara G (2001) Lateralization of response to social
674 stimuli in fishes: a comparison between different methods and species. *Physiology*
675 *and Behavior*, 74:237–244
- 676 63. Vallortigara, G (1992) Right hemisphere advantage for social recognition in the
677 chick. *Neuropsychologia*, 30:761-768
- 678 64. Rosa Salva O, Regolin L, Mascalon E, Vallortigara G (2012) Cerebral and
679 behavioural asymmetries in animal social recognition. *Comparative Cognition and*
680 *Behavior Reviews*, 7:110-138
- 681 65. Rogers LJ, Vallortigara G (2019) Complementary specializations of the left and
682 right sides of the honeybee brain. *Frontiers in Psychology*, 10:280
- 683 66. Wagner BR, Breed M D (2000). Does honey bee sting alarm pheromone give
684 orientation information to defensive bees? *Annals of the Entomology Society of*
685 *America*, 93:1329-1332. doi: 10.1603/0013-8746(2000)093[1329:dhbsap]2.0.co;2
- 686 67. Free JB (1961). The stimuli releasing the stinging response of honeybees. *Animal*
687 *Behaviour*, 9:193–196. doi: 10.1016/0003-3472(61)90008-2
- 688 68. Hunt GJ (2007) Flight and fight: a comparative view of the neurophysiology and
689 genetics of honey bee defensive behaviour. *Journal of Insect Physiology*, 53:399–410
690 doi:10.1016/j.jinsphys.2007.01.010
- 691 69. Anfora G, Frasnelli E, Maccagnani B, Rogers LJ, Vallortigara G (2010) Behavioural
692 and electrophysiological lateralization in a social (*Apis mellifera*) but not in a non-

693 social (*Osmia cornuta*) species of bee. Behavioural Brain Research, 206:236–239.
694 doi:10.1016/j.bbr.2009.09.023

695 70. Nouvian M, Mandal S, Jamme C, Claudianos C, d'Ettorre P, Reinhard J, Barron AB,
696 Giurfa M (2018) Cooperative defence operates by social modulation of biogenic amine
697 levels in the honey bee brain Proceedings of the Royal Society B: Biological Sciences,
698 285:20172653

699 71. Rogers LJ, Rigosi E, Frasnelli E, Vallortigara G (2013) A right antenna for social
700 behaviour in honeybees. Scientific Reports, 3: 2045. doi: 10.1038/srep02045

701 72. Frasnelli E, Iakovlev I, Reznikova Z (2012) Asymmetry in antenna contacts during
702 tropallaxis in ants. Behavioural Brain Research, 232:7-12

703 73. Rogers LJ, Frasnelli E (2016) Antennal asymmetry in social behavior of the
704 Australian stingless bee, *Tetragonula carbonaria*. Journal of Insect Behavior, 29:491-
705 499

706 74. Romano D, Benelli G, Stefanini C (2017) Escape and surveillance asymmetries in
707 locusts exposed to a Guinea fowl-mimicking robot predator. Scientific Reports,
708 7:12825

709 75. Romano D, Benelli G, Stefanini C (2019) Encoding lateralization of jump kinematics
710 and eye use in a locust via bio-robotic artifacts. Journal of Experimental Biology,
711 222:jeb187427

712 76. Schnell AK, Hanlon RT, Benkada A, Jozet-Alves C (2016) Lateralization of eye use
713 in cuttlefish: Opposite direction for anti-predatory and predatory behaviors. Frontiers
714 in Physiology, 7:620

715 77. Casperd LM, Dunbar RIM (1996) Asymmetries in the visual processing of
716 emotional cues during agonistic interactions in gelada baboons. Behavioural
717 Processes, 37:57-65

- 718 78. Vallortigara G, Cozzutti C, Tommasi L, Rogers LJ (2001) How birds use their eyes:
719 Opposite left-right specialisation for the lateral and frontal visual hemifield in the
720 domestic chick. *Current Biology*, 11:29-33
- 721 79. Robins A, Lippolis G, Bisazza , Vallortigara G, Rogers, L.J (1998) Lateralization of
722 agonistic responses and hind-limb use in toads. *Animal Behaviour*, 56:875-881
- 723 80. Robins A, Rogers LJ (2006) Lateralized visual and motor responses in the green
724 tree frog (*Litoria caerulea*). *Animal Behaviour*, 72:843-852
- 725 81. Deckel AW (1995) Laterality of aggressive responses in *Anolis*. *Journal of*
726 *Experimental Zoology*, 272:194-200
- 727 82. Austin NA, Rogers LJ (2012) Limb preferences and lateralization of aggression,
728 reactivity and vigilance in feral horses (*Equus caballus*). *Animal Behaviour*, 83:239-247
- 729 83. Stor T, Rebstock GA, Borboroglu PG, Boersma PD (2019) Lateralization
730 (handedness) in Magellanic penguins. *PeerJ*, 7:e6936
- 731 84. Lemaire BS, Viblanc VA, Jozet-Alves C (2019) Sex-specific lateralization during
732 aggressive interactions in breeding king penguins. *Ethology*, 125:439-449
- 733 85. Ariyomo TO, Watt PJ (2013) Aggression and sex differences in lateralization in the
734 zebrafish. *Animal Behaviour*, 86:617-622
- 735 86. Rogers LJ, Frasnelli E, Versace E (2016) Lateralized antennal control of aggression
736 and sex differences in red mason bees, *Osmia bicornis*. *Scientific Reports*, 6:29411.
737 doi: 10.1038/srep29411
- 738 87. Schnell AK, Jozet-Alves C, Hall KC, Radday L, Hanlon RT (2019) Fighting and
739 mating success in giant Australian cuttlefish is influenced by behavioural
740 lateralization. *Proceedings of the Royal Society B*, 286, 20182507
- 741 88. Benelli G, Donati E, Romano D, Stefanini C, Messing RH, Canale A (2015)
742 Lateralisation of aggressive displays in a tephritid fly. *The Science of Nature*, 102:1251

- 743 89. Benelli G, Romano D, Messing RH, Canale A (2015) Population-level lateralized
744 aggressive and courtship displays make better fighters not lovers: evidence from a fly.
745 Behavioural Processes, 115:163-168
- 746 90. Heuts BA, Lambrechts DYM (1999) Positional biases in leg loss of spiders and
747 harvestmen (Arachnida). Enomologische Berichten (Amst) 59:13-20
- 748 91. Romano D, Canale A, Benelli G (2015) Do right-biased boxers do it better?
749 Population-level asymmetry of aggressive displays enhances fighting success in
750 blowflies. Behavioural Processes 113:159-162
- 751 92. Backwell PRY, Matsumasa M, Double M, Roberts A, Murai M, Keogh JS, Jennions
752 MD (2007) What are the consequences of being left-clawed in a predominantly right-
753 clawed fiddler crab? Proceedings of the Royal Society B 274:2723-2729
- 754 93. Rogers LJ, Zappia JV, Bullock SP (1985) Testosterone and eye-brain asymmetry
755 for copulation in chickens. Experientia, 41:1447-1449
- 756 94. Ventolini N, Ferrero EA, Sponza S, Chiesa AD, Zucca P, Vallortigara G (2005)
757 Laterality in the wild: preferential hemifield use during predatory and sexual behaviour
758 in the black-winged stilt. Animal Behaviour, 69:1077-1084
- 759 95. Workman L, Andrew RJ (1991) Population lateralization in zebra finch courtship:
760 an unresolved issue. Animal Behaviour, 41:545-546
- 761 96. Templeton JJ, McCracken BG, Sher M, Mountjoy DJ (2014) An eye for beauty:
762 Lateralized visual stimulation of courtship behaviour and mate preferences in male
763 zebra finches, Taeniopygia guttata. Behaviour Processes, 102:33-39
- 764 97. George I, Hara E, Hessler NA (2006) Behavioral and neural lateralization of vision
765 in courtship singing of the zebra finch. Journal of Neurobiology, 66:1164-1173
- 766 98. Benelli G, Romano D, Stefanini C, Kavallieratos NG, Athanassiou CG, Canale A
767 (2017) Asymmetry of mating behaviour affects copulation success in two stored-
768 product beetles. Journal of Pest Science, 90:547-556

- 769 99. Romano D, Kavallieratos N, Athanassiou C, Stefanini C, Canale A, Benelli G (2016)
770 Impact of geographical origin and rearing medium on mating success and
771 lateralization in the rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae).
772 *Journal of Stored Products Research*, 69:106-112
- 773 100. Boukouvala MC, Romano D, Kavallieratos NG, Stefanini C, Canale A, Benelli G
774 (2021) Behavioral asymmetries affecting male mating success in *Tenebrio molitor*
775 (Coleoptera: Tenebrionidae), an important edible species. *Journal of Economic*
776 *Entomology*, 114:454-461
- 777 101. Boukouvala MC, Romano D, Kavallieratos NG, Athanassiou CG, Stefanini C,
778 Canale a, Benelli G (2019) Asymmetric courtship boosts male mating success in the
779 red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae). *Journal of*
780 *Stored Products Research*, 81, 1-6
- 781 102. Romano D, Donati E, Canale A, Messing R, Benelli G, Stefanini C (2016) Lateralized
782 courtship in a parasitic wasp. *Laterality*, 21:243-254
- 783 103. Benelli G (2018) Mating behavior of the West Nile virus vector *Culex pipiens* –
784 role of behavioral asymmetries. *Acta Tropica*, 179:88-95
- 785 104. Benelli G, Romano D, Messing RH, Canale A (2015) First report of behavioural
786 lateralisation in mosquitoes: right biased kicking behaviour against males in females
787 of the Asian tiger mosquito, *Aedes albopictus*. *Parasitology Research*, 114:1613-1617
- 788 105. Romano D, Benelli G, Kavallieratos N, Athanassiou C, Canale A, Stefanini C (2020)
789 Beetle-robot hybrid interaction: sex, lateralization and mating experience modulate
790 behavioural responses to robotic cues in the larger grain borer *Prostephanus truncatus*
791 (Horn). *Biological Cybernetics*, 114:473-483
- 792 106. Romano D, Benelli G, Stefanini C (2022) Lateralization of courtship traits impacts
793 pentatomid male mating success – Evidence from field observations. *Insects*, 13:172
- 794 107. Boutet A (2017) The evolution of asymmetric photosensitive structures in
795 metazoans and the Nodal connection. *Mechanisms of Development*, 147:49-60

- 796 108. Oberst P, Agirman G, Jabaudon D (2019) Principles of progenitor temporal
797 patterning in the developing invertebrate and vertebrate nervous system. Current
798 Opinion in Neurobiology, 56: 185-193