



Relationships between personality and lateralisation of sensory inputs

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Animal Behaviour

DOI:

[10.1016/j.anbehav.2018.05.016](https://doi.org/10.1016/j.anbehav.2018.05.016)

Published: 01/07/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Kareklas, K., Elwood, R. W., Arnott, G., & Holland, R. (2018). Relationships between personality and lateralisation of sensory inputs. *Animal Behaviour*, 141, 127-135.

<https://doi.org/10.1016/j.anbehav.2018.05.016>

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1 Title:

2 Relationships between personality and lateralisation of sensory inputs

3

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25 **ABSTRACT**

26

27 In humans and other vertebrates, sensory information is sometimes lateralised towards
28 one brain hemisphere that dominates the control of a task. Although sensory lateralisation
29 may depend on the stimuli being processed, the degree or direction of lateralisation can differ
30 according to behavioural phenotype. Accordingly, personality may play an important role in
31 lateralisation, yet there is a lack of evidence regarding how laterlisations are utilised to
32 process information and promote a personality-based response to a particular situation. Here
33 we show that simultaneous stimulus processing and organisation of personality-based
34 responses can be accomplished via differences in laterality between senses. We demonstrate
35 this by examining novel-object inspection in the weakly-electric fish *Gnathonemus petersii*.
36 Our findings reveal that electrosensing is lateralised in this species, but differently between
37 personality phenotypes; bold fish lateralise towards the right and timid fish the left
38 hemisphere. By contrast, visual laterality did not vary with personality; rather the left
39 hemisphere was dominant across the population, as is common for fish when visually
40 analysing unfamiliar objects. This evidence demonstrates differences in functional laterality
41 between sensory systems and the role of personality in eliciting these differences. The species
42 has a stronger input of electrical than visual signals in its brain, therefore, sensory
43 representation in the brain might drive the laterality differences.

44

45 **Keywords:** electrosensing; hemispheric functions; novel-object inspection; personality;
46 sensory laterality

47

48 INTRODUCTION

49 Vertebrate sensory systems extract information from the environment and pass it to
50 the brain, where it can be processed and used for cognitive tasks and for adjusting
51 behavioural responses (Shettleworth, 2001; Dall, Giraldeau, Olsson, McNamara & Stephens,
52 2005). Due to the bilateral organisation of the brain, each hemisphere can be more strongly
53 involved than the other hemisphere in a particular cognitive or behavioural function (Toga &
54 Thompson, 2003; Ocklenburg & Gunturkun, 2012). For example, the left parietal cortex of
55 humans is more prominently involved in visual attention towards limb movement
56 (Rushworth, Krams & Passingham, 2001) and the right parietal cortex in processing sound
57 movement (Griffiths et al., 1998). Because of the specialisations of each hemisphere, it is
58 often the case that a required task relies on asymmetric inputs of sensory information between
59 hemispheres (Bisazza, Rogers & Vallortigara, 1998; Rogers, 2014). This is termed sensory
60 laterality and examples include asymmetric inputs of sound (Griffiths et al., 1998), smell
61 (Zatorre, Jones-Gotman, Evans & Meyer, 1992) and visual information (Sovrano, 2004).

62 An important function of sensory laterality is that by relegating information to a
63 specialised area of the brain, other areas are free to engage in other tasks (Levy, 1977;
64 Vallortigara, Rogers & Bisazza, 1999). Sensory lateralisations can be exhibited at both the
65 population and at the individual level (Bisazza et al., 1998; Vallortigara & Rogers, 2005).
66 When lateralisations are similar amongst a proportion of the population that exceeds what
67 would be expected by chance (i.e. 50%), the degree and hemispheric direction of
68 lateralisations is often found to depend on the cognitive requirements of a particular situation,
69 such as recognising a familiar stimulus or assessing an unfamiliar one (Sorvano, 2014).
70 Arguably, the adaptive value of these population-level lateralisations is that they enable
71 coordination of social behaviour during group activities, including responses to predators in
72 fish (Bisazza, Cantalupo, Capocchiano & Vallortigara, 2000; Brown, 2005). However,

73 solitary individuals may also coordinate different responses towards a situation or attain
74 different levels of cognitive performance, and this may involve differing levels or directions
75 of laterality (Rogers, 2014; Lucon-Xiccato & Bisazza, 2015). More strongly lateralised
76 individuals may have stronger phenotypic expressions (Magat & Brown, 2009), better
77 cognitive performance (Dadda, Agrillo, Bisazza & Brown, 2015) or the ability to multitask
78 (Rogers, Zucca & Vallortigara, 2004), whereas differing directions of laterality in strongly
79 lateralised individuals may promote different behavioural phenotypes (Irving & Brown,
80 2013). These individual differences are often attributed to structural asymmetries in the brain,
81 presumably because of the differing behavioural functions of each hemisphere (Galaburda,
82 Rosen & Sherman, 1990; Facchin, Argenton & Bisazza, 2009). For instance, the direction of
83 asymmetries in the zebrafish epithalamus determines both the direction of visual laterality
84 and behavioural phenotypes, with right-sided asymmetries linked to constantly faster
85 approaches towards a novel cue and left-sided asymmetries linked to increasing avoidance of
86 novel cues over successive trials (Barth et al., 2005).

87 Although some studies argue that functional links between sensory lateralisation and
88 behaviour depend on personality, research on non-human vertebrates often fails to provide
89 one of two significant pieces of evidence: (1) the expression of personality by testing
90 phenotypic consistency or repeatability, as described for personality traits in the literature
91 (Bell, 2007; Stamps & Groothuis, 2010; Toms, Echevarria & Jouandot, 2010), or (2) a
92 measure of laterality specific to the context personality traits are tested in. For example, a
93 study of convict cichlids *Archocentrus nigrofasciatus* argues for a relationship between the
94 strength of laterality and boldness, but measures boldness only once and uses a single
95 measure (Reddon & Hurd, 2009). A study of rainbow fish *Melanotaenia nigrans* measures
96 boldness in the context of novel-environment exploration, but tests links to visual laterality in
97 a social interaction context, by utilising mirror tests (Brown & Bibost, 2014). As a result,

98 while links between laterality and behaviour may be observed, the direct attribution of
99 individual differences to personality-dependent lateralisation remains inconclusive. Despite
100 the gap in evidence from behavioural observations, developmental studies provide further
101 support to the argument that personality may indeed be related to the functional lateralisation
102 of information. A particularly important contribution comes from recent examples of
103 asymmetry development in the zebrafish brain, showing hemispheric asymmetries that
104 develop in early-life affecting later behaviour (Andrew, 2006; Dadda, Domenichini, Piffer,
105 Argenton & Bisazza, 2010). Collectively, the evidence suggests that functions of population-
106 level sensory laterality are linked to the cognitive requirements of a task and functions of
107 individual-level laterality are related to the expression of individual phenotypes, arguably due
108 to personality. However, to our knowledge, there is no evidence on the role of sensory
109 laterality when cognitively processing a stimulus and organising a personality-dependent
110 behavioural response towards it. We propose that the two functions may be carried out
111 simultaneously because of laterality differences between sensory systems.

112 Vertebrates frequently rely on the simultaneous use of multiple senses, which enable
113 the extraction of different types of information and the integrated use of this information for a
114 required function, such as object inspection and recognition (Schumacher, Burt de Perrera,
115 Thenet & von der Emde, 2016). However, the integration of lateralisation across different
116 senses remains largely unexplored. A rare example, in the blue gourami *Trichogaster*
117 *trichopterus*, found vision and touch to be strongly lateralised and in the same direction
118 during novel-object inspection (Bisazza, Lippolis & Vallortigara, 2001). Senses can work
119 synergistically (Moller, 2002), but some senses can be dominant depending on external
120 conditions and on the value of the information each sense provides for a particular task. For
121 example, individuals may use visual information when foraging to detect distant food but
122 may increase their use of smell and other senses in conditions where visibility is low (von der

123 Emde & Bleckmann, 1998). Alternatively, different senses may attend to different stimuli,
124 such as is the case when dividing attention between auditory and visual stimuli during
125 detection and identification tasks (Bonnell & Haftser, 1998). Thus, sensory laterality may also
126 be exhibited differently across sensory modalities at any one situation, which could be a
127 means of carrying out separate functions simultaneously.

128 The weakly-electric mormyrid fish *Gnathonemus petersii* uses information gathered
129 by vision and electrosensing when inspecting objects (Moller, 2002; Schumacher et al.,
130 2016). Both the photosensory cells of each eye and the electrosensory cells on either body-
131 side project to the contralateral hemisphere, i.e. left-to-right and right-to-left (Lázár,
132 Libouban & Szabo, 1984; Vélez, Kohashi, Lu & Carlson, 2017). Lateralisations towards one
133 hemisphere can thus be detected by observing side biases during sensing. Eye preference has
134 been noted for *G. petersii* populations, engaging in mirror-image inspections that exclusively
135 rely on vision (Sovrano, Bisazza & Vallortigara, 2001). Electrosensory laterality has not
136 been examined before, but a typical electrosensory behaviour by *G. petersii* is to align their
137 body parallel to an object and move back and forth alongside it (Toerring & Moller, 1984).
138 Therefore, switching between left and right alignments enables the detection of side biases
139 specific for electrosensing. The inspection of unfamiliar objects is particularly interesting
140 because individuals respond differently depending on their personality, with bolder
141 individuals being consistently more eager to approach and inspect (Toms et al., 2010). This is
142 linked to individual tendencies in aversion to risk from unfamiliar settings (Wilson, Clark,
143 Coleman & Dearstyne, 1994), as shown in *G. petersii* (Kareklas, Arnott, Elwood & Holland,
144 2016). As a result, observations on how unfamiliar objects are approached and inspected can
145 help elucidate functional lateralisation by each sense and reveal links to personality.

146 Here we examine novel-object inspection in this species to test links between
147 laterality and personality. We also examine how context-specific laterality compares between

148 different senses in vertebrates. The cognitive processing of objects, by attending to features,
149 categorising and identifying unfamiliar stimuli, is a left hemisphere function in many
150 vertebrates (Vallortigara & Rogers, 2005; Ocklenburg & Gunturkun, 2012) and the
151 inspection of novel or unfamiliar stimuli is a left-hemisphere function in fish, as ascertained
152 by biases towards the right eye (Sovrano, 2004). For population-level lateralisations in *G.*
153 *petersii*, therefore, we expect to see right-side preference when inspecting a novel object.
154 Alternatively, if laterality is linked to the organisation of a behavioural response towards a
155 novel object (e.g. approach and inspection tendency), differences in the degree and direction
156 of laterality could manifest within the population between bold and timid personalities.
157 Although functional lateralisations could be consistent between electrosensing and vision, we
158 hypothesise that functional differences may exist between the two senses and that they may
159 be discriminated by testing whether laterality is similar across the population for inspecting
160 novel-objects or varies between personalities differing in their behaviour towards novel-
161 objects.

162

163 **EXPERIEMNTAL PROCEDURES**

164 **Animals and husbandry**

165 Wild-caught *G. petersii* (70-100 mm, $N = 20$) of unidentifiable gender (phenotypic
166 dimorphism is lost in captivity; Moller, 2002) were provided by a local supplier and first used
167 in a separate behavioural study but were naïve to the tests employed here. Animals were kept
168 individually in 15L tanks enriched with plants, toys and shelter. Tank water was filtered,
169 heated, aerated and changed twice-weekly, kept at 26 ± 1 °C, 7.2 ± 0.4 pH, 225 ± 75 μ S/cm
170 conductivity and a regulated bacterial cycle. Fish were fed daily, each with 15 ± 5 chironomid
171 larvae, and exposed to regular photoperiods, 12 h light to 12 h dark (0700-1900).
172 Experiments were carried out during light periods (350-600 nm and 300 lux at water surface).

173 **Ethical note**

174 All applicable animal-welfare guidelines were followed (ASAB, 2016) and sample
175 size was kept the minimum required. Veterinary inspections by DHSSPS, Northern Ireland,
176 deemed no need for licensing. Following the conclusion of the study, animals were kept for
177 separate non-invasive tests.

178 **Behavioural tests of boldness**

179 Boldness is characterised by consistent risk-taking tendencies, including the tendency
180 to approach and inspect unfamiliar objects (see review by Toms et al., 2010). Therefore, we
181 tested boldness by presenting individuals with a novel/unfamiliar object on three separate
182 occasions, with a 48h interval between each test. The objects included a ~10 cm long green
183 plastic soldier figurine (Test 1), a ~5 cm long brass fishing weight (Test 2) and a ~7 cm long
184 yellow silicon fishing lure (Test 3). These were presented to all individuals in this order to
185 control for carryover effects (Wilson, de Boer, Arnott & Grimmer, 2011, Kareklas et al.,
186 2016). At each presentation, the object was lowered via a pulley system to the bottom of
187 each housing tank, thus ensuring that only the object was novel and not the environment.
188 Each individual fish was given up to 5 min to approach within 15 cm distance from the object
189 (1.5 of maximum body-length; Toms et al., 2010), estimated through a grid placed under the
190 tank and visible through the glass bottom. Following approach, 5 min of inspection was
191 allowed, during which the time spent within the 15 cm distance was recorded. Behaviour was
192 scored via observations of live video feeds to a computer and opaque sheets kept tanks
193 invisible to neighbours and limited interference by the observer during tests.

194 Preliminary mixed-model analyses confirmed repeatability across the three novel-
195 object tests in individual latency to approach ($ICC = 0.970$, $F_{19,38} = 16.01$, $P < 0.001$) and
196 individual inspection times ($ICC = 0.833$, $F_{19,38} = 98.77$, $P < 0.001$), as expected for a
197 personality trait (Bell, 2007; Stamps & Groothuis, 2010). Mean latency times to approach and

198 mean exploration times, from across tests, were strongly negatively correlated (Pearson's, $r =$
199 -0.84 , $P < 0.001$), as predicted for boldness (Toms et al., 2010). Similar to other studies
200 (Herczeg Gonda & Merilä, 2009; Magnhagen & Borcharding, 2008; Wilson et al., 2011),
201 Principal Component Analysis (PCA) was used to produce composite scores from the
202 repeated measures (sampling adequacy: $KMO > 0.7$; sphericity: Bartlett's $\chi^2_{15} = 214.1$, $P <$
203 0.001 ; determinacy of multicollinearity: $\rho = 3.95 \times 10^{18}$). Given scales were similar for latency
204 and inspection times (0-300s), PCA was conducted on the covariance matrix (Jolliffe, 1986;
205 Borgognone, Bussi & Hough, 2001). Only the first component had an eigenvalue greater than
206 the mean of eigenvalues from random data (parallel analysis selection; O'Connor, 2000) and
207 was retained for scoring boldness (loadings: Table 1). Regression-based scores extracted
208 from the PCA strongly predicted approach and inspection times as would be expected by
209 increasing boldness (Fig. 1), with bolder animals showing lower avoidance and greater
210 exploration tendencies (Wilson et al., 1994; Toms et al., 2010). The PC scores were thus
211 retained for inter-individual comparisons, whereas for comparisons between bold and timid
212 phenotypes, fish with an above-median score (> -0.27 , $N = 10$) were considered bold and fish
213 with a below-median score (< -0.27 , $N = 10$) were considered timid.

214 **Laterality tests**

215 To examine laterality, a separate unfamiliar object (~20 cm long multi-coloured clay
216 gnome) was presented to individuals both through a transparent screen, for the visual test, and
217 from up close without the screen for the electrosensory test. Viewing the object through the
218 screen ensured that the object was not approached closely and thus sensing was limited to
219 vision during the visual test. By contrast electrosensory laterality was observed during close
220 approach and indicated by lateral electrosensing acts (Toerring & Moller, 1984). Tests were
221 recorded from above using a tripod-supported *Sony HDR CX190E handycam* video camera.
222 The experimental tank (25 cm Length x 40 cm Width; 25 L) was surrounded by opaque

223 plastic sheets to limit interference from external stimuli. For the visual test, fish were
224 individually introduced to a segregated section of the experimental tank (25 cm Length x 20
225 cm Width; ~10 L), created by the transparent screen and an opaque divider behind it.
226 Individuals were given 10 min to acclimatise to the tank, but also to the transparent screen.
227 This ensured that fish would not approach to inspect the screen instead of viewing the object
228 behind it during testing. The visual test started by removing the opaque divider behind the
229 transparent screen so that the object could be seen but not approached. Fish were then
230 recorded for 10 min. For the electrosensory test, each fish was again given a 10 min
231 acclimatisation in an equally sized segregated section created by an opaque divider. The
232 divider was then removed to allow fish close-up access to the object and behaviour recorded
233 for 10 min. Tests were carried out in sequence, with the 10 min acclimation period before the
234 second test acting as an interval between tests. The order of the test sequence (i.e. visual or
235 electrosensory test first) was balanced across fish.

236 The distance from which each sense is utilised can be a confounding factor on how
237 boldness to approach and inspect relates to sensory laterality. However, the low ability of *G.*
238 *petersii* to visually detect detail in bright environments suggests that they need to be closer to
239 objects than other fish species (Kreysing et al., 2012). This made it ecologically sound to
240 minimise the distance of visual inspections and limit the likelihood of effects by inter-sense
241 differences in distance. The minimum distance allowed during visual inspections was kept
242 equal to the maximum distance for electrosensing. This distance was set to the maximum
243 body-length from the sample population (10 cm) and represents the ~1 body-length distance
244 where electrolocation is possible (von der Emde, 2004). Visual inspection was measured
245 between 10 and 20 cm distance (i.e. 1-2 body-lengths; Toms et al., 2010). To calibrate
246 distances, we used marks on the bottom of the tank: a line running 10 cm away, parallel to the
247 viewing screen (visual tests) and an oval shape marked around the object (gnome) with a

248 distance of ~10 cm from the object to any point on the shape's circumference. These were
249 standard, clear markings of distance during scoring from videos, given the camera was not
250 moved and the test tank was recorded from above.

251 From the recordings of the visual test, any instance that the tail of the fish was within
252 10 cm from the screen (behind which the object was also at a 10 cm distance) and lateralised
253 up to 90^o was tallied as left or right sided. From the recordings of the electrosensory test, any
254 instance a fish was within 10 cm from the object and exhibiting lateral electrosensory acts
255 was tallied as left or right sided. Lateral electrosensory acts were identified by alignments of
256 either side of the body towards the object followed by slight curving towards the object, and
257 backwards and forward movement. These acts are specific for the active electrolocation of
258 objects and require close approach by all individuals (Toerring & Moller, 1984). Therefore,
259 we eliminated the chance of mistaking visual inspection for electrolocation during tests of
260 electrosensory laterality.

261 Because we cannot be sure that sensing time procures similar amounts of information
262 in both senses, the number of alignments over the recording period were used, instead of the
263 time each body-side was used. This provided a more comparable measure between visual and
264 electrosensory tests. As a typical measure of lateralisation (review: Vallortigara & Rogers,
265 2005), and in line with other studies (e.g. Bisazza et al., 2000; Sorvano, 2004), laterality
266 index (LI) was calculated to indicate asymmetries during electrosensory and visual
267 inspections (Table A1). This was calculated by the formula:

268

$$LI = \frac{(\text{Number of right alignments} - \text{Number of left alignments})}{(\text{Number of right alignments} + \text{Number of left alignments})}$$

269

270 Individual laterality indices can range between values of -1 (where all inspections were by the
271 left side) and 1 (where all inspections were by the right side). The 0 value indicates isometric
272 inspections, with equal left to right alignments. By transforming all LI values to positive we
273 further provide a measure of the strength of lateralisation regardless of direction, termed
274 absolute laterality, and ranging from 0 (non-lateralised or symmetric) to 1 (fully lateralised).

275 **Analysis**

276 Calculations, analyses and graphical representations were carried out in the statistics
277 software Minitab[®] version 17 (Minitab Inc., State College, PA, USA) and some of the
278 preliminary analyses in SPSS version 20 (IBM Corp., Armonk, NY, USA). Poisson-rate tests
279 showed that bold fish made more visual ($z_{10} = 3.72, P < 0.001$) and electrosensory ($z_{10} =$
280 $4.76, P < 0.001$) inspections than timid fish during the laterality tests, but no fish made fewer
281 than 5 inspections during the 10-min test period. Visual LI values were normally distributed,
282 but electrosensory LI values were not. Therefore, non-parametric one-sample sign tests (z)
283 were used to indicate if the median (\tilde{x}) of absolute and directional laterality indices of either
284 sense, vision and electrosensing, were significantly different from symmetrical (i.e. $\neq 0$) for
285 the population and for either personality-type, bold and timid. Mann-Whitney U -tests were
286 used to compare electrosensory and visual laterality between bold and timid phenotypes.
287 Effect sizes for the laterality differences were calculated by the rank-biserial correlation
288 coefficient (r), using the U statistic (Wendt, 1972):

$$r = 1 - \frac{2U}{N_1 \times N_2}$$

289 where N_1 is the sample size of bold individuals and N_2 of timid individuals. Finally, correlation
290 analyses (Spearman's r_s) were used to test whether individual boldness (PC scores) related to
291 individual visual and electrosensory laterality (absolute and directional LI values).

292

293 **RESULTS**

294 The *G. petersii* sample-population was strongly lateralised during the visual
295 inspection of the novel-object (absolute: $\tilde{x}_{20} = 0.261$, $P < 0.001$; Fig. 2a), towards the right
296 eye (directional: $\tilde{x}_{20} = 0.218$, $P = 0.008$; Fig. 2b). However, although individuals were on
297 average also strongly lateralised when electrosensing the same object (absolute: $\tilde{x}_{20} = 0.333$,
298 $P < 0.001$; Fig. 2a), there were no population biases in lateral body-alignments when
299 electrosensing (directional: $\tilde{x}_{20} = -0.020$, $P > 0.05$; Fig. 2b).

300 Visual laterality was noted in both personality types, with laterality strength being
301 significantly greater than symmetrical for timid (absolute: $\tilde{x}_{10} = 0.289$, $P = 0.004$) and bold
302 (absolute: $\tilde{x}_{10} = 0.177$, $P = 0.001$) individuals. Comparisons between personality types show
303 no significant differences in either the strength ($W_{10} = 92.5$, $U_{10} = 37.5$, $P = 0.364$, $r = 0.25$;
304 Fig. 3a) or the direction of lateralisation in eye use ($W_{10} = 97.5$, $U_{10} = 42.5$, $P = 0.597$, $r =$
305 0.15 ; Fig. 3b), being strongly lateralised to the right eye in both timid and bold individuals
306 (directional: $\tilde{x}_{10} > 0.15$, $P < 0.05$). Electrosensory laterality was also noted for both bold
307 (absolute: $\tilde{x}_{10} = 0.292$, $P = 0.02$) and timid (absolute: $\tilde{x}_{10} = 0.333$, $P = 0.02$) fish, showing no
308 differences in strength ($W_{10} = 99$, $U_{10} = 44$, $P = 0.678$, $r = 0.12$; Fig. 3a). However, the
309 direction of body-alignments during electrosensing differed between personality types ($W_{10} =$
310 72 , $U_{10} = 17$, $P = 0.014$, $r = 0.66$; Fig. 3b), being left-sided in bold individuals (directional:
311 $\tilde{x}_{10} = -0.225$, $P = 0.022$) and right-sided in timid individuals (directional: $\tilde{x}_{10} = 0.314$, $P =$
312 0.022).

313 Individually, visual laterality was not significantly related to boldness, with only weak
314 links to PC scores noted for both laterality strength (absolute: $r_s = 0.378$, $P = 0.100$; Fig. 4a)
315 and direction (directional: $r_s = 0.288$, $P = 0.219$; Fig. 4b). On the contrary, while an increase
316 in boldness did not relate to the strength of individual electrosensory laterality (absolute: $r_s =$

317 0.033, $P = 0.889$; Fig. 4a), it significantly related to shifts in laterality direction from a strong
318 right to a strong left preference (directional: $r_s = 0.479$, $P = 0.033$; Fig. 4b).

319

320 **DISCUSSION**

321 We demonstrate that the direction of lateralisation for one sense is population wide
322 and not affected by personality, but for another sense the direction is strongly linked to
323 personality. Eye-use and lateral body-alignments for electrosensing were both strongly
324 lateralised in the *G. petersii* sample population during the inspection of a novel object (Fig.
325 2a). Given the strong contralateral connections of peripheral sensory cells, both photosensory
326 (visual) and electrosensory (Lázár et al., 1984; Vélez et al., 2017), this indicates that sensory
327 information is dominantly transferred to one hemisphere and suggests that it is used for a
328 particular brain function (Rogers, 2014). Although absolute laterality indices of *G. petersii*
329 show some individual variation in strength, both for vision and electrosensing (Fig. 4a), these
330 do not follow a pattern consistent with personality score. Indeed, the strength of laterality is
331 similar between bold and timid fish for both vision and electrosensing (Fig. 3a), which shows
332 that personality does not affect the extent to which laterality is utilised when inspecting
333 objects. Instead we find a preference amongst the population for lateralisations that are
334 consistent in direction for visual inspection, but differ in direction with personality for
335 electrosensory inspection (Fig. 3b and 4b).

336 In particular, the population exhibits strong visual lateralisation towards the right eye
337 (Fig. 2b), which reveals the dominant use of the left hemisphere during visual inspection. As
338 predicted, this finding is consistent with findings for other fish species during novel-object
339 inspection, such as the Sarasins minnow *Xenopoecilus sarasinorum* (Sovrano, 2004), and is
340 linked to the cognitive analysis of unfamiliar stimuli. However, our findings differ from
341 many studies identifying behavioural phenotypes to be related to the strength of visual

342 laterality (Reddon & Hurd, 2009; Irving & Brown, 2013), often more than the direction (e.g.
343 in the rainbowfish *Melanotaenia nigrans*; Brown & Bibost, 2014). This is not only
344 inconsistent with our findings for visual laterality, but also for electrosensory laterality, where
345 the strength is similar between phenotypes but the direction differs instead (Fig. 3b). Bolder
346 individuals had a left-side bias, whereas more timid individuals showed a preference for the
347 right body-side when electrosensing (Fig. 4b). This difference reflects a contralateral reversal
348 in control (Vélez et al., 2017) from the left hemisphere in timid individuals to the right
349 hemisphere in bold individuals. This differs from findings in other vertebrates, including
350 humans and other primates, where the right hemisphere is more strongly involved in
351 emotional and behavioural responses linked to increased timidity instead of increased
352 boldness (Rogers, 2002; Vallortigara & Rogers, 2005). However, it is consistent with
353 findings in fish, where the right hemisphere is associated to increased approach tendency and
354 the left hemisphere increased avoidance (Barth et al., 2005; Dadda et al., 2010). In their
355 review of collective evidence from fish, Bisazza and Brown (2011) suggest that, while the
356 strength of laterality exhibited during object inspection could be inherited, the direction may
357 rely on individual experience, which determines how objects are classified and analysed.
358 Although, this may also depend on the function of lateralisations, which may differ between
359 sensory systems.

360 Cognitive functions of the brain, such as stimulus analysis and spatial processing, are
361 often shared in a population and can thus involve shared expressions of sensory laterality
362 (Bisazza et al., 1998; Sovrano, 2004; Rogers, 2014). Laterality can enable individuals to use
363 both hemispheres simultaneously for carrying out different functions. For example,
364 lateralised chicks can discriminate pebbles from grains using their left hemisphere and
365 concurrently remain vigilant to predators by using their right hemisphere (Rogers et al.,
366 2004). However, mechanisms that control behavioural responses to perceived information

367 can be altered by individual experience and learning, during the development of their
368 personality (Stamps & Groothuis, 2010; Mathot, Wright, Kempenaers & Dingemanse, 2012).
369 Links between the direction of hemispheric asymmetries and aspects of personality, such as
370 fearfulness and aggressiveness, are found across vertebrates, including humans (Ocklenburg
371 & Gunturkun, 2012; Rogers, 2014). For example, the size of bilateral areas of the human
372 cingulate gyrus, responsible for mediating response to stimuli, is biased towards the right
373 hemisphere in more harm-avoidant individuals and towards the left in bolder individuals
374 (Pujol et al., 2002). Consequently, a personality-dependent behavioural function may rely on
375 structural asymmetries between hemispheres and related sensory lateralisations that vary in
376 direction within a population (e.g. in zebrafish; Barth et al., 2005; Dadda et al., 2010). Here
377 we get a first glimpse of shared and personality-dependent lateralisations occurring
378 simultaneously in separate senses (Fig. 2-4), and we can make some initial suggestions
379 regarding how the separation of functions between senses is brought about.

380 There is no direct phylogenetic evidence of trade-offs between the visual and
381 electrosensory system in *G. petersii*, but more cells and areas are devoted to the transfer of
382 electrosensory signals than visual signals to the brain (Stevens, Sukhum & Carlson, 2013).
383 One prominent example is the electrosensory lateral line lobe, which is exclusively reserved
384 for processing and controlling electrosensory input (Meek, Grant & Bell, 1999).
385 Another notable example is the thalamus, with neural labelling indicating the ventromedial
386 region being mostly involved in visual pathways, but the much larger preglomerular region
387 being mostly involved in electrosensory pathways (Wullimann & Glenn Northcutt, 1990).
388 Hemispheric asymmetries of input to the preglomerular region can indirectly lateralise
389 subsequent inputs from that region to the forebrain, further affecting emotional and
390 behavioural responses (Walker, 1980; Yamamoto & Ito, 2008). Even when exposed to the
391 same conditions, physiological mechanisms can appropriate individual brain structure,

392 neuronal growth and asymmetry during personality and behavioural development (Rogers et
393 al., 2004; Barth et al., 2005; Dadda et al., 2010; Rogers, 2014; Stamps & Groothuis, 2010).
394 Therefore, the effects of individual development would be greater for electrosensory
395 pathways that have a greater abundance of neurons and regions in the brain than vision
396 (Wullimann & Glenn Northcutt, 1990; Meek et al., 1999; Stevens et al., 2013), resulting in
397 electrosensing having a greater involvement in personality-related brain-functions.

398 Albeit less studied in *G. petersii*, the structure of the epithalamus may also be
399 involved in the effects of personality. The epithalamus is part of the vertebrate dorsal
400 diencephalic conduction system, involved in cognition, motivation and control of behavioural
401 response (Concha & Wilson, 2001; Golden et al., 2016). Of particular interest is the
402 habenular region, which is responsible for controlling neurotransmission from the forebrain
403 and hypothalamus to the hindbrain and is arguably associated with the development of
404 behavioral phenotypes (Andrew, 2006; Flanigan, Aleyasin, Takahashi, Golden & Russo,
405 2017). In zebrafish, the development of asymmetries in size and efferent innervation between
406 the left and right habenula (Barth et al., 2005) and the directional location of the parapineal
407 organ (Dadda et al., 2010) are linked to both the direction of sensory lateralisations and to
408 behavioural responses towards imminent risk and novel settings. Based on this combined
409 evidence, there is likelihood that asymmetries in the habenular complex may drive, at least
410 partly, the direction of sensory lateralisations, depending on personality phenotype.

411 The lateralisation of sensory input has a direct influence on brain function because of
412 the functional specialisations of each hemisphere (Ocklenburg & Gunturkun, 2012).
413 Therefore, the use of a sense for a particular function might also rely on the type of
414 information that sense can best detect. On one hand, the eye structure of *G. petersii* is adapted
415 for low sensitivity to spatial detail and visual noise (when visual conditions are not clear),
416 arguably for detecting predator movement in the murky waters they naturally inhabit

417 (Kreysing et al., 2012). On the other hand, the active use of the electric sense can provide
418 more detailed information; the sensing of autogenous electric signals enables the perception
419 of distance, shape, size and composition of objects interacting with the signals (von der
420 Emde, 2004). Therefore, electrosensing offers *G. petersii* more information than vision about
421 unfamiliar objects, which is crucial to assessing risk and for managing the uncertainty
422 imposed by novel settings when promoting a behavioural response, e.g. approach or
423 avoidance (Mathot et al., 2012). Notably, each sense is effective from different distances,
424 with electrosensing requiring closer approach than visual inspection (Schumacher et al.,
425 2016). These differences in distance were limited by our methodology, but could otherwise
426 interact with the approach tendencies of each phenotype. For example, especially timid fish
427 could invest more in visual inspections from a distance and avoid electrosensing that requires
428 closer approach. Testing the confounds of sensing distance in the future could prove
429 constructive in elucidating interactions between personality type and sense-use.

430 Collectively, our findings show that discrete senses can lateralise information
431 differently, enabling stimulus processing and response-organisation to occur simultaneously.
432 We find that this involves personality-dependent biases to laterality being specific to the
433 sense which provides more information and is more strongly represented in the brain. These
434 observations suggest that different senses can be selected for lateralisation in different ways,
435 arguably based on their information-value and input-dominance to the brain. The discrete
436 functional-lateralisation of senses has implications for how brains manage information and
437 for the evolution and development of brain structure. We look forward to future studies
438 examining this mechanism further in different vertebrates and identifying the involvement of
439 developmental processes.

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610 **Table 1.** Loadings extracted by the PCA on the covariance matrix of behaviours from the
 611 three novel-object tests (T1-3) in 20 *Gnathonemus petersii*.

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		<u>Component loadings^a</u>		
	<u>Behaviour</u>	PC1	PC2	Communalities ^b
614				
615	Avoidance			
616	Latency to approach plastic figurine (T1)	- 0.969	0.164	0.966
617	Latency to approach brass weight (T2)	- 0.951	0.305	0.997
618	Latency to approach silicone lure (T3)	- 0.950	0.282	0.983
619	Exploration			
620	Time inspecting object plastic figurine (T1)	0.842	0.078	0.715
621	Time inspecting object brass weight (T2)	0.926	0.353	0.982
622	Time inspecting object silicone lure (T3)	0.921	0.367	0.984
623				
624	<i>% variance explained</i>	<i>85.997</i>	<i>7.756</i>	
625	<i>Eigenvalue^c</i>	<i>5.106</i>	<i>0.465</i>	

626 ^a Correlation between PC and variable values

627 ^b Proportion of variable variance explained by the PC's

628 ^c Variance of transformed data used for each PC

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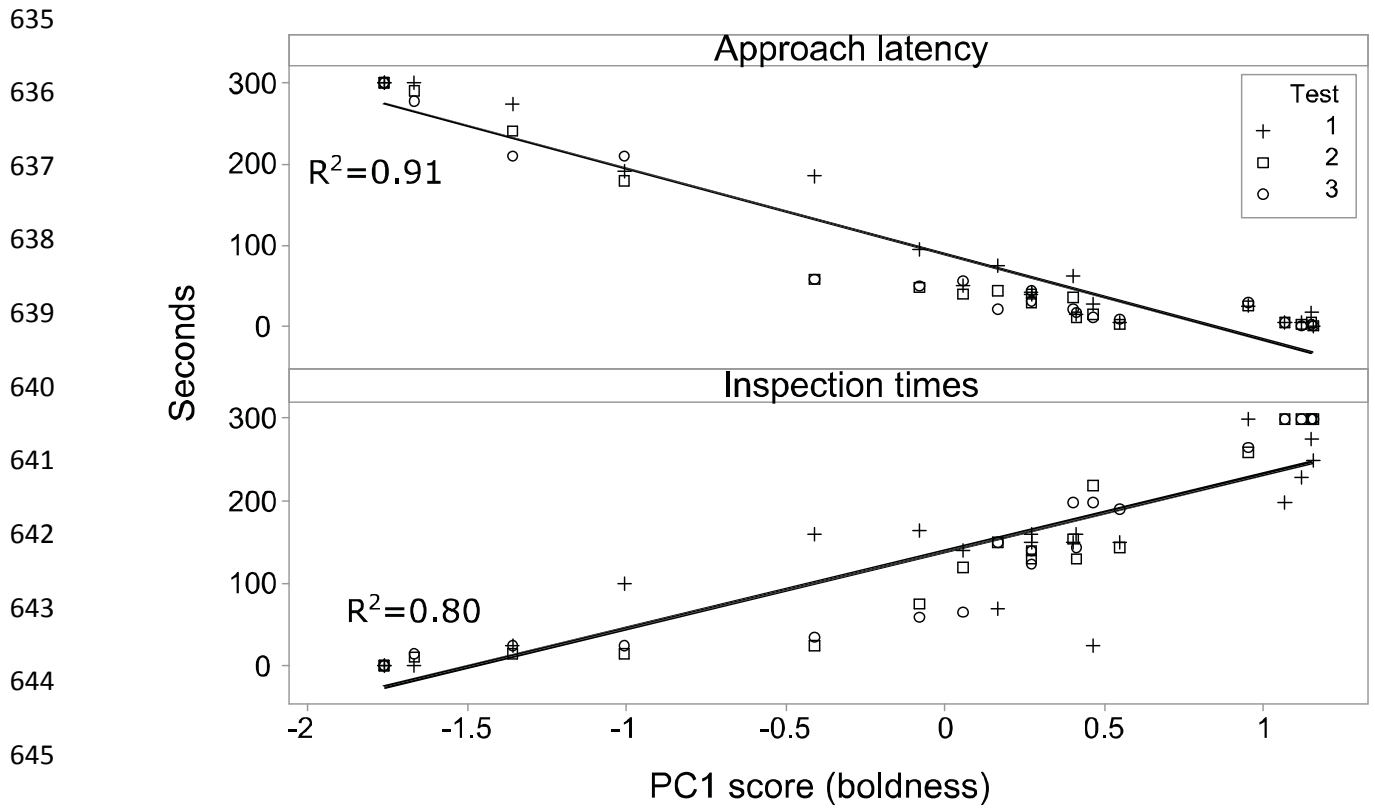
630 The first component (PC1) had the highest eigenvalue and explained most of the variance

631 from all measures, as illustrated here by comparisons to the second component (PC2). Bold

632 type indicates strong contributors to each component (coefficient > 0.3).

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648 **Figure 1:** Behavioural indicators of boldness, as they relate to the PC1 scores from the
 649 component analysis. Higher PC1 scores correspond to bolder individuals, which approached
 650 objects faster and inspected them longer across the three tests.

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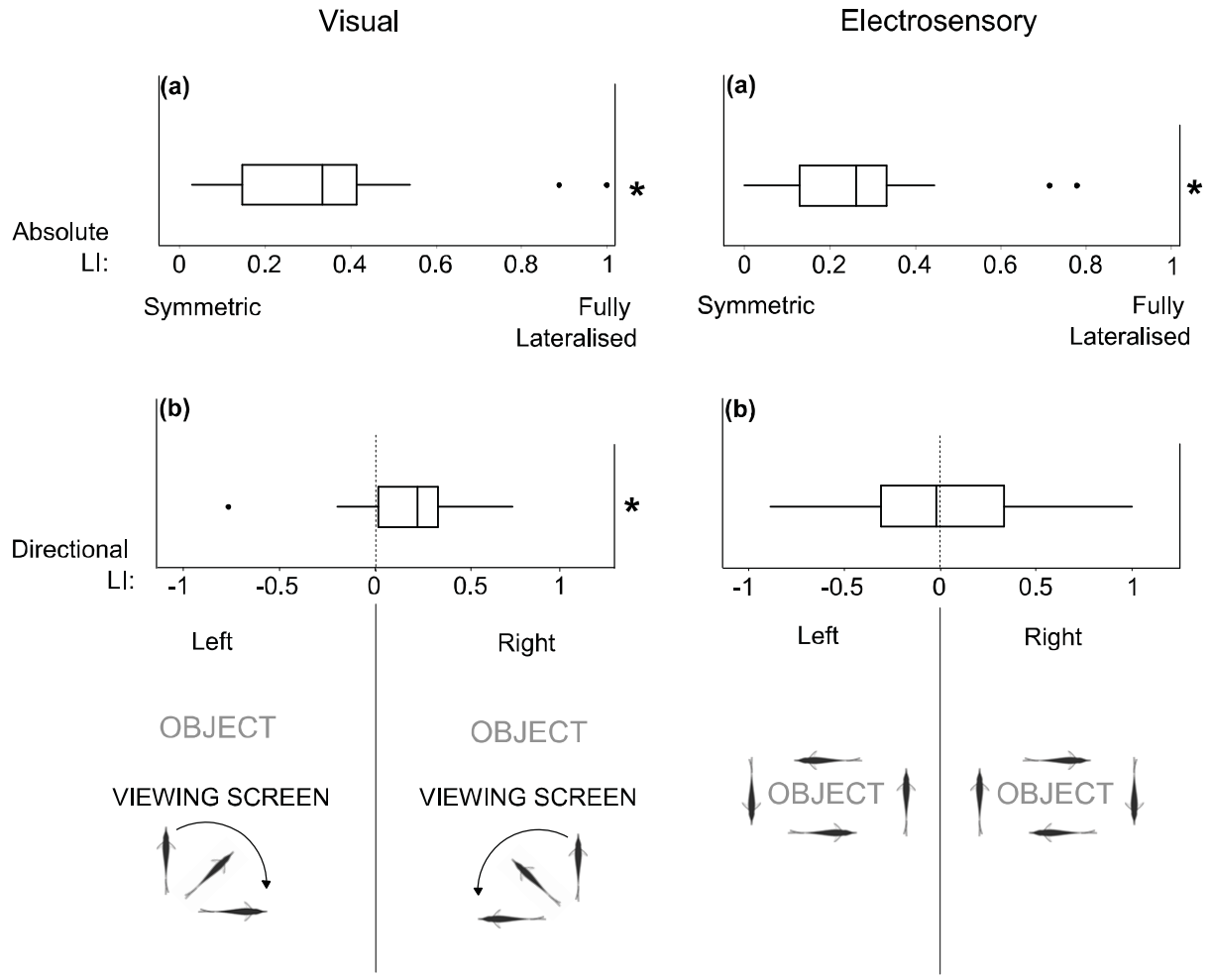
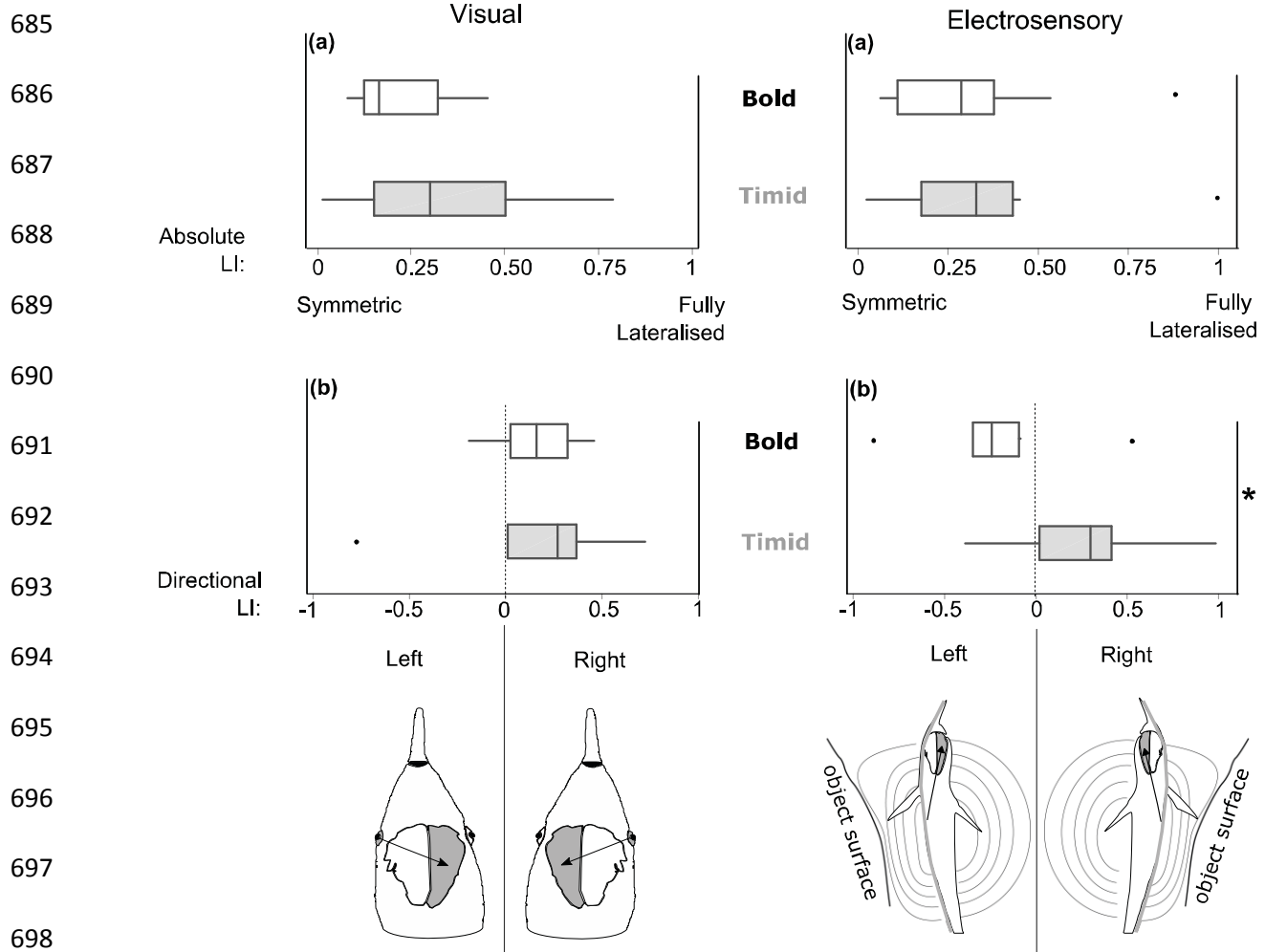


Figure 2: Population level laterality in the number of visual and electrosensory inspections as indicated by the median in individual laterality indices. The laterality of each individual was represented by the difference of left from right sided inspections as a proportion of the total number of inspections (LI), with absolute values indicating strength (a) and negative versus positive values indicating direction (b). The fish positions considered as left or right sided are illustrated below their respective direction in (b). [•outliers; * $P > 0.05$]



701 **Figure 3:** Comparisons of the strength (a) and direction (b) in visual and electrosensory
 702 laterality between bold and timid fish. Illustrations in (b) indicate how sensory input is
 703 lateralised depending on side preference during visual and electrosensory inspections, as
 704 would be expected from the strong contralateral connections of sensory cells to the brain
 705 (Lázár et al., 1984; Vélez et al., 2017). [•outliers; * $P > 0.05$]

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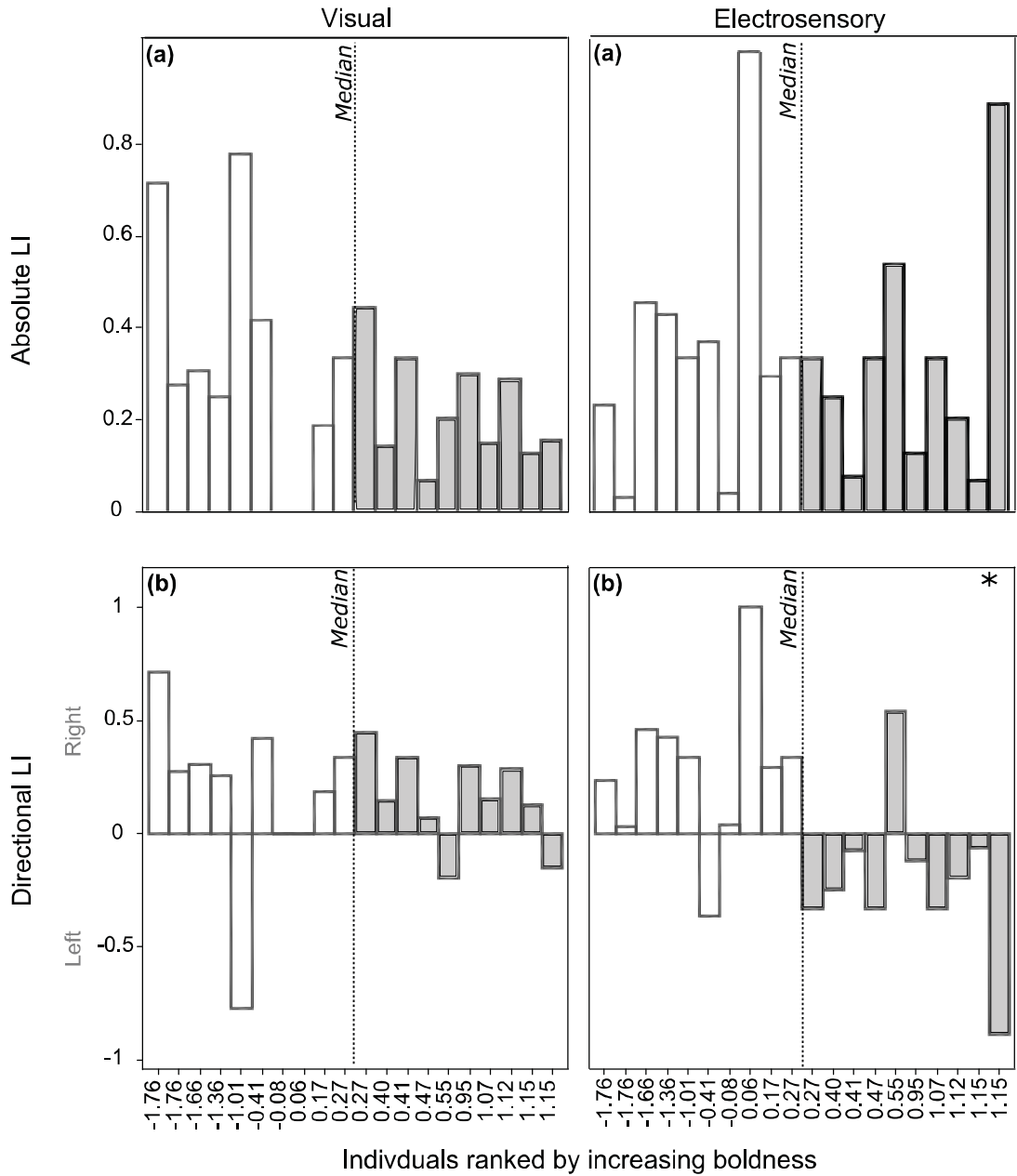


Figure 4: Absolute (a) and directional (b) laterality indices (LI) from the visual and electrosensory tests for each individual, ranked by boldness score. Timid individuals were those with below median boldness (white) and bold individuals were those with above median boldness (grey). Significant shifts were only found in the direction of electrosensory laterality with increasing boldness. [*ranked relationship with $P < 0.05$]

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735 **Table A1.** Counts of visual and electrosensory inspections and the calculated laterality index

736 (LI).

737	ID	Visual			LI	Electrosensory			LI
		<u>Count of inspections</u>				<u>Count of inspections</u>			
		Left-sided	Right-sided	Total		Left-sided	Right-sided	Total	
739	1	8	1	9	-0.778	2	4	6	0.333
	2	1	6	7	0.714	5	8	13	0.231
740	3	8	14	22	0.273	18	19	37	0.027
	4	7	17	24	0.417	13	6	19	-0.368
741	5	12	16	28	0.143	25	15	40	-0.25
	6	7	13	20	0.3	40	31	71	-0.127
742	7	6	10	16	0.25	2	5	7	0.429
	8	3	6	9	0.333	21	18	39	-0.077
743	9	11	16	27	0.185	6	11	17	0.294
	10	9	9	18	0	13	14	27	0.037
744	11	3	6	9	0.333	2	4	6	0.333
	12	15	11	26	-0.154	17	1	18	-0.889
745	13	3	2	5	-0.2	3	10	13	0.538
	14	3	3	6	0	0	5	5	1
746	15	5	13	18	0.444	4	2	6	-0.333
	16	8	15	23	0.304	3	8	11	0.455
747	17	23	31	54	0.148	14	7	21	-0.333
	18	7	8	15	0.067	6	3	9	-0.333
748	19	14	18	32	0.125	8	7	15	-0.067
749	20	10	18	28	0.286	6	4	10	-0.2

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