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ABSTRACT

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

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INTRODUCTION

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

An important function of sensory laterality is that by relegating information to a specialised area of the brain, other areas are free to engage in other tasks (Levy, 1977; Vallortigara, Rogers & Bisazza, 1999). Sensory lateralisations can be exhibited at both the population and at the individual level (Bisazza et al., 1998; Vallortigara & Rogers, 2005). When lateralisations are similar amongst a proportion of the population that exceeds what would be expected by chance (i.e. 50%), the degree and hemispheric direction of lateralisations is often found to depend on the cognitive requirements of a particular situation, such as recognising a familiar stimulus or assessing an unfamiliar one (Sorvano, 2014). Arguably, the adaptive value of these population-level lateralisations is that they enable coordination of social behaviour during group activities, including responses to predators in 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 (Bonnel & 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 e 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 ^{O}C, 7.2 ± 0.4 pH, 225 ± 75 µS/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).

Ethical note

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

Behavioural tests of boldness

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

Preliminary mixed-model analyses confirmed repeatability across the three novel-object tests in individual latency to approach (ICC = 0.970, $F_{19,38}$ = 16.01, $P < 0.001$) and individual inspection times (ICC = 0.833, $F_{19,38}$ = 98.77, $P < 0.001$), as expected for a 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 & Borcherding, 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 (Joliffe, 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° 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

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

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   were 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

RESULTS

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

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

Individually, visual laterality was not significantly related to boldness, with only weak links to PC scores noted for both laterality strength (absolute: $r_s = 0.378$, $P = 0.100$; Fig. 4a) and direction (directional: $r_s = 0.288$, $P = 0.219$; Fig. 4b). On the contrary, while an increase 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 electrosensosensory 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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Behaviour	Component loadings[a]		Communalities[b]
	PC1	PC2	
Avoidance			
Latency to approach plastic figurine (T1)	**- 0.969**	0.164	0.966
Latency to approach brass weight (T2)	**- 0.951**	**0.305**	0.997
Latency to approach silicone lure (T3)	**- 0.950**	0.282	0.983
Exploration			
Time inspecting object plastic figurine (T1)	**0.842**	0.078	0.715
Time inspecting object brass weight (T2)	**0.926**	**0.353**	0.982
Time inspecting object silicone lure (T3)	**0.921**	**0.367**	0.984
% variance explained	*85.997*	*7.756*	
Eigenvalue[c]	*5.106*	*0.465*	

[a] Correlation between PC and variable values

[b] Proportion of variable variance explained by the PC's

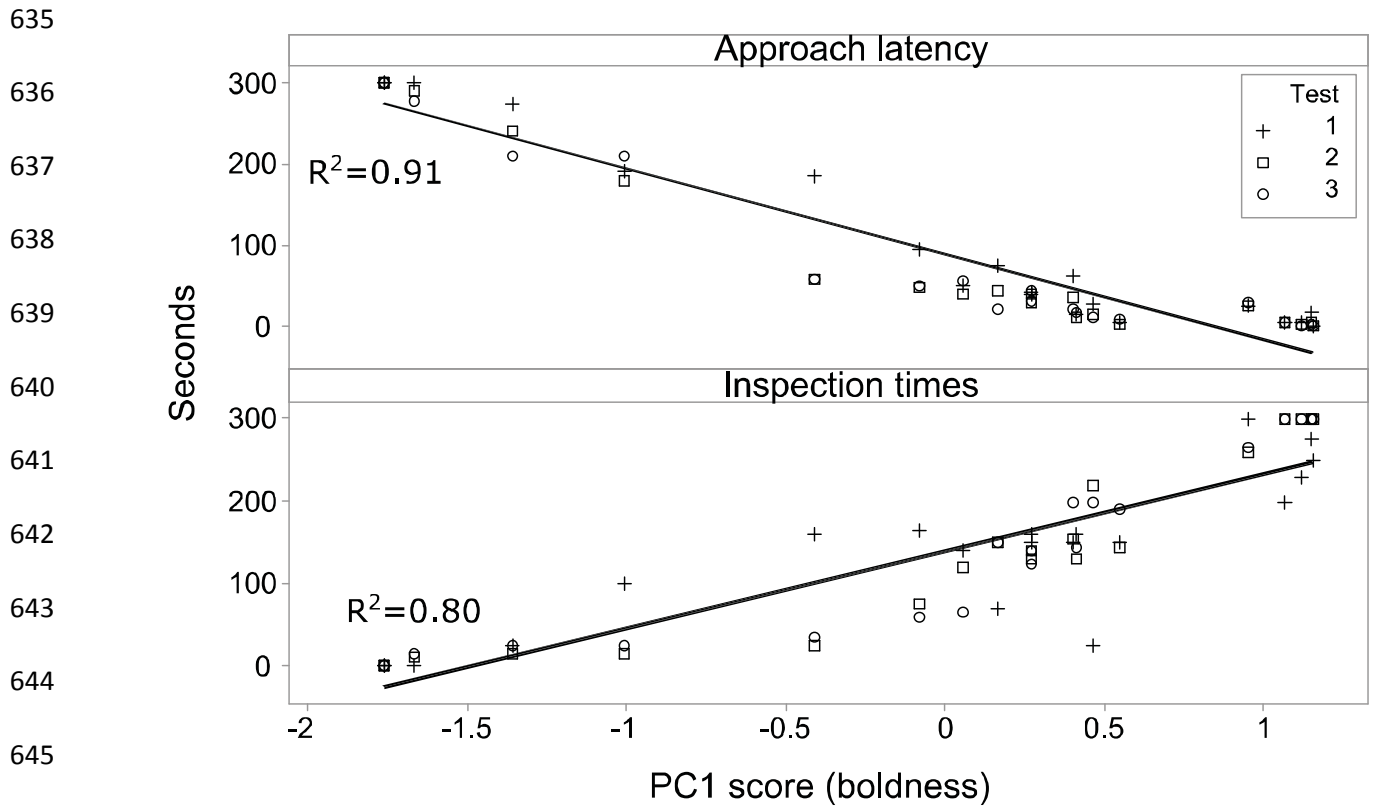[c] Variance of transformed data used for each PC

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

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

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

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Figure 1: Behavioural indicators of boldness, as they relate to the PC1 scores from the component analysis. Higher PC1 scores correspond to bolder individuals, which approached objects faster and inspected them longer across the three tests.
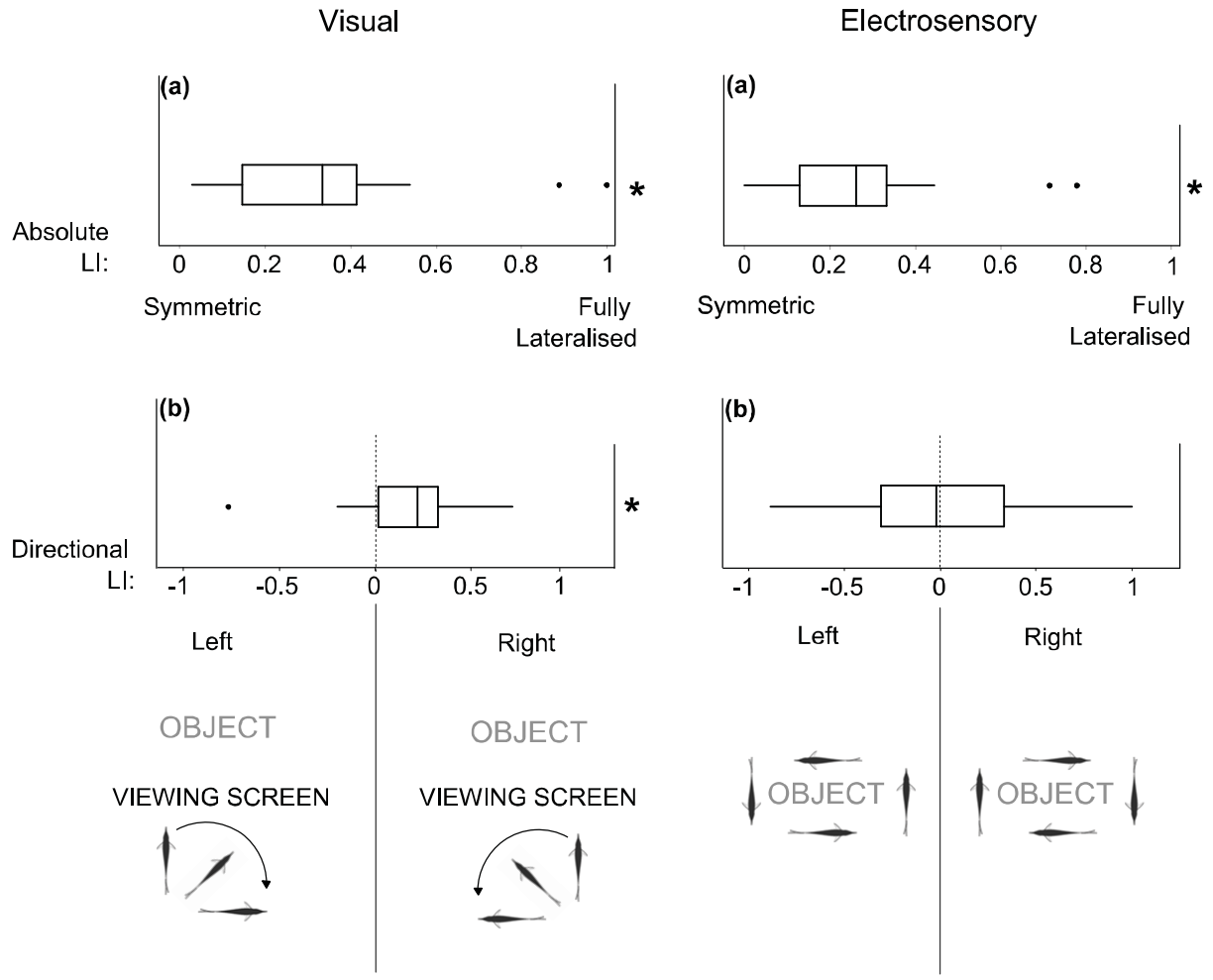
Figure 2: Population level laterality in the number of visual and electrosensory inspections as indicated by the median in individual laterality indices. The laterality of each individual was represented by the difference of left from right sided inspections as a proportion of the total number of inspections (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; *$P > 0.05$]
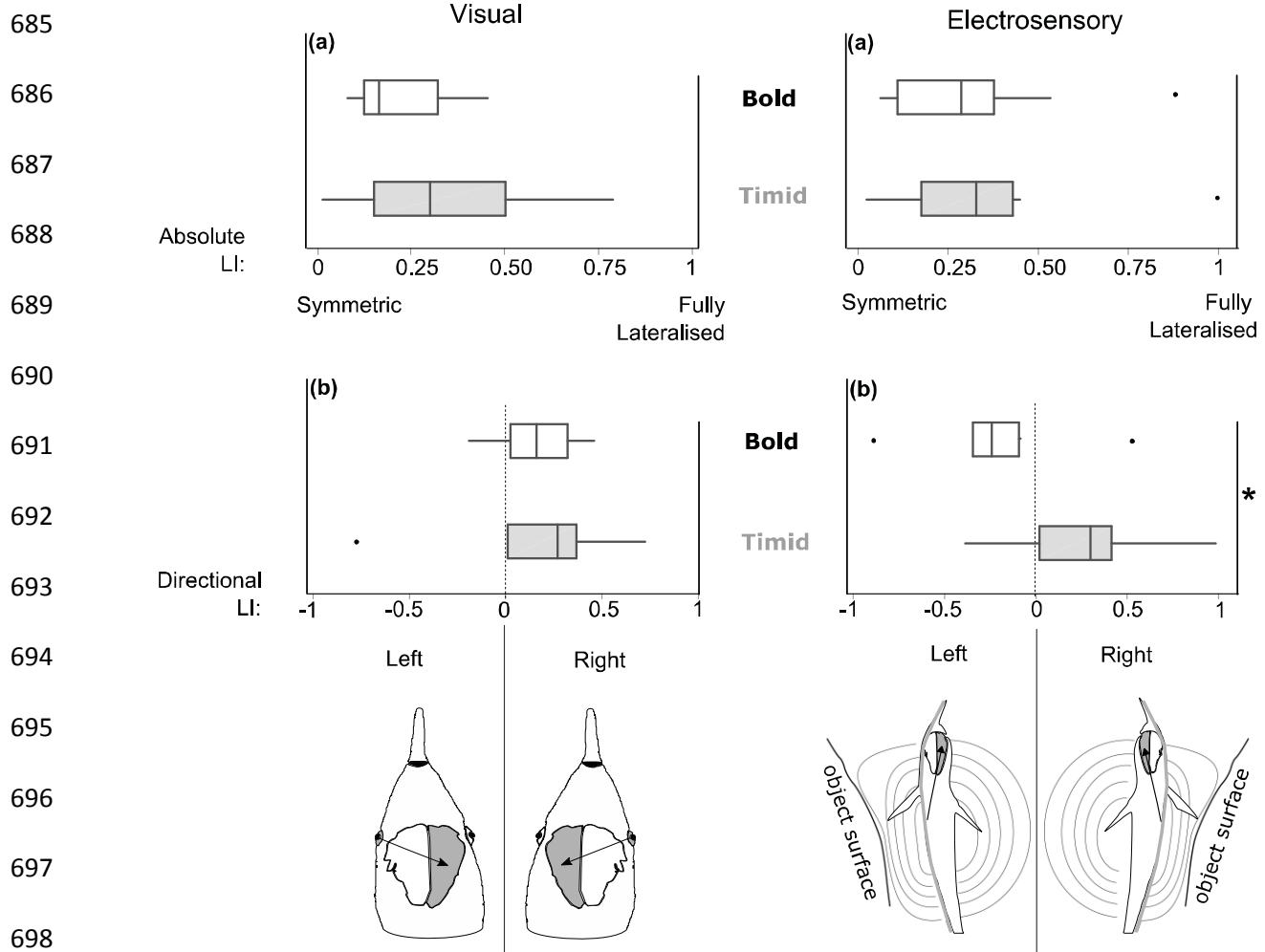
Figure 3: Comparisons of the strength (**a**) and direction (**b**) in visual and electrosensory laterality between bold and timid fish. Illustrations in (**b**) indicate how sensory input is lateralised depending on side preference during visual and electrosensory inspections, as would be expected from the strong contralateral connections of sensory cells to the brain (Lázár et al., 1984; Vélez et al., 2017). [•outliers; *$P > 0.05$]
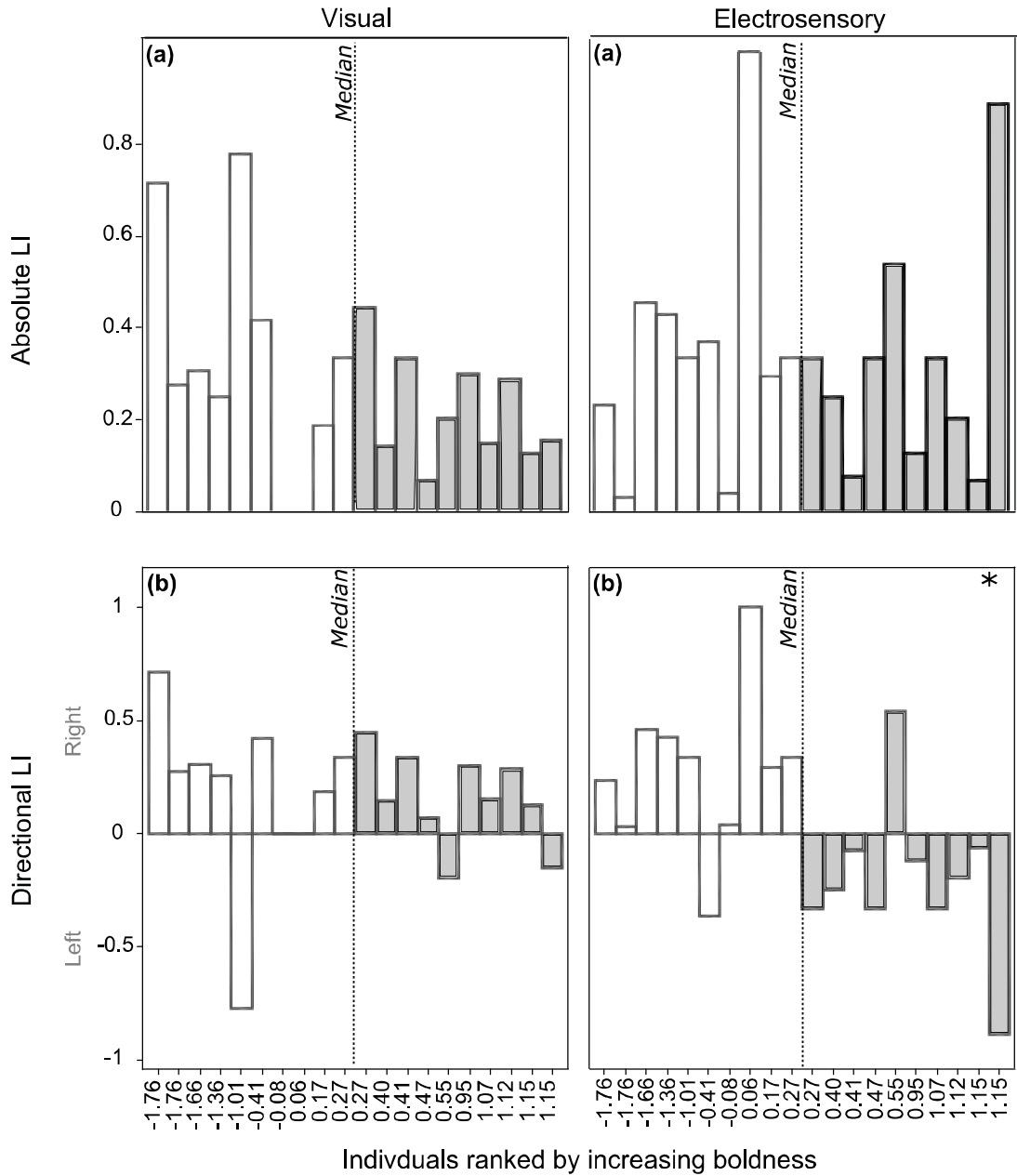
Figure 4: Absolute (**a**) and directional (**b**) laterality indices (LI) from the visual and electrosensory tests for each individual, ranked by boldness score. Timid individuals were those with below median boldness (white) and bold individuals were those with above median boldness (grey). Significant 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).

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

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