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Relationships between personality and lateralisation of sensory inputs

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ABSTRACT

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.

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

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,

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

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

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

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

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

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

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

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

EXPERIEMNTAL PROCEDURES

Animals and husbandry

Wild-caught *G. petersii* (70-100 mm, N = 20) of unidentifiable gender (phenotypic dimorphism is lost in captivity; Moller, 2002) were provided by a local supplier and first used in a separate behavioural study but were naïve to the tests employed here. Animals were kept individually in 15L tanks enriched with plants, toys and shelter. Tank water was filtered, heated, aerated and changed twice-weekly, kept at 26±1 ^{O}C, 7.2±0.4 pH, 225±75 μS/cm conductivity and a regulated bacterial cycle. Fish were fed daily, each with 15±5 chironomid larvae, and exposed to regular photoperiods, 12 h light to 12 h dark (0700-1900). 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

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

Laterality tests

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

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

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

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

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

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

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

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

Analysis

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

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

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

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 =

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

	Component loadings[a]		
Behaviour	PC1	PC2	Communalities[b]
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

The first component (PC1) had the highest eigenvalue and explained most of the variance from all measures, as illustrated here by comparisons to the second component (PC2). Bold type indicates strong contributors to each component (coefficient > 0.3).

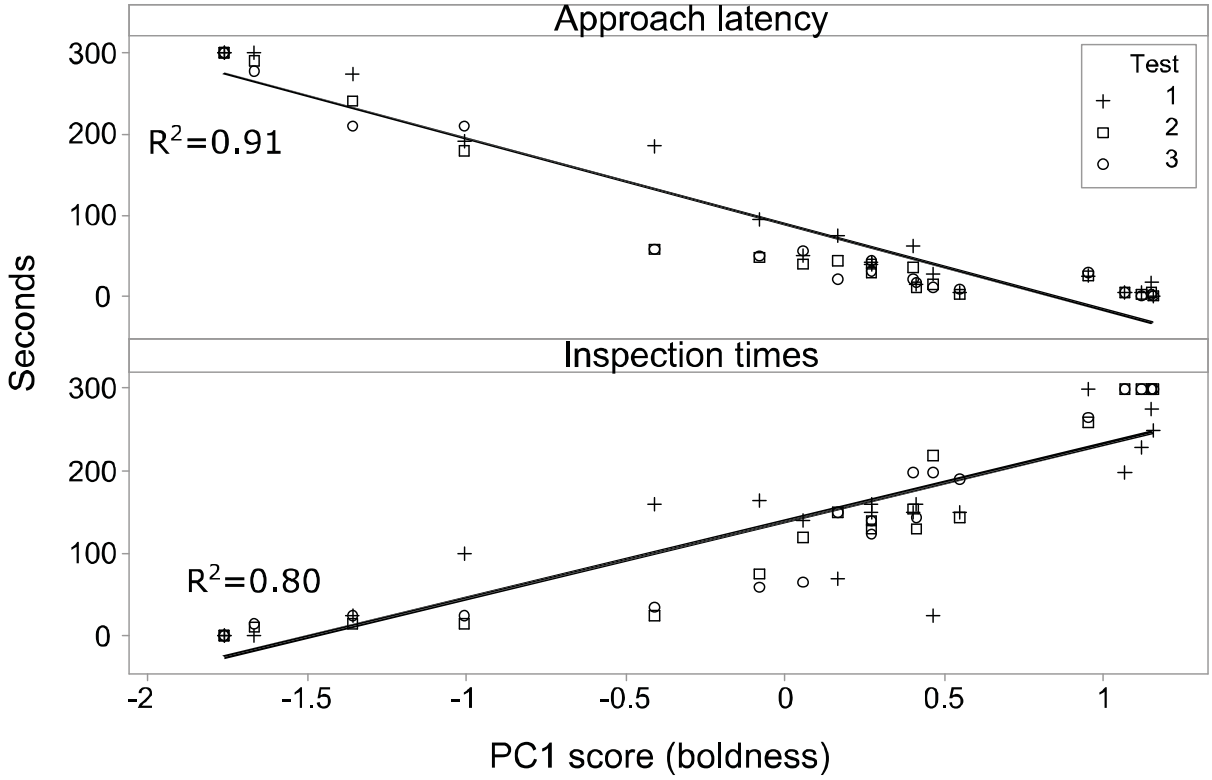

Figure 1: Behavioural indicators of boldness, as they relate to the PC1 scores from the component analysis. Higher PC1 scores correspond to bolder individuals, which approached objects faster and inspected them longer across the three tests.

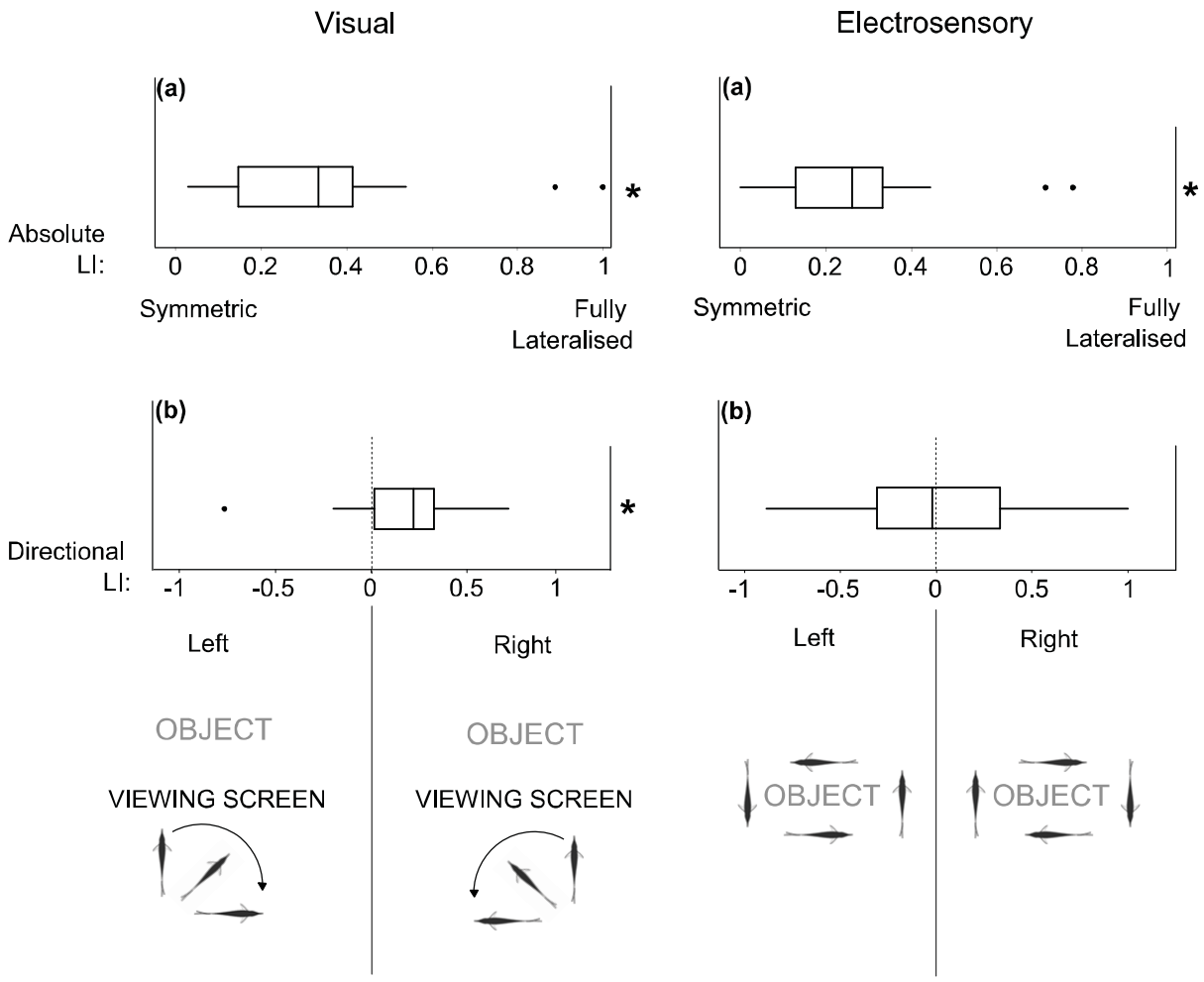

Figure 2: Population level laterality in the number of visual and electrosensory inspections as indicated by the median in individual laterality indices. The laterality of each individual was represented by the difference of left from right sided inspections as a proportion of the total number of inspections (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; *$P > 0.05$]

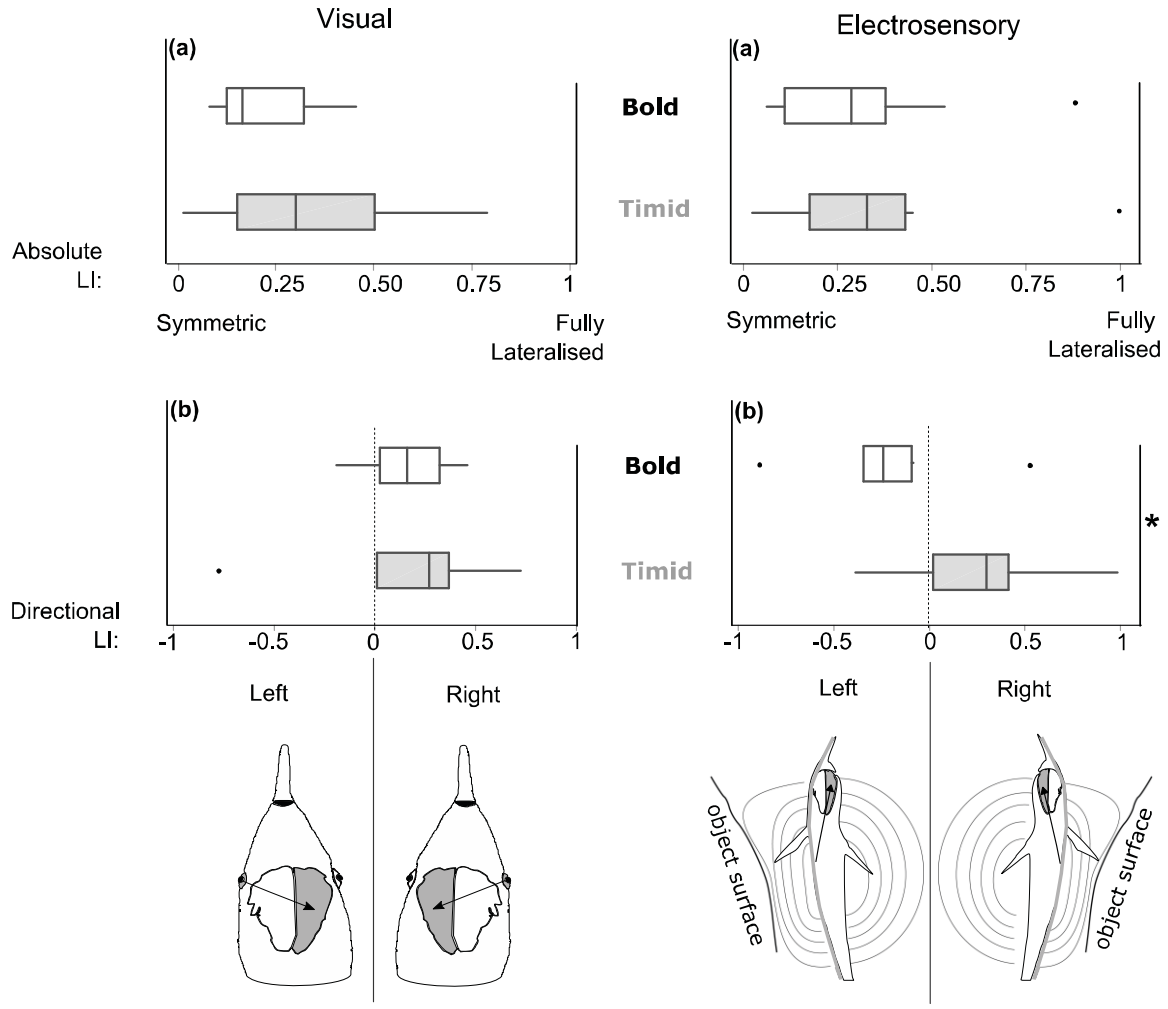

Figure 3: Comparisons of the strength (**a**) and direction (**b**) in visual and electrosensory laterality between bold and timid fish. Illustrations in (**b**) indicate how sensory input is lateralised depending on side preference during visual and electrosensory inspections, as would be expected from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

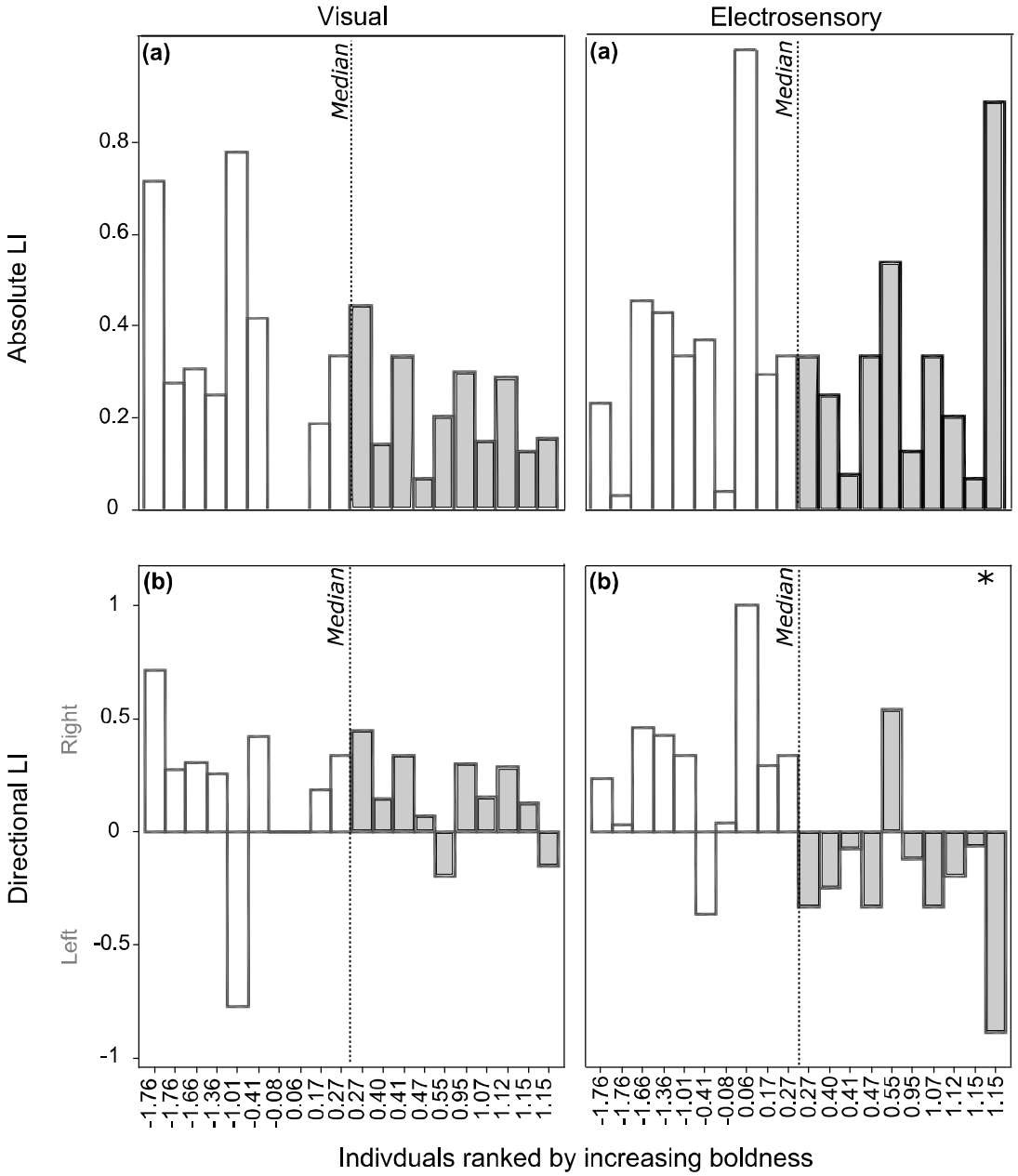

Figure 4: Absolute (**a**) and directional (**b**) laterality indices (LI) from the visual and electrosensory tests for each individual, ranked by boldness score. Timid individuals were those with below median boldness (white) and bold individuals were those with above median boldness (grey). Significant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

Table A1. Counts of visual and electrosensory inspections and the calculated laterality index (LI).

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