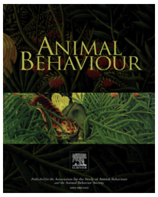
Animal Behaviour 141 (2018) 127–135

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Relationships between personality and lateralization of sensory inputs

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ARTICLE INFO

Article history:
Received 19 January 2018
Initial acceptance 1 March 2018
Final acceptance 25 April 2018

MS. number: 18-00052R

Keywords:
electrosensing
hemispheric functions
novel object inspection
personality
sensory laterality

In humans and other vertebrates, sensory information is sometimes lateralized towards one brain hemisphere that dominates the control of a task. Although sensory lateralization may depend on the stimuli being processed, the degree or direction of lateralization can differ according to behavioural phenotype. Accordingly, personality may play an important role in lateralization, yet there is a lack of evidence regarding how lateralizations are utilized to process information and promote a personality-based response to a particular situation. Here we show that simultaneous stimulus processing and organization 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*. We found that electrosensing is lateralized in this species, but differently between personality phenotypes: bold fish were lateralized towards the right hemisphere and timid fish the left. 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 reveals differences in functional laterality between sensory systems and the role of personality in eliciting these differences. The species has a stronger input of electrical signals than visual signals in its brain; therefore, sensory representation in the brain might drive the laterality differences.

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 (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Shettleworth, 2001). Owing to the bilateral organization of the brain, each hemisphere can be more strongly involved than the other hemisphere in a particular cognitive or behavioural function (Ocklenburg & Gunturkun, 2012; Toga & Thompson, 2003). 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 specializations 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 specialized area of the brain, it frees other areas to engage in other tasks (Levy, 1977; Vallortigara, Rogers, & Bisazza, 1999). Sensory lateralizations can be exhibited at both the population and the individual level (Bisazza et al., 1998; Vallortigara & Rogers, 2005). When lateralizations are similar among a percentage of the population exceeding that which would be expected by chance (i.e. 50%), the degree and hemispheric direction of lateralizations are often found to depend on the cognitive requirements of a particular situation, such as recognizing a familiar stimulus or assessing an unfamiliar one (Sovrano, 2004). Arguably, the adaptive value of these population level lateralizations 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 (Lucon-Xiccato & Bisazza, 2017; Rogers, 2014). More strongly lateralized 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

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

lateralized 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 (Facchin, Argenton, & Bisazza, 2009; Galaburda, Rosen, & Sherman, 1990). For instance, the direction of asymmetries in the epithalamus of the zebrafish, *Danio rerio*, 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 to increasing avoidance of novel cues over successive trials (Barth et al., 2005).

Although some authors have argued that functional links between sensory lateralization and behaviour depend on personality, research on nonhuman vertebrates has often failed 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 in which personality traits are tested. For example, Reddon and Hurd (2009), in a study of convict cichlids, *Archocentrus nigrofasciatus*, argued for a relationship between the strength of laterality and boldness, but measured boldness only once and used a single measure. A study of rainbowfish, *Melanotaenia nigrans*, measured boldness in the context of novel environment exploration, but tested links to visual laterality in a social interaction context, by utilizing 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 lateralization 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 lateralization 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 organizing 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 Perera, Thenert, & von der Emde, 2016). However, the integration of lateralization across different senses remains largely unexplored. A rare example, in the blue gourami, *Trichogaster trichopterus*, found vision and touch to be strongly lateralized 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 in 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 each side of the body project to the contralateral hemisphere, that is, left to right and right to left (Lázár, Libouban, & Szabo, 1984; Vélez, Kohashi, Lu, & Carlson, 2017). Lateralizations towards one hemisphere can thus be detected by observing side biases during sensing. Eye preference has been noted for *G. petersii* populations, when 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 et 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 lateralization by each sense and reveal links to personality.

Here we examined novel object inspection in this species to test links between laterality and personality. We also examined how context-specific laterality compares between different senses in vertebrates. The cognitive processing of objects, by attending to features, categorizing and identifying unfamiliar stimuli, is a left-hemisphere function in many vertebrates (Ocklenburg & Gunturkun, 2012; Vallortigara & Rogers, 2005) 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 lateralizations in *G. petersii*, therefore, we expected to see right-side preference when inspecting a novel object. Alternatively, if laterality is linked to the organization 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 lateralizations could be consistent between electrosensing and vision, we hypothesized 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.

METHODS

Animals and Husbandry

Wild-caught *G. petersii* (70–100 mm, $N = 20$) of unidentifiable sexes (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 15-litre tanks enriched with plants, toys and shelter. Tank water was filtered, heated, aerated and changed twice weekly, kept at 26 ± 1 °C, pH 7.2 ± 0.4, 225 ± 75 μS/cm conductivity and a regulated bacterial cycle. Fish were fed daily, each with 15 ± 5 chironomid larvae, and exposed to regular 12:12 h