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## The importance of understanding function and evolution

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### ABSTRACT

Ocklenburg et al. (2020, *Laterality* 2020: Entering the next decade. *Laterality*) provided the field of laterality research with a stimulating research perspective for the coming decade, based on the current state of the art in both animal and human laterality research. Although this paper takes many different approaches of laterality into account, we emphasize that the eco-evolutionary approach needs more attention. This concerns the question why organisms are lateralized in the first place, in other words, how does lateralization enhance the Darwinian fitness of the individual. We argue that laterality can be distinguished along four dimensions, and that each of them requires different ultimate explanations. Studying these functional and evolutionary explanations requires the development of ecologically relevant tests, adapted to the species at hand. It also requires experimental manipulation of laterality, testing the effect in (semi)-natural conditions on fitness parameters. Tools for such manipulation of laterality urgently require a better understanding of the developmental plasticity of lateralization, extending the field of evo-devo to that of eco-evo-devo. We also warn against seeing the minority in the distribution of direction or strength of lateralization as being a pathology as such minorities in biology can often be explained as adaptations by natural frequency dependent selection.

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Ocklenburg and colleagues (2020) did a great job in outlining both the state of the art and the future perspectives of the field of laterality research, throwing their nets widely. Their paper and the discussions it will provoke will be hugely beneficial for the field and the journal *Laterality*. Hopefully, it will

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also increase the interest for laterality research from the international community that is still somewhat undervalued in behavioural neurosciences, behavioural biology and ecology.

Given the space provided we like to focus on one in our view important aspect of laterality research that was somewhat underexposed in the paper: the question about why are we lateralized in the first place? This is the question about Darwinian function and evolution, and relates to reproduction and fitness. The discovery that lateralization of the nervous system and behaviour is a fundamental part of the design of all animals has provided us with the potential to use animal models both to extend the field from correlative and descriptive studies to experimental approaches, as well as to study the Darwinian function and evolution of lateralization, integrating biology with psychology. Moreover, studies on fossil evidence show that lateralized behaviour is indeed very old (Reisz, MacDougall, LeBlanc, Scott, & Nagesan, 2020). However, studying these issues and generating relevant hypotheses need, among others, a clarification and consensus on two issues: which aspects of lateralization are we dealing with and how to test their Darwinian function in an ecologically relevant way.

As for the first issue, we should distinguish lateralization along no less than four axes: on one axis direction versus strength (now often mixed in, for example, the classical laterality index), on the second axis preference versus skill, on the third which trait is lateralized and on the fourth the individual versus the population level. Mixing or not specifying these different components may confuse the field. Being specific about these different components may generate different hypotheses. It can be argued that for laterality at the individual level the absolute difference in skill between both limbs or the absolute skill of the best performing limb might be more important for Darwinian selection than the direction of preference. This is because how adequate a task is performed and how well it is coordinated between both limbs may be more important than with which limb it is performed. After all, evolution selects on the outcome, not directly on its underlying mechanism. At the population level direction of lateralization might be important for behaviour in order to synchronize it with conspecifics either because of social interactions within the species, to escape predators (Bisazza et al., 2000a; Vallortigara & Rogers, 2005), or to facilitate imitation for making tools (Zickert, Geuze, Tiedstra, & Groothuis, [in minor revision](#)). On the other hand, this synchronization at the population level may be less relevant for cognitive aspects that do not translate into lateralized behaviour but in cognitive skills. For the lateralization of cognitive processes at the individual level several adaptive hypotheses have been suggested, including hemispheric specialization, avoiding crowding within one hemisphere, and avoiding time consuming coordination between the

two hemispheres (e.g., Vallortigara & Rogers, 2005). The jury is still out for all these hypotheses. Moreover, the latter hypotheses do not explain why we have two hemispheres in the first place since without two separate hemispheres the need for counteracting a “crowding effect” by division of tasks over both hemispheres and mitigating hemispheric communication and coordination would not be needed. The evolutionary reasons to develop two hemispheres need to be better understood. We also do not understand why some species have a well-developed corpus callosum while others appear to have solved the need for inter hemispheric communication in other structures. Finally, the overall classification of each hemisphere in two distinct overall functional categories should be critically evaluated. It has now become apparent that at least in humans the pattern of distribution of lateralized functions over the two hemispheres differs considerable among individuals, warranting caution about generalized statements about our species specific default in this respect (Lust et al., 2011; Stroobant, Buijs, & Vingerhoets, 2009; Zickert et al., *in revision* ).

There is a tendency in the field to associate atypical handedness with pathologies, or at least traits with a negative connotation. This may stem from the common approach in the medical field where traits characterizing the majority are qualified as normal and those that deviate from this as abnormal. Hence many studies have looked at associations between atypical or left handedness and pathologies such as schizophrenia, dyslexia, ADHD, criminal behaviour and so on (e.g., Markou, Banu, & Papadatou-Pastou, 2017; Savopoulos & Lindell, 2018). However, a biologist would look at minorities in a completely different way. They would argue that the “deviation” cannot be all bad as otherwise Darwinian selection would have it weeded out. Instead, biologists look at cost–benefit trade-offs of a trait, and would hypothesize that by negative frequency dependent selection minorities can obtain equal fitness as individuals from the majority (Ghirlanda & Vallortigara, 2004; Faurie & Raymond, 2005; Groothuis, McManus, Schaafsma, & Geuze, 2013). We as scientists have to be careful not to fuel unsubstantiated negative connotation with the word left, as is the case in the majority of languages (Schiefenhövel, 2013).

Answering these important questions need, among others, and as Ocklenburg, Berretz, Packheiser, and Friedrich, (2020) bring forward, testing animals in their ecological context and comparative approaches. This brings us to the second issue mentioned in our introduction: how to design ecologically relevant tests for different species in different ecological conditions. For example, testing subjects in non-western cultures might require different lateralization tests than the prevalent ones used for western culture (e.g., Schaafsma et al., 2012). However, adapting tests to species specific behaviour and ecological conditions may create difficulties for validation and

generalization and species comparison. The introduction of consensus papers by experts on such topics would be of great help to the field.

The next step for testing the Darwinian function of lateralization should be an experimental approach. As the paper of Ocklenburg et al. rightfully state, the finding that many animals are lateralized, provides us the possibility for such experimentation. However, this is not only relevant for testing mechanistic hypotheses, but also hypotheses about their Darwinian functions. Ideally, studies would not only encompass testing the effect of the manipulation on the performance of a specific task, such as predator detection, but also whether and how this translates to survival and reproduction. This will give more insight into the cost–benefit trade-offs of the different traits by which the net detrimental effect of one trait may be compensated for by a net positive effect of another. Such studies should therefore be performed under semi-natural or field conditions for which lizards, fish and birds would be feasible subjects. Luckily, the development of lateralization is much more open for environmental factors than previously thought (see also Ocklenburg et al., 2020), and manipulations in early sensitive phases may have organizing long term effects on the brain. In addition, selection lines for different patterns of lateralization (Bisazza, Dadda, Facchin, & Vigo, 2007, Bisazza, A., Facchin, L., & Vallortigara 2000b) might be used. Apart from asymmetrical light exposure for the visual system and perhaps steroid hormones for several other traits, we are unfortunately only scratching the surface of detecting the factors affecting early developmental plasticity in lateralization, including the so called missing heritability, (Danchin, 2013). With respect to the latter, we have manipulated in a series of studies prenatal exposure to steroids within the physiological range, mimicking maternal hormone exposure in bird and fish species (Schaafsma & Groothuis, 2012), based on the correlation between indices of lateralization and testosterone concentration in human amniotic fluid (Beking et al., 2018; Lust et al., 2010, 2011). In addition, we made use of hormonal treatment of transsexuals as an experimental approach in our own species (Beking et al., 2020). These studies do reveal the effects of early exposure to gonadal hormones, in part in interaction with hormone exposure in puberty, nowadays recognized as a second sensitive period for development in at least mammalian species (Zimmermann, Kaiser, Hennessy, & Sachser, 2017). Clearly, proximate studies on development incorporating different aspects of lateralization in several traits may substantially fertilize ultimate studies on lateralization in the future, leading to an integrative eco-evo-devo approach to the study of laterality.

### Disclosure statement

No potential conflict of interest was reported by the author(s).

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