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Comment

Phenotypes in hemispheric functional segregation as by-products of the evolution of lateralization population structure
Comment on "Phenotypes in hemispheric functional segregation? Perspectives and challenges" by Guy Vingerhoets

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I would like to comment on Guy Vingerhoets's [1] excellent essay on the different phenotypes associated with brain and behavioural lateralization focusing on the issue of the origin of directional asymmetries, and on how a theory based on mathematical theory of games can account for the population structure of typical and atypical lateralization phenotypes.

There is growing consensus that a certain (moderate) degree of left-right asymmetry in the nervous system can convey computational and thus fitness advantages to vertebrate [2–4] and perhaps also to invertebrate organisms [5–8]. The list of the suggested possible computational advantages comprises *(i)* increased neural capacity because specialization of one side of the brain for a cognitive function avoids useless duplication of cognitive functions between the two sides of the brain [2], *(ii)* the possibility to take charge of control of unilateral response from lateralized sensory input [9], *(iii)* the decrease of reaction times as a result of increased learning with one perceptual or motor system, giving rise to a time advantage of the dominant side [10], *(iv)* the possibility of simultaneous and parallel processing in the two hemispheres [11]. However, it is apparent that all these advantages held at the individual level and do not require, to be effective, the alignment of asymmetries at the level of population. Besides, the structure of population-level lateralization is not uniform, i.e., with all individuals showing the same direction of bias. We know from a long time that handedness in humans shows a peculiar structure at the population level, with a majority of individuals favouring one hand (right-handers) and a minority the other one (left-handers) [12]. Now, as clearly pointed out in Vingerhoets's [1] paper we recognize that variations in the standard blueprint of animal brain lateralization exist and take at least two forms: that of complete mirror reversal of typical lateralization, and that of atypical lateralization in which some, but not all, functions show mirror reversal, and thus there could be crowding of functions that usually (i.e., in the majority of individuals) would not share the same side of the brain.

A crucial question in my view is *why* the structure of population lateralization in vertebrates has the form it has, namely why left- and right-type phenotypes are often in a definite proportion different from 50:50. Why aren't left-

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and right-phenotypes equally common? The explanations offered for lateralization of brain function (e.g., that it may avoid unnecessary duplication of neural circuitry and reduce interference between functions etc., see above) cannot account this fact, because increased individual efficiency is unrelated to the alignment of lateralization at the population level. A further puzzle is that such an alignment may even be a disadvantage, as it makes individual behaviour predictable to other organisms [13]. Some years ago I proposed with my colleagues that alignment of the direction of behavioural asymmetries in a population can arise as an "evolutionarily stable strategy" – a basic concept in evolutionary biology conveying the simple idea that what is best to do for an individual may depend on what the majority of the individuals of the group do [14,15]. The formal proof of the hypothesis requires some mathematics [16,17] but the basic idea can be conveyed straightforwardly: I argued that directional behavioural lateralization as we know it in humans and other species may have evolved when individually asymmetrical organisms have been in the need to coordinate their behaviour with that of other asymmetrical organisms. This does not necessarily mean that social species should be lateralized at the population level and solitary ones at the individual level, as the theory has sometimes been misinterpreted (see for a discussion [18]). The nature of social interaction can generate evolutionarily stable strategies of lateralization at both the individual- or population-level depending on ecological contexts. For instance, population-level asymmetries have been observed in aggressive and mating displays in so-called "solitary" insects [19,20], suggesting that engagement in specific inter-individual interactions rather than "being social" in general does generate population-level lateralization [18].

The type of interactive behaviour is also important [17]. For example, if predators can attack prey on either right or left sides it would be more convenient for them to be unpredictable. This is the case of sailfish, which have been shown to be lateralized at the individual-level in attacking schooling sardines on one side. The stronger they are lateralized, the more successful they are at capturing their preys but overall they do not show any population-level bias [21]. In contrast, the alignment within a population may be linked to the need of an individual to position itself in a congruent way from a postural/motor point of view, as it happens for instance during shoaling [22].

This sort of analyses, which admittedly are more common in evolutionary biology than in cognitive neuroscience, could inform, in my view, a proper understanding of phenotypic variation in hemispheric functional segregation. Complete mirror reversal of typical hemispheric complementary can be expected simply because left- and right-phenotypes do not have any intrinsic advantage in themselves. The point to stress, however, is that such a stable polymorphism is possible only if one phenotypic variation is limited to a minority of individuals. Theoretical analyses [16] have shown that stable polymorphisms in population structure – with a minority showing complete mirror reversal – can spontaneously emerge and be maintained by frequency-dependent selection (see also [23]). Consider a situation like prey-predator interaction in which prey dilute the risk of predation by shoaling: since there is not any intrinsic benefit of left or right lateralization, there are always two specular solutions, one with a majority of left-type prey and one with a majority of right-type prey. The majority of prey get protection by keeping together (shoaling), but pay a cost because predators are better at handling them; thus, a minority of prey manages to enjoy the same escape probability by trading-off protection from the group with an advantage in the face of predators [16].

Reversal of typical laterality segregation would be expected whether symmetry breaking occurred as a single event, with all the different types of functional lateralization being derived from it. This seems unlikely, however. Symmetry breaking events should have been occurring at the level of individuals, to whom asymmetry conveys computational/cognitive (and thus fitness) advantages. Whether or not these individual-level asymmetries need to be aligned at the population level (with frequency-dependent minorities phenotypes) clearly depends on tasks and ecological demands. Some functions could have been segregated independently from each other and at different times during evolution. There could be also asymmetries in the nervous systems that are not producing any bias in overt behaviour (and thus that would be not subjected to any selective pressure for aligning at the population level because of the absence of any inter-individual "social" constraint). Thus, atypical segregation could be also maintained by frequency-dependent selection which would be operating on specific tasks or functions.

Nonetheless, I concur with Vingerhoets that for atypical functional segregation phenotype a major impact on behaviour should be expected. I would speculate that this may be related to the particular logical demands associated with phenomena of functional incompatibility within neural mechanisms originally devoted to the solution of a particular and circumscribed problem when they have to be coopted for novel tasks [24]. Separate and independent segregation of functions associated with different task demands may have promoted arrangement in which the minority phenotypes have frequency-dependent advantage for single tasks but do experience disadvantages associated with the combination of functionally incoherent and incompatibles functions within each hemisphere. I would predict disadvantages should be apparent while performing two tasks simultaneously rather than single tasks [11].

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