A Critique on Studies of Brain Lateralization

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Abstract. Giorgio Vallortigara has been devoting his life to neuroscience and has made great strides in brain lateralization. The current paper mainly critiques his and his colleagues' two studies and one related study on brain lateralization, which have mainly covered individual and population- level asymmetry. The first paper claimed that the putative advantages associated with lateralization could not explain the specific disadvantages associated with directional asymmetry. They assumed that population-level asymmetries arise due to the need to coordinate behavior among individuals behaviorally asymmetric. The second article summarized recent experiments conducted by scientists and presented them in conceptual models. They explained the causes of individual brain lateralization from three main perspectives. The third paper concluded that the ESS (Evolutionarily Stable Strategy) remains the most potent and widespread evolutionary hypothesis to explain lateralization, and individual-level or population-level lateralization emerges as an ESS. This paper concludes that the orientation of individual lateralization has an essential impact on the stability of population behavioral asymmetry with ESS tendencies. Additionally, some innovative ideas and prospects for future research potentials are discussed.

Keywords: asymmetry, brain lateralization, individual-level, population-level, lateralization of behavior, directional asymmetry, ESS model.

1. Introduction

Brain lateralization studies include neuroethology, biology, psychology, and evolution, which is too often a conceptual science in brain research. Neuroscientists also have been making theoretical breakthroughs from multiple perspectives [1,2,3]. From the very beginning in this field, Gott-fried Reinhold Treviranus described for the first time apparent asymmetries of the human cortex: "Humans have multitude and deep convolutions that are asymmetrically organized in the two hemispheres [4]. This is different from the cortex of monkeys". Since then, scientists have analyzed and summarized various studies to solve the mystery of brain asymmetry. Giorgio Vallortigara is an Italian neuroscientist from the Department of Psychology and BRAIN Centre for Neuroscience, University of Trieste. He has been doing several studies on brain lateralization. In 2005, by analyzing the mechanism and results of such studies ranging from individual-level advantages and drawbacks to population-level, the first paper he wrote provided a general overview of the benefits and disadvantages of brain lateralization. The article highlights population-level asymmetry versus individual behavioral asymmetry and makes appropriate assumptions about how hormones affect brain lateralization [1]. However, in 2018, he published another paper with much the same focus on brain lateralization. The second paper further summarizes the advantages and disadvantages of individual lateralization and reviews two ESS models [2]. This paper adds a third article [3] to update the understanding of individual-level lateralization to show the limitation of the first paper. Additionally, this paper will compare and analyze the differences between these three articles, expound on the calculation principles and mechanism of the two ESS models, and summarize the maturity and defects of their arguments.

2. Summary

2.1. The factors that affect individual-level brain lateralization

In recent years, the study of asymmetries has just moved from human-centered to non-human animal groups. This research area remained outside biology because of a focus on causal mechanisms rather than their function. However, Vallortigara and Rogers find evidence for lateral biases affecting everyday behavior in the natural environment of various species, which leads the research into a new area: biology [1].

In 2020, Onur, Felix, and Sebastian [5] found that a single genetic factor is insufficient to explain any lateralized function's ontogeny. Instead, it may be a mixture of several genetic, environmental, and epigenetic factors. They analyzed the impact on the population level from three initial factors: Genetic, environmental, and Epigenetic Factors.

To analyze the influence of genetic factors, they set an experiment to test the role of cilia function in the emergence of hemispheric asymmetries. Firstly, the embryo image shows the asymmetric expression of Nodal on the left side. It has been affected by a viral phenomenon, "Nodal flow." However, due to their protein and cytoskeletal structure, these rotations can only occur in one direction, causing a weak fluid movement at the surface of or in the node. This phenomenon explains the association with genetic factors from the view of structural function. Only a few pieces of evidence mentioned the specific bond between gene expression and the results, one of which is that it has been shown in both mice and zebrafish that the flow causes a stronger calcium influx in the cells on the left than on the right side of the nod, which demonstrates the higher gene expression directly [5]. In the early days, single-gene inheritance was the primary research factor that scientists used. In the first paper, they claimed that the allele which specifies left- handedness or right-handedness at random determines the presence of lateralization but not its direction. Since such issues of handedness can only be explained by epigenetic factors instead of genetic factors, this claim can be proved inadequate. After nearly a decade of research,

epigenetic factors gradually entered the field of study. The epigenetic mechanism changes gene expression through modification, such as DNA methylation, without changing nucleotide sequence, leading to phenotypic changes. This explains the previous problem that single-gene inheritance cannot entirely solve handedness. However, the current research objects are essential but limited, and more experimental samples are needed to explain the more direct mechanism.

Additionally, Individuals are influenced by specific environmental factors. They reviewed a well-researched example, comparing chicks exposed to light before hatching with those incubated in the dark showed that light exposure aligned and enhanced visual lateralization in some tasks [5]. In contrast, visual lateralization is weak when hatched in the dark. Through a controlled experiment, it was proved that light caused functional lateralization. As a result, the ability of visual capture and discrimination of strongly lateralized individuals is much higher than that of lightly lateralized individuals. There is much debate about the correlation between individuals and populations and the evidence that lateralization evolution at the individual level must lead to dominance at the population level.

2.2. The determination of the incentives for population-level asymmetry through the advantages and drawbacks of individual-level brain lateralization

In the first article, Vallortigara and Rogers proposed that population-level asymmetries are related to lateralized species' diverse aspects of social interactions [1]. They focused on similar questions: Population-level asymmetries arise due to the need to coordinate behavior among behaviorally asymmetric individuals. They claimed that brain lateralization has two advantages for individuals: it can increase neural capacity and be a convenient way of preventing the simultaneous initiation of incompatible responses in organisms with laterally placed eyes. Based on this, they used predator-prey relationships to clarify the advantages and drawbacks of population-level brain lateralization: If the prey group can predict the predator's strategy and benefit from the "dilution effect," the individuals in the prey group choose the same behavior as other individuals, which can increase the survival probability, which is beneficial to the prey.

However, at the same time, predators will also use the lateralized characteristics of the target to attack the target, which is unfavorable for a major of individuals with the same lateralization; in contrast, a small number of individuals with the inverse lateralization can save lives. Changes in brain organization may occur due to stress coordinated with the behavioral lateralization exhibited by other individuals; ultimately, it leads to asymmetries in population-level behavior.

2.3. Two ESS models about population-level lateralization

It can be seen from the first and the third paper that the ESS model plays a crucial role in explaining the direction of population-level asymmetry. The ESS concept conveys that assuming that individual behavior is lateralized, the population tends to an evolutionarily stable strategy, which is an ideal model. Vallortigara applied the ESS model to biology for the first time based on natural selection and game theory. Ghirlanda and Vallortigara innovatively created the survival probability model of prey in the context of predator-prey interaction [6]. In this ESS model, l(x) represents the cost of having the same directional bias as a proportion x, which provides the theoretical basis for this ESS model. Equating p(a*) with p(1-a*) as a condition for balanced evolution of prey with opposite lateralization. In 2009, Ghirlanda and colleagues innovatively extended this view by proposing an intra-evolutionary stabilization strategy that postulates that population-level asymmetries can arise through the balance of competitive interactions: antagonism function and synergism function [3]. They devised two parameters, ka and ks. They respectively represent the adaptation of the two functions in the population. Also, two functions, a(x) and s(x), are used to quantify the relative magnitude of the two actions.

They study the model varying the relative importance, c, of synergistic and antagonistic interactions in terms of these parameters. They set the fitness of left-right lateralized individuals in the population as f (x*) and f (1-x*) and used the first-order Taylor expansion of equation to represent the stable conditions of population lateralization.

In this paper, we argue that the introduction of Taylor expansion expands the applicable group of population-level lateralization and makes the prediction model more practical and reliable.

3. Discussion

3.1. Uncertain association between individual laterality and population-level laterality

Individual brain lateralization influences the direction of behavioral lateralization and ultimately determines the asymmetry of population evolution. However, a similar question was raised in the first paper [1]: does group-level lateralization require the coordination of individual behavioral lateralization? They gave various examples and hypotheses for this uncertain connection: For example, the directionality of population lateralization may be due to social pressure, or "social" factors such as solitary or group living may influence the lateralization of populations and individual brains, etc. In the third paper, they used the ESS model in 2009 to explain the connection that the ESS theory is a way to predict individual-level or population-level lateralization in the form of ESS [3].

There are no experimental or direct results proving a direct link between the individual and population levels, and only idealized predictions of this relationship can be made using ESS.

3.2. Limitations of the two ESS model

An idealized model requires large species and population data to verify its generalizability and fitness. ESS remains the single most powerful and widespread evolutionary hypothesis to explain lateralization [3]. However, we need to distinguish the claims of the ESS theory as an evolutionary hypothesis. It still has two limitations: first, the evidence of the feasibility of ESS is insufficient. Based on the ESS model of Ghirlanda and Vallortigara [6], Six of the twenty species-specific populations did not fit the ESS model (no population effect). However, due to the limitation of the number of experimental species, we still need to conclude the generalizability of this ESS model in populations with population effects or the degree of fitting of the ESS model for most populations. It is still necessary to collect a large amount of data between populations to fit the ESS equilibrium condition.

Secondly, the limitations of related factors in the ESS model. Taylor expansion can contain only two variables, so it is possible to combine external and intraspecies factors to study the ESS model. Increasing the number of parameters will increase the difficulty of the fitting equation several times.

This article argues that future research on population lateralization will focus on two aspects: more adequate population data and more efficient ESS models. The following is an innovative discussion of the future development of the ESS model.

3.3. The potential to introduce AI deep learning algorithms to compute fitted models

In recent years, AI technology has rapidly evolved and has had a profound impact on neuroscience. The ease and advantages of AI deep learning algorithms for categorizing biological information are demonstrated in areas such as brain-computer interfaces, prosthetics, etc.

Nowadays, ESS model population range applicability is at the bottleneck stage. And using a classifier, population lateralization can be successfully directed. The experimenter uses supervised learning to organize and classify multiple pieces of information about the sample population, finally arriving at a reasonably fitting model [7].

4. Conclusion

This paper reviews and analyzes three articles on brain lateralization. In the research process from individual behavior lateralization to population lateralization, it is found that the two ESS models play a specific role in explaining the evolution of population-level lateralization.

However, the fitted curve is controversial because of the limitations and inadequacy of factors considered in both ESS models. So far, we have yet to find a more reasonable ESS model, but it is probably more effective to use an AI training model and deep learning algorithm to determine the fitted curve. Using AI to innovate a more adaptable ESS model should be an important direction of future research in this field, but the specific method still needs further investigation.

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