

# Beyond the mosaic model of brain evolution: Rearing environment defines local and global plasticity

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## Abstract

Comparative animal studies have identified a trend toward a more global structural organization as brains become larger, suggesting that brain regions grow in sync as predicted by the concerted model of brain evolution. At the same time, brain plasticity studies have identified a boost in local brain structure triggered by the environment, suggesting that brain regions grow independently, as predicted by the mosaic model. Nevertheless, it is unclear whether the environment can also trigger shifts toward a more global brain structure, that is, whether phenotypic plasticity proceeds in a concerted fashion. Here, we examined the impact of radically different rearing environments on brain organization in a teleost fish, the three-spined stickleback (*Gasterosteus aculeatus*). We computed novel indices of local and global brain structure across groups reared in the two environments and entered them as predictors of differences in brain and body sizes. Changes in local brain structure predicted differences in both body and brain sizes, whereas changes in global brain structure only predicted differences in brain size. Our findings highlight the emergence of brain plasticity in a population as local and global changes that are both compatible with the concerted model.

## KEYWORDS

concerted model, global index, local index, mosaic model, plastic brain structure, three-spined stickleback

## INTRODUCTION

The regions composing the vertebrate brain support bodily functions that maintain life-promoting processes. For example, in teleost fish and across vertebrates, the telencephalon is the center of cognition and decision making that integrates inputs from sensory areas, including the olfactory bulbs and optic tecta. Another key region is the hypothalamus, which regulates body functions, motivation, and social behavior, whereas the cerebellum is involved mainly in sensorimotor coordination but also in cognitive processing.<sup>1–6</sup> Optic tecta and olfactory bulbs are well represented in fish and insectivores because, for them, survival is largely dependent on sensory informa-

tion, whereas the telencephalon and the cerebellum are disproportionately represented in primates and marine mammals because these regions are instrumental in supporting complex cognitive abilities.<sup>7</sup> Comparative studies have shown that, in species where specific functions are relevant for survival, these are supported by enlarged brain regions.<sup>4,8,9</sup> By virtue of its dual contribution to motion and sensory processing, the cerebellum may also become enlarged to support specific sensory functions, for example, an electrosensory system in mormyrid fish<sup>10</sup> and in other fishes.<sup>11</sup> However, current evidence is insufficient for answering the bigger question of whether, in the end, behavior shapes brain structure or the other way around.

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At the same time, comparative studies have identified a trend toward greater integration among regions as brains become larger,<sup>12</sup> as well as an increase in the size of the telencephalon and a remapping of brain functions over emerging brain (sub)regions.<sup>13</sup> Nevertheless, it is unclear whether selective pressures in the environment can trigger changes in brain structure and function during the lifetime of individuals in the same direction as those outlined in comparative studies. In other words, it is unclear whether environmental differences induce brain plasticity along a local-to-global axis such that brain regions become better integrated with each other. For teleost fish, predictions are rather complex. On the one hand, their modular brain structure strongly supports local organization, which makes such changes rather unlikely. On the other hand, in contrast to mammals and birds, fish continue to undergo neurogenesis throughout adulthood,<sup>14–19</sup> which affords lifelong brain plasticity in either direction. Here, we used a novel analysis to determine whether changes in the environment could shift brain structure from local to global, where these types of organization approximate those captured, respectively, by the *mosaic* and by the *concerted* models of brain evolution. In the following, we briefly review current evidence supporting both models of brain evolution. We then review evidence from phenotypic plasticity studies that largely support mosaic changes in brain structure before turning to our analysis of rearing effects on brain plasticity.

The central tenet of the mosaic model<sup>20–22</sup> is that brain regions vary in size independently of each other. In contrast, according to the concerted model,<sup>4,23,24</sup> the size of brain regions is constrained by specific developmental programs and responds to selection by growing or shrinking in sync with other parts of the brain. The mosaic and concerted models of brain evolution are not mutually exclusive but rather embody orthogonal axes of brain evolution that account for variation in brain region sizes.<sup>11,25,26</sup> Indeed, current evidence suggests that both concerted and mosaic evolution contribute to diversity in brain anatomy, especially in teleost fish. To wit, the size of each region, with the exception of the olfactory bulb, is a good predictor of total brain size,<sup>27–29</sup> thus supporting the concerted model, which predicts unaltered brain functions irrespective of changes in size. Furthermore, body parts conserve their scaling with body size, indicating that changes in brain size are often driven by changes in body size,<sup>30</sup> as predicted by the concerted model.

Evidence for evolutionary mosaic changes in the teleost brain includes the study by Protas et al., who identified independent loci regulating the evolution of eye phenotypes in a quantitative genetic analysis of the cave-dwelling fish *Astyanax mexicanus*.<sup>31</sup> Similarly, in the same species, Yoshizawa and Jeffery found a concurrent increase in the number and size of superficial neuromasts that was independent of body size development.<sup>32</sup> Moreover, Hager et al. identified independent loci controlling variations in the size of brain region, which in turn did not correlate with phenotypic traits,<sup>22</sup> thereby arguing against strong developmental constraints on allometric measures. In brief, although the mosaic model predicts size changes only in brain areas that are important in certain environments, the con-

certed model predicts size changes in all areas of the brain even when selective pressures target functions that are driven by a subset of regions.

Interestingly, although evidence from evolutionary studies favors both the mosaic and the concerted models, evidence from studies on brain plasticity in fish largely supports the mosaic model<sup>14,17,33–36</sup> (for a recent discussion of brain evolution vs. plasticity, see Ref. 37). In a study on the effects of rearing environment on cerebellar growth in salmon, Kihlslinger and Nevitt<sup>38</sup> reported that alevins reared in empty tanks developed proportionally smaller cerebellums compared to alevins reared in slightly improved conditions (i.e., tanks with stones added). Moreover, group-reared nine-spined sticklebacks (*Pungitius pungitius*) developed larger optic tecta and smaller olfactory bulbs compared to individually reared fish.<sup>39</sup> More recently, Noreikiene et al.<sup>40</sup> explored the quantitative genetics of brain architecture in the three-spined stickleback (*Gasterosteus aculeatus*) and provided strong support of the mosaic model. The authors reported that heritability and genetic correlations among different brain regions were low, which suggests that selection is not strongly constrained by genetic and phenotypic correlations.

In sum, there is currently no account of why and how shifts in brain structure could have emerged as a result of environmental changes. We thus set out to investigate whether, in response to specific environmental differences, phenotypic plasticity and evolution could act in similar ways, that is, whether plasticity follows both mosaic and concerted patterns. We chose to investigate changes in brain structure that occur in fish reared in radically different environments, as there is substantial literature on mosaic changes triggered by environmental constraints but no mention of concerted changes. The lack of evidence supporting concerted plasticity in fish is surprising, given that, from an evolutionary perspective, there is a robust tendency across species toward a reorganization of brain structure in concerted fashion. We hypothesize that the main reason for unidirectional findings in the plasticity literature on teleosts, that is, for documenting largely mosaic changes triggered by the environment, is a rather vague conceptualization of local versus global brain structure and their relationship. We know that mosaic size shifts occur in one or a few brain areas that support functions relevant to survival in specific environments, which do not require overall reorganization of brain structure, whereas concerted size shifts occur in all brain areas, even in those that are not relevant to functional adjustments. However, we argue that mosaic changes are better described as being local and concerted changes as being both local and global, because global changes require local changes.

We further note that size shifts in multiple brain regions may not always result in global change. In other words, size shifts could signal independent development of brain regions, as defined by the mosaic model, or express, at the same time, a complex dynamic of binary directions of growth or shrinking among multiple brain areas. This dynamic could be captured by a more narrowly conceived concerted model. So, for example, some areas may become larger and, at the same time, other areas may become smaller in systematic fashion, such that their absolute (i.e., unsigned) volumes are overall proportional to each other.

Local (signed) changes that occur in most brain areas and are proportional with respect to total brain size but not to each other are currently described as “concerted,” whereas they would be considered as merely local from a narrow perspective. Thus, in a narrowly conceived concerted model, global size shifts would automatically involve mutually defined local changes, that is, brain region volumes that are proportional to each other. In other words, a change in size for a particular brain region might modify inter-regional proportions, resulting in global reorganization of brain structure. This is a possibility that both the mosaic and the concerted models fail to consider.

Another reason for the dominance of the mosaic model in research on phenotypic plasticity in teleost fish could be the lack of finely tuned analytical tools for detecting changes in global brain structure that would support the concerted model more narrowly viewed to involve proportional and unsigned size shifts. Sometimes, volume changes may not reach significance according to current statistical tests (i.e., ANOVA, covariation/correlation structure among regions between two groups) when considered in isolation (e.g., when comparing the size of the hypothalamus across groups reared in different environments), but their relative change in size to each other may be considerable and needs to be captured. These patterns would follow a narrowly conceived concerted model. For example, most studies run ANOVAs over model parameters computed for each brain region. As the number of (sub)regions increases, this becomes highly impractical. Yet another reason for the unidirectional findings supporting the mosaic model is that differences between environments may not be large enough to detect global structural changes.

In the current study, we investigated the impact of radically different environments on brain region sizes in a teleost fish, the three-spined stickleback (*G. aculeatus*). We analyzed a freely available dataset<sup>40</sup> using a global index (GI) and a local index (LI), which are novel mathematical versions of the distance index and the laterality index, respectively, as recently defined in a brain asymmetry study.<sup>41</sup> The indices allow us to estimate local (LI) and global (GI) changes in brain structure between groups raised in different environments: a group raised in simple (bare-minimum) conditions and another group raised in an enriched environment that approximates the fish natural habitat. Differences in local structure are computed for each brain region separately across groups, whereas differences in global brain structure are computed for each brain region compared to all other brain regions for each group and subsequently compared across groups. By computing local and global changes in the size of brain regions across groups, we can also assess the extent to which the brain of three-spined stickleback develops in mosaic or in concerted fashion. Environmentally triggered plasticity may take the form of local size shifts among individuals reared in the two environments, yielding significant results for LI models. Plasticity may also take the form of global size shifts, resulting in proportional differences in size across brain regions of the two groups, which should yield significant results for GI models. Importantly, we may observe both local and global size shifts in the same dataset, thus providing support for the concerted model.

## MATERIALS AND METHODS

### Sampling and measurements

Out of 231 individuals included in the freely available dataset,<sup>40</sup> we randomly selected a sample of 208 individuals, so they could be divided into 2 groups with equal numbers of males and females. Individuals in the first group were reared in a simple environment (tanks were filled with water and nothing else), whereas individuals in the second group were reared in an enriched environment (tanks contained a gravel substrate, plastic horizontal and vertical cylinders, and artificial plants). The study was carried out according to international guidelines for experimental research and was licensed by the Finnish National Animal Experiment Board (STH223A).

Digital photographs were taken from the dorsal, lateral, and ventral sides of the brain from a standard distance and angle. Width, height, and length were measured for several brain regions (bulbus olfactorius, telencephalon, tectum opticum, cerebellum, hypothalamus), and their volumes were derived using the ellipsoid model.<sup>34,42</sup> Standard length was also measured. Detailed methodology can be found in Herczeg et al.<sup>18</sup> as well as in Noreikiene et al.<sup>40</sup>

### Computing local and global brain structure

We obtained global GI and local LI values for five brain regions of interest (ROIs) (i.e., telencephalon, optical tectum, olfactory bulb, hypothalamus, and cerebellum) by applying Equations (1) and (2), respectively. Equation (1) shows that, for each region  $i$ ,  $GI_i$  can be computed by first deriving two vectors,  $Vector_{Simple}$  and  $Vector_{Enriched}$ , as absolute differences between the size of that region and the sizes of each of the remaining four regions for two individuals randomly chosen from the simple environment and from the enriched environment, respectively. We thus obtained four values in each vector, corresponding to differences between the volume of one region and the volumes of the remaining four. Next, we entered the two vectors in a Pearson correlation coefficient formula where  $a_{iSimple}$  is the volume of a given brain region (e.g., telencephalon) for an individual drawn from the simple environment group,  $\overline{Vector_{Simple}}$  is the mean of the volumes for all five brain regions for the same individual,  $a_{iEnriched}$  is the volume of the same brain region previously measured in the simple group (i.e., telencephalon), this time for an individual drawn from the enriched environment group, and  $\overline{Vector_{Enriched}}$  is the mean of the volumes for all five brain regions for this individual. We derived the absolute value of the Pearson correlation coefficient and subtracted this value from 1 to obtain the global index  $GI_i$  for a given brain region (telencephalon) for a randomly chosen pair of individuals drawn from the simple and from the enriched environment group. We repeated the computation for each randomly selected pair of individuals, one from each environment, thus obtaining a vector of coefficients with the arity of all pairs of individuals across environments. The higher the mean GI value, the greater the difference between environments for a particular region.

The same procedure was used to derive GI values for each of the five brain regions investigated.

$$GI_i = 1 - \frac{\sum (a_{i,Simple} - \overline{Vector}_{Simple}) (a_{i,Enriched} - \overline{Vector}_{Enriched})}{\sqrt{\sum (a_{i,Simple} - \overline{Vector}_{Simple})^2 \sum (a_{i,Enriched} - \overline{Vector}_{Enriched})^2}} \quad (1)$$

$$\overline{Vector}_{Simple} = [ |a_{i,Simple} - a_{i+1,Simple}| \cdots |a_{i,Simple} - a_{n,Simple}| ]$$

$$\overline{Vector}_{Enriched} = [ |a_{i,Enriched} - a_{i+1,Enriched}| \cdots |a_{i,Enriched} - a_{n,Enriched}| ]$$

$$LI_i = \frac{|a_{i,Simple} - a_{i,Enriched}|}{|a_{i,Simple} + a_{i,Enriched}|} \quad (2)$$

Equation (2) illustrates the formula for computing  $LI_i$  for each region  $i$ . We first subtracted the volume of that region for an individual randomly selected from the first group from the volume of the same region for an individual randomly selected from the second group, then dividing the result by the sum of the two values before deriving the absolute difference. We repeated the computation for each randomly selected pair of individuals and obtained a vector of values. The higher the mean LI value, the greater the difference between groups for a particular region.

To summarize, GI estimates volume proportions between multiple brain regions as global structural differences among groups. In the context of our analysis, GI values for the five ROIs will be entered as predictors in a random forest model where differences in total brain size (i.e., volume) and differences in body size (i.e., weight) between groups are the response variables. The LI estimates pairwise volume differences among groups for each brain region. As for GI, LI values will be entered as model predictors of differences in total brain size and in body size among groups.

## Predicting brain volume and body weight using random forest regression models

We used R version 2022.07.2<sup>43</sup> to carry out all analyses. First, we computed GI and LI values across volumes for the five brain regions and included them as predictors in GI and LI random forest regression models.<sup>44</sup> Next, we divided the data into a training set (80%) and a test set (20%). As responses, we included absolute values of differences in total brain volume in brain LI and GI models, or differences in total body weight between groups in body LI and GI models. We aimed to determine whether differences in rearing environment are predicted by differences in local (LI models) or global (GI models) structure. Models were fitted using the best  $R^2$  and RMSE estimators, and optimized models were applied to the test sample. Finally, we applied 10-fold

grid leave-one-out cross-validation over test values and evaluated the prediction accuracy of the test set.

## RESULTS

### Index values

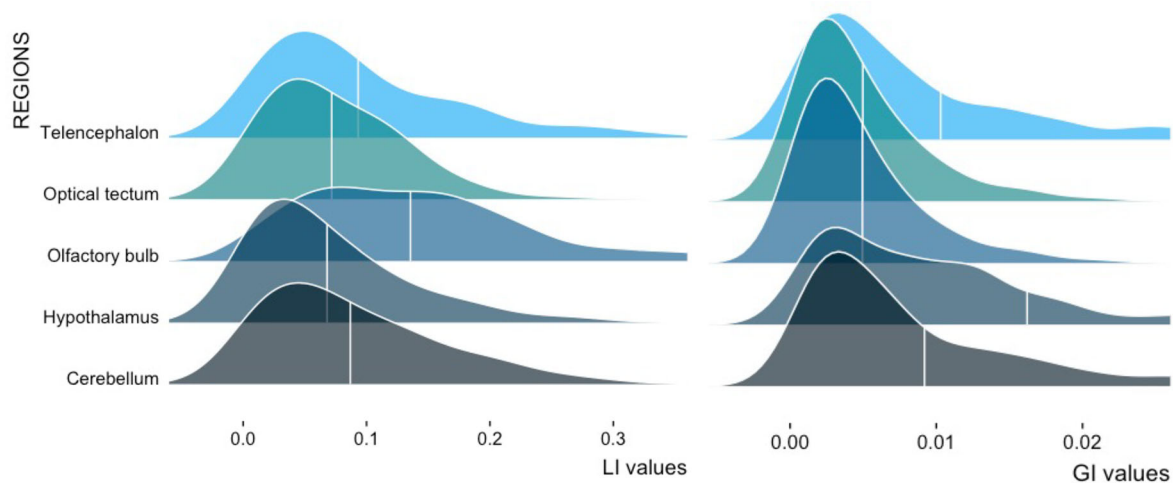
GI and LI values computed for each of the five brain ROIs are summarized in Figure 1. The hypothalamus scored the highest GI values, whereas the olfactory bulb and the optic tectum were tied for lowest GI values. As for LI, the olfactory bulb scored the highest values, whereas the hypothalamus scored the lowest values.

### Random forest regression models

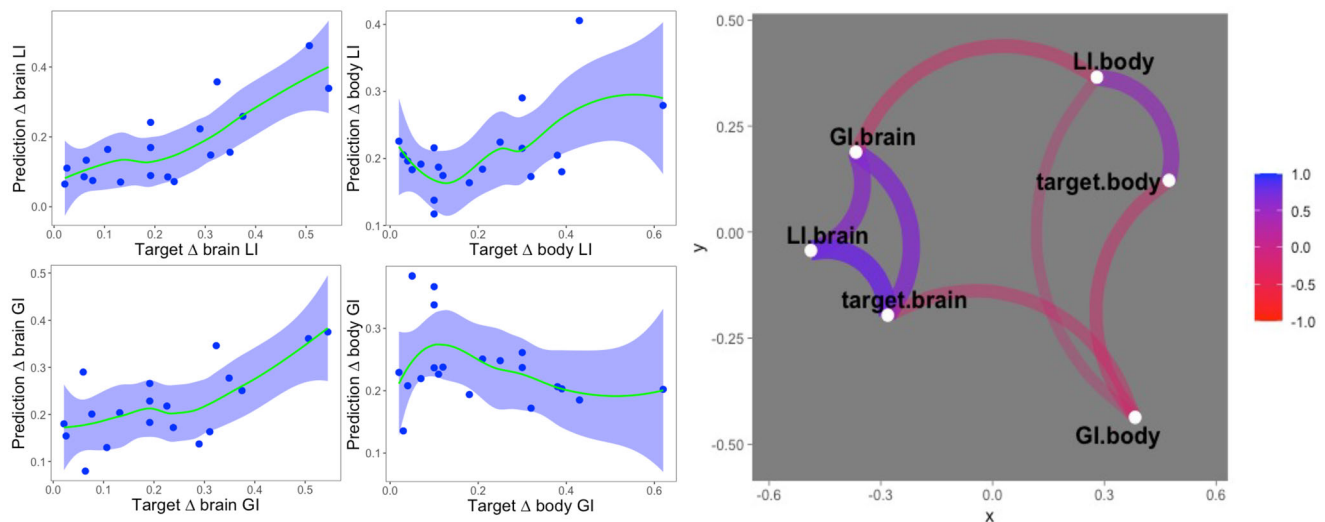
We predicted differences in brain size and body size for global and local brain measures by computing random forest regression models separately for GI and LI scores, respectively. For each model, we obtained RMSE values (0.085 for LI brain, 0.165 for GI brain, 0.163 for LI body, and 0.199 for GI body) and  $R^2$  values (0.684 for LI brain, 0.081 for GI brain, 0.310 for LI body, and 0.130 for GI body).

Figure 2 summarizes the performance accuracy of GI and LI brain and body models as correlations between predicted and target values on the y and x axes, respectively, and also provides correlation coefficients of predicted differences between rearing groups, on the one hand, and target differences on the other. A brief examination of the values reveals better performance for LI models compared to GI models and better performance for brain differences models compared to body differences models:  $r = 0.78$ ,  $p < 0.001$  for the LI brain predicted versus target values,  $r = 0.53$ ,  $p = 0.016$  for the LI body predicted versus target values,  $r = 0.67$ ,  $p = 0.001$  for the GI brain predicted versus target values, and  $r = -0.32$ ,  $p = 0.173$  for GI body predicted versus target values. In the right panel of Figure 2, the network of Pearson correlation coefficients highlights the adaptive changes in brain structure. Differences in brain size ("target.brain") were predicted by differences in local structure ("LI.brain") and in global structure ("GI.brain"), supporting the mosaic and the development model of brain evolution, respectively. Differences in body size ("target.body") were predicted by differences in local structure ("LI.body") but not in global structure ("GI.body").

The predictor (ROI) importance hierarchy that is part of the output of each random forest model illustrated in Figure 3 reveals that, among the brain measures investigated, optic tectum size as well as telencephalon size correlate positively with total brain size and total body size in LI models. For GI models, hypothalamus size correlated positively with total brain size but not with total body weight. Partial dependence plots reveal positive relationships between the magnitude of GI and LI values for each brain region and differences in either brain size or body size among groups.



**FIGURE 1** Local index (LI) and global index (GI) values as density plots with mean lines for five brain regions. The hypothalamus had the highest GI values, whereas the olfactory bulb and the optic tectum were tied for lowest GI values. The olfactory bulb had the highest LI values, whereas the hypothalamus scored the lowest LI values.



**FIGURE 2** Correlation plots and network plot for global index (GI) and local index (LI) models. Model-predicted versus target (actual) GI and LI differences in brain size and body size across the simple- and enriched-environment groups (prediction and target  $\Delta$ ) are plotted on the y and x axes, respectively. Data are fitted with the green curve (95% confidence intervals are represented by the purple shaded area). Correlations were all positive and significant for LI and GI models of brain size as well as for the LI model of body size. The network plot summarizing the magnitude of Pearson correlation coefficients shows a link between model-derived and actual differences between total brain size and body size across groups. Links are color-coded to indicate correlation coefficients greater than 0.2.

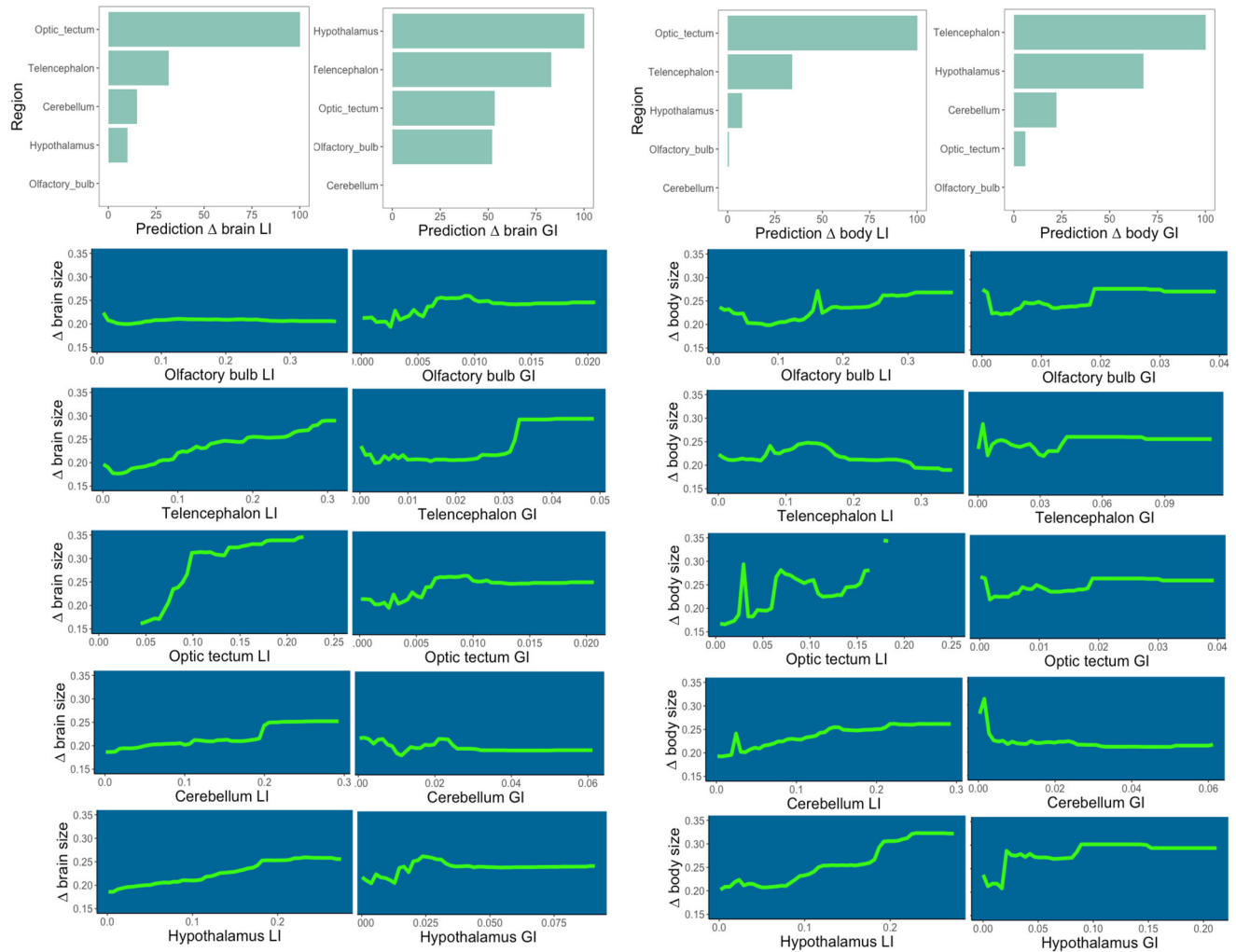
## DISCUSSION

We investigated whether and how brain regions scale with brain size as a result of plasticity induced by radically different rearing environments. We found both local and global changes in the teleost brain, which are both compatible with the concerted model. The results contrast with previous evidence in the literature that plastic changes triggered by selective pressures in the environment largely follow the mosaic pattern, thus yielding size changes in brain regions that are independent of each other.<sup>14,17,35,36,45,46</sup> Indeed, in addition to changes

in local brain structures, that is, an increase or decrease in size for selective brain regions in one group compared to the other, we found significant, albeit small, global changes compatible with the concerted model.

Orchestrated changes are noteworthy, as they are more costly than independent local changes. Indeed, when brain regions increase or decrease proportionately in size in response to environmental pressures, they override the internal competition for resources. As a rule, sensory systems compete for space in teleost fish,<sup>46</sup> and a larger brain where all regions increase in size will impose hydrodynamical





**FIGURE 3** Brain region contributions to local index (LI) and global index (GI) model performance and partial dependence plots. Bar charts show the hierarchy of brain regions in terms of their contribution to model performance: The optic tectum is the best predictor of differences in brain and body size between the simple- and enriched-environment groups in LI models, whereas the hypothalamus and the telencephalon are the best predictors in GI models. The partial dependence plots shown underneath were computed for each brain region. GI and LI values (on the x-axis) increase across the board with the difference in total brain size (on the y-axis) between the simple- and enriched-environment groups.

disadvantages for swimming as well as increased detection risk.<sup>47</sup> In contrast, studies supporting the expensive brain hypothesis<sup>48</sup> document advantages in maintaining a large brain<sup>49–53</sup> despite the costs involved.<sup>8,26,33,54</sup> Unlike mosaic changes, which target a small set of brain regions, concerted changes involve increased volumes for all brain regions.<sup>8,29,27</sup> The link between larger brains and greater cognitive ability in fish<sup>27–29</sup> is in line with our findings that large differences in rearing environments (i.e., simple vs. enriched) are accompanied by changes in brain size that are predicted by changes in brain regions. This supports the hypothesis that different environments select for larger brains because they require increased cognitive abilities.<sup>55,56</sup>

The differences we found in brain size across rearing groups are not only plastic but also adaptive or otherwise warranted by evolutionary selection. A common finding is that body size displays higher evolutionary rates than brain size,<sup>8,57,58</sup> such that selective

requirements on body size progressively trigger correlated requirements on brain size.<sup>12,53,59</sup> Alternatively, rearing environments can trigger plasticity of brain and body simultaneously, such that the latter can adequately support the functions of the former. Nevertheless, it is also possible that a strong plastic response of body size to the environment can subsequently impact relative brain size. In other words, changes in brain size could be driven by adaptive changes in body size rather than by a direct trade-off with the environment.<sup>53,60</sup> However, this was not evident in our results, where differences in body size between groups were not associated with global differences across brain regions. Moreover, the genetic bases of stickleback phenotypes in the two rearing environments featured in our dataset were weak,<sup>40</sup> indicating that brain regions are free to respond to environmental demands with either individual or global plasticity. Indeed, differences between groups in brain region sizes computed with the LI predicted both brain and body size,

which suggests that local changes in brain size proceed in sync with changes in body size,<sup>57,61</sup> as predicted by both the mosaic and the concerted models. However, differences between groups for brain region sizes computed with the GI predicted brain size but not body size, which suggests that global changes in brain size adapt directly to selective pressure in the environment despite the high costs incurred by neural development.

Changes estimated by the GI were largest for the hypothalamus, whereas individual brain region changes estimated by the LI across groups were largest for the optical tectum, which is the same area showing significant size shifts in a previous study using the same dataset.<sup>18</sup> The differences in brain growth that we observed may have an adaptive explanation. For example, because the hypothalamus is involved in the release of growth hormones,<sup>60,62</sup> larger hypothalami could facilitate increased growth rates for one group relative to the other. Similarly, larger optical tecta may facilitate body-centered orientation abilities,<sup>63</sup> which are required to a greater extent in one group relative to the other. Overall, brain regions that are important for rapid growth and cognitive development are similar in teleost fish and mammals, consistent with the hypothesis that vertebrates share a common pattern of brain and behavioral organization.

## CONCLUSION

By documenting global changes in brain structure, we demonstrated that environmental constraints can alter brain organization along a local-to-global axis, as predicted by a more narrowly conceived concerted model of brain evolution. In this model, local and global size shifts co-occur; that is, the latter should entail the former. However, the implications of our hypothesis remain to be tested in future work. We have also shown that global brain structure was a successful predictor of differences in brain volume but not in body size, which mitigates the assumptions of the classic concerted model. In sum, our analysis suggests that brain plasticity is both local and global, thus supporting some but not all assumptions of both models.

## AUTHOR CONTRIBUTIONS

**Magda L. Dumitru:** Conceptualization; investigation; methodology; software; formal analysis; writing—original draft preparation; visualization. **Anders Martin Frugård Opdal:** Investigation; writing—reviewing and editing; both authors have agreed to the final submitted version of the manuscript.

## CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data are made freely available online, as described in Noreikiene et al. (2015)<sup>40</sup> and in Herczeg et al. (2015)<sup>18</sup>.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/nyas.15267>.

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**How to cite this article:** Dumitru, M. L., & Frugård Opdal, A. M. (2024). Beyond the mosaic model of brain evolution: Rearing environment defines local and global plasticity. *Ann NY Acad Sci.*, 1542, 58–66. <https://doi.org/10.1111/nyas.15267>