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Functional hemispheric segregation of sensory-motor laterality

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ABSTRACT

Background: Functional laterality manifests across motor and sensory domains, yet analysis of their combined organization within individuals remains underexplored. Gerrits' 2024 (doi: 10.1007/s11065-022-09575-y) segregation bias model provides theoretical support that allows testing specific predictions for the lateralization of brain functions and their phenotype distributions in the population. We applied this approach to investigate sensory-motor laterality on the behavioral level (handedness, footedness, and eyedness) using a large sample (n = 900; 11–70 years).

Methods: Participants completed the Global Lateral Preference Inventory, and laterality indices were computed to categorize individuals into typical functional segregation (all preferences to the same side) or deviation patterns (either 1 or 2 deviations from the handedness side). We compared the observed distribution with Gerrits' (2024) predictions and analyzed associations with handedness, sex, and age.

Results: Our findings partially supported the segregation bias model, as non-right-handers exhibited more atypical segregation patterns, confirming one of the model's primary predictions. However, exact percentages differed, likely due to methodological differences between behavioral inventories and neuroimaging, and differences in the lateralized functions being assessed. Contrary to expectations, no sex differences in segregation patterns emerged, suggesting the organizational principles for segregation bias in sensory-motor laterality may override sex-linked variability. Age effects were observed, with young adults displaying higher deviation rates, potentially reflecting continued neural and motor refinement during early adulthood.

Conclusions: These findings extend the segregation model framework to sensory-motor domains, highlighting its potential for neurodevelopmental, clinical, and research contexts, further emphasizing the importance of multidimensional assessments of laterality beyond handedness alone.

1. Introduction

Humans show functional lateralization across multiple motor and sensory domains, prominently as preferences in hand, foot, and eye use (Ocklenburg and Güntürkün, 2024; Reiss et al., 1999). Among these, handedness is the most extensively studied, with a robust population-level bias towards right-handedness (Ocklenburg et al., 2025; Ocklenburg and Güntürkün, 2025). Meta-analysis showed that approximately 89.4 % of individuals exhibit right-hand preference, though this figure varies depending on assessment criteria and cultural context (Papadatou-Pastou et al., 2020). Footedness shows a similar, though slightly less pronounced asymmetry: around 80 % of the population is right-footed (Packheiser et al., 2020). Eye preference, or eyedness, tends to be less lateralized overall, standing at around 70 % right-eyedness in the population (Bourassa et al., 1996; Mandal et al., 1992). Even though these lateral preference dimensions are often aligned, this is not always the case. Most individuals do show a consistent preference pattern (e.g., right-handedness, footedness, and eyedness), but a minority can display crossed laterality pattern types (Marcori et al., 2019).

The relationship between hand, foot, and eye preference has been previously explored, revealing different results depending on the sensory-motor laterality pair being under analysis. Agreement between handedness and footedness, for instance, is the most robust among the

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possible pairings at around >90 % of right-handers being right-footed, with research consistently reporting a significant positive correlation between these dimensions (Marcori et al., 2023; Packheiser et al., 2020). Handedness and eyedness, on the other hand, show only a weak relationship: approximately 70 % of right-handers are right-eyed (Bourassa et al., 1996; Dargent-Paré et al., 1992). This proportion closely matches the population base rate of right-eyedness, thus indicating that, unlike hand-foot concordance, hand-eye concordance adds only a small predictive value beyond the overall distribution. The congruence for left-handers is reported at around 60 % for both footedness (Packheiser et al., 2020) and eyedness (Bourassa et al., 1996; Dargent-Paré et al., 1992) – highlighting how non-right (NR) handers have a more atypical pattern of lateralization. Foot and eye agreement values, however, are missing in most research, even though these two measures have been collected in previous investigations. Behavioral clustering and latent-variable analyses have revealed that lateral preferences across hand, foot, and eye tend to group into discrete phenotypes (e.g. Peters and Murphy, 1992; Tran et al., 2014)). In a large sample, Tran et al. (2014) found evidence for three categories (right, mixed, left) across multiple effector systems, further identifying footedness as a particularly strong indicator of generalized sidedness. More recently, Rodway et al. (2024) used cluster analysis and machine learning to show that footedness, along with throwing arm, and handedness, can jointly predict eyedness, supporting the idea of structured interdependence among motor and perceptual laterality systems, while also showing some individuals cluster into a crossed lateralization patterns. As such, studies have strengthened the view that lateral preferences across different domains are not always fully aligned. For instance, Marcori et al. (2023) found evidence supporting the notion that sensory-motor lateral preference in different dimensions is developed in a dissociated fashion, showing that individuals may present crossed or mixed profiles within normal developmental conditions. Taken together, these findings support a multifactorial and dimension-specific view of laterality, such that sensory-motor lateralized functions may develop through overlapping but not necessarily identical influences, thus displaying distinct patterns depending on the form of analysis.

The behavioral organization of lateral preferences can reflect underlying patterns of neural architecture. Handedness and footedness are primarily organized through contralateral corticospinal projections that mediate fine and gross motor control (Corballis, 2009; Sainburg, 2002). In contrast, eyedness involves a more complex interplay between contralateral retinocollicular projections and bilateral cortical processing, with partial ipsilateral integration at higher visual areas (Bourne, 2006; Goodale and Milner, 1992; Milner and Goodale, 2008). Evidence from neuroimaging and neurophysiology highlights that these pathways are lateralized to different degrees, which may, therefore, explain why effector systems differ in the strength of their expressed asymmetries and laterality patterns (Corballis, 2009; Milner and Goodale, 2008).

Within this context, the concept of hemispheric functional segregation offers a crucial framework for understanding how lateralized functions organize within the brain, challenging previous simplistic models of lateralization as isolated and independent phenomena (Vingerhoets, 2019). Traditionally, the lateralization of cognitive functions – such as language, praxis, and emotion – has been interpreted either through a statistical model, in which each function independently acquires its hemispheric dominance or through a causal model, where the lateralization of one function constrains the lateralization of others (Badzakova-Trajkov et al., 2016). In a landmark study, Gerrits et al. (2020) tested these hypotheses by examining five distinct lateralized brain functions within the same individuals. Their findings demonstrated that most participants exhibited a coherent pattern of segregation, either following the typical organization (e.g., left hemisphere for language and handedness, and right for attention, face recognition, and prosody) or a complete reversal of this pattern. These findings led to the proposal of a novel framework: the segregation bias model. According to this model, hemispheric functions are guided by a developmental blueprint that favors a balanced distribution across hemispheres, reducing interference of similar functions requiring equally specialized neural networks, and thus optimizing processing efficiency (Gerrits, 2024). While this model has been developed considering handedness, language, and spatial attention, its application to sensory-motor laterality – hand, foot, and eye preference –, even though perfectly viable, has not yet been tested. Therefore, investigating whether similar segregation biases operate in these domains represents an expansion of the model, with the potential to reveal whether the motor-sensory systems are similarly constrained by these hemispheric organizational principles.

The segregation of functional asymmetries, however, may not follow a uniform pattern across individuals, such that sex and age are key variables that can potentially shape asymmetries organizational profiles (Gerrits, 2024). Indeed, age (Marcori et al., 2019a; Michel et al., 2013; Scharoun and Bryden, 2014) and sex (Papadatou-Pastou et al., 2008) are important moderating factors known to affect both sensory-motor laterality expression and the relationship between preference dimensions (Marcori et al., 2023). Large-scale meta-analyses have consistently shown that males are more likely to exhibit NR preferences, particularly left-handedness, and mixed-footedness (Packheiser et al., 2020; Papadatou-Pastou et al., 2008). Age-related differences are also present in other scenarios, as children, for instance, display higher rates of NR or inconsistent lateral preferences (Packheiser et al., 2020; Scharoun and Bryden, 2014). However, correlations between preference dimensions, such as hand and foot or hand and eye, tend to diminish with aging (Marcori et al., 2023), possibly suggesting higher segregation variability in older age groups. Given this variability, testing the segregation bias model across different age groups and sexes could yield relevant insights and further advance our understanding of the model. If functional segregation patterns differ systematically by sex or developmental stage, it would indicate that the organizational principles guiding lateralization of motor-sensory dimensions are not necessarily fixed, but rather shaped dynamically by maturation, environmental, and sex-specific neurodevelopmental trajectories.

The present research aims to test whether the predictions of Gerrits' general mechanistic model (2024) for functional segregation bias of hemispheric specificity holds for sensory-motor domains of laterality, as assessed by inventory. We have three main goals: 1) compare Gerrits' (2024) predictions to our data, checking if expected and observed percentages are similar; 2) analyze if the main predictions of the model also apply to motor-sensory domains of laterality, such as non-right handers (NRHs) presenting higher frequency of atypical hemisphere functional segregation phenotypes; and 3) explore the relationship between the functional segregation phenotypes of sensory-motor laterality domains and age and sex. Based on the abovementioned literature, we hypothesized that: H1) our data would significantly match the model's predictions; H2) right-handers (RH) have fewer cases of atypical segregation phenotypes as compared to NRHs; H3) older individuals and H4) men display higher frequencies of atypical segregation patterns.

2. Methods

2.1. Participants and ethics

A sample of 900 volunteers (400 men) participated in the present research, with ages ranging from 11 to 70 years old (mean of 31 ± 18). Individuals were selected for convenience and did not receive any kind of reward for participating. All methodological procedures were conducted according to the 1964 Helsinki Declaration and its later amendments or comparable ethical standards, and this study was approved by the Londrina State University ethical committee (certificate no.: 92987718.4.0000.5231). Adults provided written informed consent and for the under-aged participants signatures were collected from their parents or legal guardians, who accompanied the children/adolescents during data acquisition. The younger individuals also provided their verbal assent before participation.

For analyses, participants were divided into four age groups corresponding to meaningful developmental and lifespan stages: adolescence (11–17 years), young adulthood (18–30 years), middle adulthood (31–50 years), and older adulthood (51–70 years). This categorization reflects evidence that motor and cognitive lateralization consolidates during adolescence, remains stable in young adulthood, begins to show subtle compensatory shifts in midlife, and may weaken in older adulthood (Bishop, 2013; Cabeza, 2002; Porac, 2016).

2.2. *Laterality preference measures*

To assess preference for each of the laterality dimensions (i.e., handedness, footedness, and eyedness), we used the Global Lateral Preference Inventory (Marim et al., 2011), specifically the three sections related to hand, foot, and eye preference. Fifteen questions composed the handedness assessment, while five questions each composed the footedness and eyedness section. For further details, content validity and reliability measurements on the Inventory, please refer to previous literature (Bazo et al., 2022; Marcori et al., 2019a; Marcori et al., 2023; Marim et al., 2011). Since handedness is deemed adult-like from the ages of 10–12 (Scharoun and Bryden, 2014), applying a questionnaire to the younger individuals in our sample is a valid approach. Aiming to reduce potential bias in the outcomes, inventory application was made with a computer and all participants were assisted by a researcher to guarantee the accuracy of data acquisition and solution of eventual doubts in the procedures. This dataset is part of larger research project investigating issues beyond only lateral preference and individuals went to the laboratory for testing other motor skills not included in the present analysis.

The individual answers to each question were computed on a score ranging from −2 to +2, meaning: −2 always left; −1 mostly left; 0 indifferent; +1 mostly right; +2 always right. Based on the individual answer of each score, a Laterality Index (LI) was calculated according to the formula: $\left(\frac{R-L}{(Rc+Lc+IDc)^{*}2}\right)$. The R-value represents the sum of all positive values, while the L-value represents the sum of all negative values. This procedure was used for properly weighting the results of strong preference answers, as a strong-sided answer accounts for 2, while a moderate-sided answer accounts for 1. The bottom part of the fraction is obtained by summing the count (c) of answers in each category and multiplying by two. With this approach, the LI of the participants range from −1 (all 'always left' answers) to +1 (all 'always right' answers).

After determining the LI, cut-off points were set to divide the sample in either right- or left-sided. Gerrits et al. (2020) experimental research used 0 as a cut-off for classifying right- (>0) or left-sided (<0) participants based on the LI of neural measurements. Therefore, aiming to compare our findings to the model, we ran the analysis with the same 0.0 cut-off in our data. From this point, individuals were classified either into right- or left-handed, as well as right- or left-footed and right- or left-eyed. The typical functional segregation pattern was assumed when all three preferences were measured to the same side (i.e., all right- or all left-sided). One deviation would be considered when a right-hander (RH) presented either left foot or left eye preference, as well as when a left-hander (LH) presented either a right foot or right eye preference. The two-deviations category was considered when both foot- and eye preference were opposite to handedness. With this approach, individuals had the possibility of falling into one of eight categories, as shown in Table 1, below.

Table 1
Sensory-motor laterality phenotypes of hemispheric functional segregation patterns.

Handedness	Footedness	Eyedness	Combination
R	R	R	TFS
R	R	L	1-dev (eye)
R	L	R	1-dev (foot)
R	L	L	2-dev
L	L	L	TFS
L	L	R	1-dev (eye)
L	R	L	1-dev (foot)
L	R	R	2-dev

Note. R = right; L = left; TFS = typical functional segregation; dev = deviation.

2.3. *Statistical analysis*

To compare our data with Gerrits' model (2024), parameters for the predicted phenotypes of right-footedness and right-eyedness were drawn from previous literature and adjusted accordingly in the model. For footedness, we applied 80 % of bias toward right-sided preference (Packheiser et al., 2020). For eyedness, we applied 70 % of bias toward right-sided preference (Kumar et al., 2010; Mandal et al., 1992; Marcori et al., 2019). Reversed patterns of typical segregation were maintained at 1 %. Predicted values for each of the eight phenotypes of the model can be found in the link by inputting the above-mentioned parameters (https://robingerrits.shinyapps.io/segregation_bias_model/). Frequency analysis from our data provided the observed percentage and count values, and comparisons with the model were made with a Goodness-of-Fit Chi-Square test normalizing the count data to our sample size from the expected percentages given by the model. Chi-square and Cohen's w values were calculated for each of these comparisons.

To test if LHs have a more atypical pattern of lateralization, the Chi-Square test of independence was applied to compare the frequency of TFS, 1-dev (either eye or foot), and 2-dev categories between RHs and LHs in our sample. This same approach was used to compare the different age groups (11–17, 18–30, 31–50, and 51–70 years old) and sex (men and women), with the additional layer of handedness. For the age and sex comparisons, the Chi-square test of independence was also applied to analyze the distribution of the 8 possible phenotypes (Table 1) between these groups. Whenever necessary, standardized residual measurements (SRM) were calculated to see in which cell frequency count was significantly different than expected, with values > |2| being considered significant (Haberman, 1973). All analyses were conducted in SPSS (IBM Statistics, v.23.0). Aiming to correct for multiple comparisons, p-value significance was divided by 2 and set at $p < 0.025$.

An additional exploratory analysis was conducted. Because questionnaire data is of a different nature as compared to neurophysiological asymmetries (Vingerhoets et al., 2023), using the 0.0 cut-off does not necessarily provide a 1:1 comparison of our behavioral data to the model. Traditionally for questionnaires, the LI range from −0.3 to +0.3 is usually regarded as the "mixed/indifferent" category (Papadatou-Pastou et al., 2020; Vingerhoets et al., 2023). Therefore, we sought to determine which cut-off values used to divide individuals into left or right-sided would produce outcomes closer to Gerrits' model. For that purpose, we have conducted 6 further exploratory analyses in the sample, each with a modification in cut-off value: 0.1, 0.2, 0.3, 0.4, 0.5, and 0.6. The selection of these values was based on recent evidence suggesting that 0.6 values for the Edinburgh Handedness Inventory are meaningful for screening non-RHs in clinical neuropsychological contexts (Mundorf et al., 2024). Therefore, besides the 0.0 value that dichotomizes the sample into either "left" or "right", all other values would theoretically produce the outcome of a "left", "mixed" (individuals between the positive and negative value of the cut-off; e.g., −0.1 to +0.1) and "right" sided lateralized groups. For comparisons to Gerrits's segregation-bias model, however, we had to collapse "left" and "mixed" into a single "non-right" category, to parallel the binary structure of Gerrits's framework – otherwise the analyses would not be possible. Both the LI calculation procedure and cut-off determination were based on previous research (Fazio et al., 2013; Marcori et al., 2023; Oldfield, 1971) and methodological recommendations for laterality research (Vingerhoets et al., 2023). After calculating the frequencies of TFS pattern with each cut-off, the same Goodness-of-fit Chi-Square test was conducted. The cut-off value that produced the lowest Chi-square and Cohen's w values when compared to Gerrits' model was considered as producing outcomes closer to the model (Agresti, 2002; Haberman, 1973).

3. Results

3.1. *Comparison of observed data and Gerrit's model (H1)*

Results of the goodness-of-fit Chi-square test showed significant differences between our data and the expected values from Gerrits' model ($\chi^2 = 230.350$; df = 7; $p < 0.001$; w = 0.506). SRM showed a greater proportion of RHs in the TFS category, with significantly fewer individuals in all other deviation categories – atypical footedness, eyedness, and both. For the LHs, proportions were only significantly different according to SRM for the 1-dev pattern of atypical eyedness, with our data showing significantly less individuals in that category (1.33 vs. 2.56 %). General proportions of lateral preferences were the following: right-handedness, 90.8 % (n = 817); right-footedness, 88.3 % (n = 795); right-eyedness, 80.1 % (n = 721) – thus 9.2 % left-handedness, 11.7 % left-footedness, and 19.9 % left-eyedness. Descriptive analyses of the comparisons are displayed in Table 2, below.

A full description of the frequency of each preference (handedness, footedness, and eyedness), divided by age and sex, along with their respective laterality index values (total of 16 groups – lateral preference x age x sex), can be found on the Supplementary Material 1.

3.2. *Comparison of typical segregation patterns between left- and right-handers (H2)*

Continuing with the proposed investigation, the Chi-square test of independence was conducted to compare the proportion of deviation from the TFS pattern between RHs and LHs in our sample. Results were significant ($\chi^2 = 59.345$; df = 2; $p < 0.001$), showing proportionally more LHs in both 1- and 2-deviations categories (SRMs of 2.5 and 6.4, respectively), as predicted by the model. Accordingly, proportionally less LHs were represented in the TFS (SRM = −2.5), and less RHs were represented in the 2-deviations category (SRM = −2.0). Results are shown in Fig. 1, below.

The distribution of all eight possible categories of phenotypes is presented in Fig. 2, along with the hemispheric dominance for foot and eye preference conditioned on handedness. The general outline of the data follows Gerrits' predictions for the distribution magnitude of prevalence between each phenotype is maintained – even though exact percentages are different. Of notice, the 0.0 cut-off produced an over-representation of the TFS in RHs (Fig. 2A and B). Also, LHs displayed a greater proportion of 2-dev as compared to either single 1-dev categories (Fig. 2B).

Table 2
Comparison of 0.0 cut-off observed data and expected values from Gerrits (2024) model, considering all eight possible phenotypes (n = 900).

	Right-handers		Left-handers	
	Our data	Gerrits' model	Our data	Gerrits' model
TFS (tH-tF-tE)	73.89 %	50.00 %	5.00 %	5.56 %
	10.13		−0.71	
1-dev (tH-tF-aE)	11.56 %	21.33 %	1.33 %	2.56 %
	−6.35		**−2.29**	
1-dev (tH-aF-tE)	3.33 %	12.44 %	1.33 %	1.56 %
	−7.75		−0.53	
2-dev (tH-aF-aE)	2.00 %	5.44 %	1.56 %	1.11 %
	−4.43		1.26	

Note. Data presented as percentage and SRM (below). TFS = typical functional segregation; t = typical; a = atypical; H = hand preference; F = foot preference; E = eye preference; dev = deviation. **Bold** cells = SRM > | 2 |.

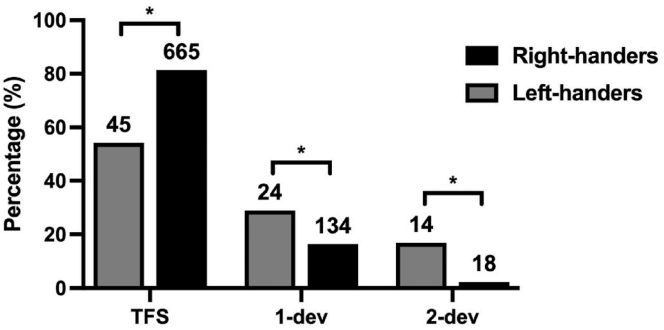

Fig. 1. Comparison of frequency of deviation from typical segregation patterns between right- and left-handers (0.0 cut-off; n = 900).
Note. * = SRM > | 2 | in either columns of the right-vs. left-handers' comparisons. Numbers above column indicated count of individuals in that category.

3.3. *Comparison of typical segregation patterns between age groups (H3)*

The distribution of the 8 phenotypes was compared across age groups, and the Chi-square analysis showed significant results ($\chi^2 = 39.682$; df = 21; p = 0.008), with SRM values being higher in the young adults group (18–30 years old), showing more cases of 1-dev in both LHs and RHs. Additionally, the 31–50 years old group had significantly more individuals in the 2-dev category for LHs. Descriptive data is available in Table 3, below.

Analysis comparing the number of deviations from the TFS pattern found mixed results. Layered Chi-square test found no significant association between age and the number of deviations in LHs ($\chi^2 = 9.196$; df = 6, p = 0.163), but significant differences were observed when comparing RHs ($\chi^2 = 14.555$; df = 6; p = 0.024). The SRM values were >2 only for the 18–30 age group in the 1-dev category. Overall Chi-square findings (age vs. n-devs) were also significant ($\chi^2 = 21.140$; df = 6; p = 0.002), having SRM >2 for 18–30 years old RHs in the 1-dev category and also 31–50 years old in the 2-dev category. These findings are illustrated below, in Fig. 3.

3.4. *Comparison of typical segregation patterns between male and female (H4)*

The distribution of the 8 phenotypes was compared across sex groups, and the Chi-square analysis did not show significant results ($\chi^2 = 9.596$; df = 7; p = 0.213), indicating both men and women participants have a similar distribution regarding the number of deviations from the TFS pattern. Descriptive data is available in Table 4, below. Additional analysis specifically comparing the number of deviations from the TFS pattern found equivalent null results. Layered Chi-square test found no significant association between sex and the number of deviations in both LHs ($\chi^2 = 1.594$; df = 2, p = 0.451) and RHs ($\chi^2 = 4.200$; df = 2; p = 0.122). Thus, overall Chi-square findings (sex vs. n-devs) were also not significant ($\chi^2 = 2.809$; df = 2; p = 0.246), suggesting a lack of sex-related effect on the distribution of the number of deviations from the TFS pattern. These findings are illustrated below, in Fig. 4.

3.5. *Comparison of different cut-off values between observed data and gerrits' model*

Results of the goodness-of-fit Chi-square test showed significant differences between the observed and the expected values for all of the models in different cut-offs (Table 5). Interpreting the coefficients, the 0.2 cut-off produced the smallest χ^2 and w values, thus being considered

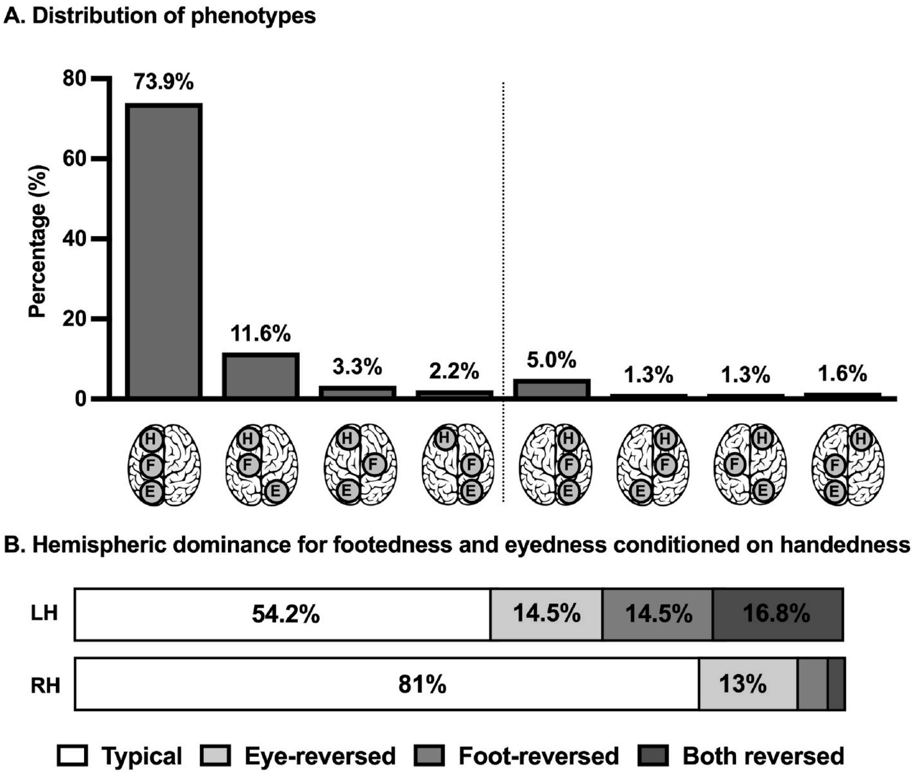

Fig. 2. Patterns of phenotypes regarding hemisphere dominance distribution on the whole sample (A) and divided by handedness (B) – 0.0 cut-off.

Table 3
Comparison of hemisphere segregation phenotypes between age groups (0.0 cut-off; n = 900).

	11-17 (n = 306)	18-30 (n = 180)	31-50 (n = 226)	51-70 (n = 188)
R, TFS (RH-RF-RE)	77.1 % 0.7	70.6 % −0.5	68.6 % −0.9	78.2 % 0.7
R, 1-dev (RH-RF-LE)	9.8 % −0.9	**17.8 %** **2.5**	12.4 % 0.4	7.4 % −1.7
R, 1-dev (RH-LF-RE)	2.6 % −0.7	3.3 % 0.0	4.0 % 0.5	3.7 % 0.3
R, 2-dev (RH-LF-LE)	2.0 % 0.0	1.7 % −0.3	3.5 % 1.6	0.5 % −1.4
L, TFS (LH-LF-LE)	5.6 % 0.4	2.2 % −1.7	5.8 % 0.5	5.9 % 0.5
L, 1-dev (LH-LF-RE)	1.6 % 0.5	0.0 % −1.5	1.8 % 0.6	1.6 % 0.3
L, 1-dev (LH-RF-LE)	0.7 % −1.0	**3.3 %** **2.3**	0.4 % −1.2	1.6 % 0.3
L, 2-dev (LH-RF-RE)	0.7 % −1.3	1.1 % −0.5	**3.5 %** **2.4**	1.1 % −0.5

Note. Data presented as percentage within age group and SRM (below). TFS = typical functional segregation; R = right; L = left; H = hand preference; F = foot preference; E = eye preference; dev = deviation. **Bold** cells = SRM > | 2 |.

as producing outcomes closer to the model. We have conducted all of the same analysis as seen in topics 3.1 to 3.4 with the 0.2 cut-off, and despite changes in the exact percentages, results are virtually the same (i.e., more LHs with 2 deviations from the TFS, young adults with more 1 deviation as compared to the other age groups, and no difference between men and women). Therefore, we have opted to include this information into the Supplementary Material 2 – results from 0.2 cut-off. For descriptive purposes, the direct percentage comparisons can be seen on Table 6, below.

For the 0.2 cut-off comparison, SRM showed a greater proportion of RHs in the TFS category, with significantly fewer individuals in the RH 1-dev (both atypical eye and atypical foot preference). There were also fewer non-RHs with 1-dev atypical patterns (right-eyed left-handers) in our sample (Table 6). Even though statistically different from Gerrits' prediction values, the general distribution of percentages followed the proposed pattern, with more occurrences of deviation in the laterality dimension with weaker segregation tendency (e.g., eyedness) and with non-RHs presenting more cases of atypical patterns – as shown and tested below. Of the 900 participating individuals, inventory data with the 0.2 cut-off value revealed our sample to be 89.2 % right-handed (n = 803). Additionally, 705 participants were right-footed (78.3 %) and 616 were right-eyed (68.4 %). The proportion of non-right preference, consequently, was 10.8 % for handedness, 21.7 % for footedness, and 31.6 % for eyedness. These values are in agreement with the preference distribution found in the literature and the values inputted in Gerrits' model to generate the 8-phenotype approaches (see 2.3 Statistical analyses), providing further evidence that the 0.2 cut-off produced values closer to the model's predictions.

Further descriptive analyses of the Goodness-of-fit comparisons from the other cut-offs are available in the Supplementary Material 3 – descriptive TFS data from other cut-offs.

4. Discussion

This research had two main goals: 1) to test whether Gerrits' model (2024) of functional segregation of hemisphere asymmetries holds for sensory-motor dimensions of laterality as assessed by questionnaires, and 2) to test whether LHs have more atypical patterns of lateralization as compared to RHs. From the results presented above, we have rejected our hypothesis of similarity between our data and the model (H1), while accepting H2 due to finding more cases of 2-deviations in LHs – one of the model's predictions (both 0.0 and 0.2 cut-offs). A higher prevalence of atypical segregation patterns was found in the young adults (18–30 years old; Table 3), and not in the older participants, thus leading us to reject H3. Because men and women presented an equal distribution of segregation pattern phenotypes, we also rejected H4. These results are separately discussed below.

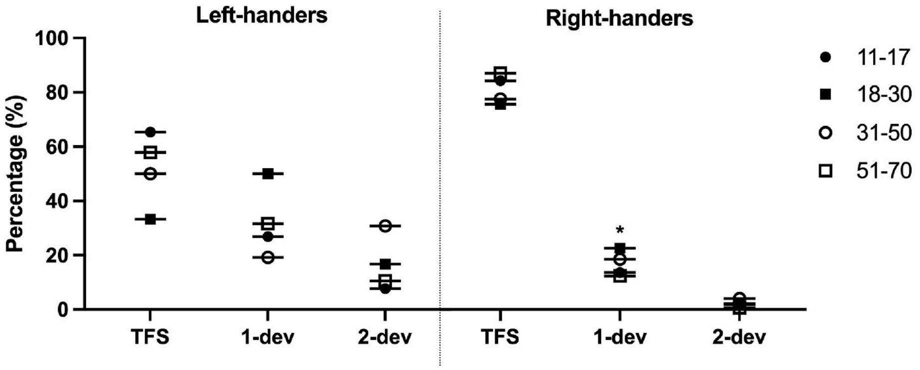

Fig. 3. Comparison of frequency of deviation from typical functional segregation patterns among left- and right-handers between age groups (0.0 cut-off; n = 900). **Note.** * = SRM > | 2 |.

Table 4
Comparison of hemisphere segregation phenotypes between sex (0.0 cut-off; n = 900).

	Women (n = 500)	Men (n = 400)
R, TFS (RH-RF-RE)	76.4 %	70.8 %
	0.7	−0.7
R, 1-dev (RH-RF-LE)	11.4 %	11.8 %
	−0.1	0.1
R, 1-dev (RH-LF-RE)	2.2 %	4.8 %
	−1.4	1.6
R, 2-dev (RH-LF-LE)	1.4 %	2.8 %
	−0.9	1.1
NR, TFS (LH-LF-LE)	4.2 %	6.0 %
	−0.8	0.9
NR, 1-dev (LH-LF-RE)	1.6 %	1.0 %
	0.5	−0.6
NR, 1-dev (LH-RF-LE)	1.4 %	1.3 %
	0.1	−0.1
NR, 2-dev (LH-RF-RE)	1.4 %	1.8 %
	−0.3	0.3

Note. Data presented as percentage within sex group and SRM (below). TFS = typical functional segregation; R = right; L = left; H = hand preference; F = foot preference; E = eye preference; dev = deviation.

4.1. Application of gerrits' segregation bias model to sensory-motor laterality

Our findings partially agree with Gerrits' segregation bias model, as percentages in each phenotype differed from the predictions, but overall data distribution and higher variability in LHs were observed. The reason for these results might be twofold: 1) differences in the nature of data acquisition methods and classification of participants; and 2) distinct lateralized functions being assessed and fitted into the model.

Firstly, the segregation bias model considered brain asymmetries as directly assessed via brain-imaging techniques, and not questionnaire-based research. Even though asymmetries in brain activation patterns have been shown to replicate asymmetries in laterality questionnaires (Packheiser et al., 2020), this may not be completely valid for all dimensions of lateral preference, such as eyedness. Laterality questionnaires offer an accessible and reliable way to characterize behavioral asymmetries, but they do not directly measure hemispheric functional specialization. While empirical evidence indicates that hand and foot preference show a relatively strong correspondence with contralateral motor control pathways (Corballis, 2009; Sainburg, 2002, 2014), eye preference reflects more complex interactions involving both contralateral and ipsilateral projections (Bourne, 2006; Goodale and Milner, 1992). Collectively, these findings support the notion that lateralized behavior often parallels, but does not perfectly mirror, the underlying neural organization. Indeed, prior work has shown that the strength of behavioral laterality is only moderately correlated with the degree of neural lateralization observed in neuroimaging or electrophysiological measures (Carey and Johnstone, 2014; Knecht, 2000) – in line with our

Table 5
Goodness-of-fit Chi-square test coefficients when comparing different cut-off with expected values from Gerrits' model.

Cut-off value	df	p	χ^2	Cohen's w
0.0	7	<0.001	230.350	0.506
0.1	7	<0.001	118.410	0.363
0.2	7	<0.001	44.369	0.222
0.3	7	<0.001	76.514	0.292
0.4	7	<0.001	306.618	0.584
0.5	7	<0.001	749.036	0.912
0.6	7	<0.001	1560.296	1.317

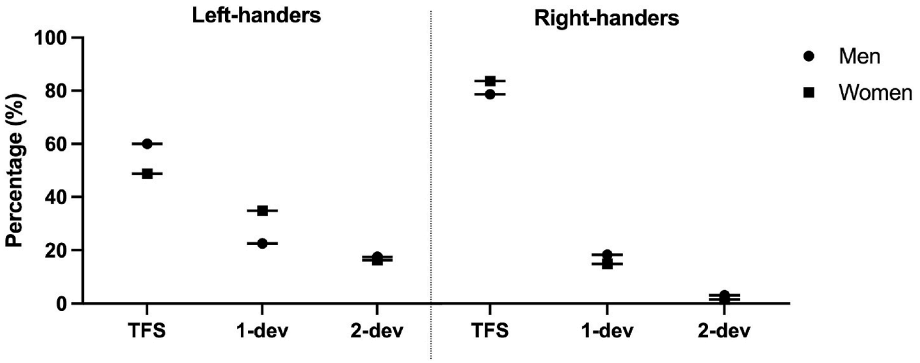

Fig. 4. Comparison of frequency of deviation from typical functional segregation patterns among left- and right-handers between men and women (0.0 cut-off; n = 900).

Table 6
Comparison of 0.2 cut-off observed data and expected values from Gerrits (2024) model, considering all eight possible phenotypes (n = 900).

	Right-handers		Non-right-handers	
	Our data	Gerrits' model	Our data	Gerrits' model
TFS (tH-tF-tE)	58.0 %	50.0 %	7.0 %	5.6 %
	3.4		1.8	
1-dev (tH-tF-aE)	17.8 %	21.3 %	1.2 %	2.6 %
	−2.3		**−2.5**	
1-dev (tH-aF-tE)	7.8 %	12.4 %	1.1 %	1.6 %
	−3.9		−1.1	
2-dev (tH-aF-aE)	5.7 %	5.4 %	1.4 %	1.1 %
	0.3		0.9	

Note. Data presented as percentage and SRM (below). TFS = typical functional segregation; t = typical; a = atypical; H = hand preference; F = foot preference; E = eye preference; dev = deviation. **Bold** cells = SRM > | 2 |.

findings of partially matching the predictions of Gerrits' model. Consequently, the current study interprets questionnaire-based laterality patterns as indirect behavioral markers of lateralized neural organization, acknowledging that individual variability and modality-specific differences may attenuate this correspondence.

Secondly, the segregation bias model was developed considering three lateralized functions: handedness, language, and spatial attention bias. Because we are trying to fit three dimensions of lateral preference into the model, it could be expected some differences in outcomes. Language has been shown to be as lateralized as handedness (Ocklenburg et al., 2014), while the preference dimensions assessed here (e.g., footedness and eyedness) are not so strongly lateralized in the population (Bourassa et al., 1996; Packheiser et al., 2020). These two distinct aspects of our methodological approach – questionnaire assessment and different lateralized functions – could account for the deviations observed in our data as compared to Gerrits' model. However, we should highlight that one of the main predictions, that LHs would display a higher frequency of deviations from the TFS, was observed in our data, showing LHs to have more often an opposed preference for right-footedness and right-eyedness.

From the neural processing efficiency standpoint, having the three sensory-motor laterality dimensions allocated within the same hemisphere could prove an advantage. Neural networks specialized in dynamic motor control would be present in a single side of the brain, fine-tuning both hand and foot fine motor control, with its counterpart impedance-related specialization located in the other hemisphere (for dynamic and impedance control concepts, see Sainburg, 2014). Eyedness, however, is less understood in this context, as it does not participate directly in the motor effector apparatus (i.e., musculoskeletal system), even though visual information is highly regarded to regulate and fine-tune motor control in a variety of scenarios (Elliott and Bennett, 2021). One possible interpretation is that the alignment of handedness and eyedness may be associated with more streamlined sensorimotor integration, given that both effectors would be predominantly represented in the same hemisphere (e.g., Bourne, 2006; Corballis, 2009; Sainburg, 2002). This hemispheric convergence could, in theory, facilitate more efficient coordination between perceptual and motor processes. However, this interpretation remains to be tested: questionnaire data alone cannot demonstrate neural efficiency or pathway shortening, and direct testing with performance measures and brain imaging would be required to confirm this hypothesis.

The opposite notion of neural efficiency in this context would be crowding, where segregation takes place in such a way that a given hemisphere is already occupied by other lateralized functions, thus causing competition for neural resources (Gerrits, 2024). Indeed, atypical patterns of hemisphere segregation of cognitive functions may be associated with poorer cognitive ability even in neurologically healthy individuals (Gerrits et al., 2020; Lust et al., 2011; Powell et al., 2012; Vingerhoets et al., 2018). However, that may not necessarily be the case with sensory-motor functions as assessed in the present research. Future investigations with brain imaging and motor performance measurements are necessary to solve this issue.

4.2. Potential effects of aging on segregation variability of sensory-motor laterality dimensions

When comparing the four different analyzed age groups (e.g., 11–17, 18–30, 31–50, and 51–70 years old), we found significant differences in the frequency of deviations (see Table 3 and Fig. 3). That result was attributed to the 18–30 group showing more cases of deviation from the TFS, specifically the right-handers (Fig. 3). It has been previously shown that each dimension of lateral preference follows its own developmental path after adolescence, thus leading to reduced correlation between preference dimensions in adulthood (Marcori et al., 2023). Additionally, the development of the neural system leads to the specialization of each cortical area in its function, being accompanied by functional reorganizational processes (Stiles and Jernigan, 2010) – which is thought to be completed in the early twenties (de Graaf-Peters and Hadders-Algra, 2006). This age range also represents a moment in life where motor skills are already fully developed (Goodway et al., 2019), such that exploration to expand the motor repertoire and participation in sports and physical activity can freely happen. Together with the neurodevelopmental process, this potentially varied motor practice can lead to both modulation of lateral preference (Marcori et al., 2019b) and neural plasticity modifications in motor control areas (Marcori and Okazaki, 2019), causing higher frequencies of deviation from the TFS. Furthermore, because changes in lateral preference based on recent motor experiences are transient and can be lost without additional practice (Teixeira and Okazaki, 2007), further aging without active practice could lead to a 'return to normal' lateral preference – causing the reduction in the deviation frequency as shown in our data. Taken together, these aspects could explain why both adults' group presents more individuals in the deviation categories, as those age groups may be more prone to exploring and using the non-preferred limb in their daily activities, thus skewing their questionnaire data towards a non-right preference. Therefore, that does not necessarily mean their lateralized functions are allocated in the other hemisphere, which could only be confirmed by brain-imaging methods, but rather show how questionnaire assessment might suggest this interpretation.

4.3. Lack of sex differences in prevalence of atypical patterns of segregation

Although previous research has consistently shown that males are more likely than females to exhibit non-right lateral preferences – particularly in handedness and footedness (Packheiser et al., 2020; Papadatou-Pastou et al., 2008), but not necessarily in eyedness (Bourassa et al., 1996) – our study found no significant sex differences in the expression of typical or deviated functional segregation phenotypes of sensory-motor laterality dimensions (see Table 4). This finding rejects our initially raised hypothesis of sex differences, thus appearing counterintuitive; however, it aligns with recent pieces of evidence emphasizing the complexity and multidimensionality of laterality organization. Gerrits (2024) suggests that the segregation of lateralized functions may follow a global organizational principle with the goal of minimizing hemispheric interference, rather than being governed solely by genetic or hormonal influences. Therefore, while sex-linked factors are known to increase the frequency of individual non-right preferences, they may not necessarily disrupt the overarching pattern of hemispheric segregation when considering multiple laterality domains together. Furthermore, crossed or mixed lateral profiles can happen in the general neurotypical population (Marcori et al., 2019a) and may not systematically cluster by sex. Cultural and social factors, such as previous motor experiences and social practices (Bazo et al., 2022; Marcori and Okazaki, 2020), may also modulate biological predispositions, contributing to a homogeneous pattern of segregation across sexes. Therefore, the absence of a sex difference in our data does not contradict established sex-related trends in single-dimension laterality (Bourassa et al., 1996; Packheiser et al., 2020; Papadatou-Pastou et al., 2020). Instead, it suggests that the expression of segregation phenotypes may operate under broader, integrative mechanisms unconstrained by sex-based variability.

4.4. Why the 0.2 cut-off had the best fit for the model?

The choice of the ±0.2 cut-off for classifying left, mixed, and right preference was both theoretically and methodologically motivated. Laterality indices derived from questionnaires differ from neuroimaging-based LI measures because they reflect behavioral preference patterns, rather than direct hemispheric activation measurements. Within questionnaires results, values close to zero are known to be unstable and more susceptible to measurement noise, which can lead to the misclassification of weak preferences – specially if zero is treated as the set threshold (Carey and Johnstone, 2014; Knecht, 2000; Seghier, 2008, 2019). To address this, laterality studies also from neuroimaging have established a neutral or "indifferent" band around zero, most commonly at ± 0.2, to distinguish individuals with meaningful lateralized preferences from those showing near-symmetry (Carey and Johnstone, 2014; Seghier, 2008, 2019). This approach is especially appropriate for preference questionnaires, which are less sensitive to subtle gradations in laterality strength than neural measures and often display clustering toward extreme values (Peters and Murphy, 1992; Rodway et al., 2024; Tran et al., 2014). Moreover, the classification of right vs. non-Right reflects the dichotomic structural asymmetry in Gerrits's framework (making our comparisons possible) while also preserving the integrity of the indifferent/mixed category, avoiding artificial inflation of the right-sided group. Although alternative thresholds (e.g., 0.0) were examined, they produced equivalent results but marked shifts in the distribution of phenotypes, as shown in our analyses, without altering the underlying pattern of effects. Thus, ±0.2 represents a conceptually justified and empirically stable threshold for classifying sensory-motor preference in this behavioral context.

4.5. What can be drawn from this approach and its applicability in clinical and practical contexts

Applying the segregation framework to sensory-motor laterality offers some venues for clinical research and practice, particularly in understanding atypical neural organization among neurological populations. A consistent observation in neuropsychology is the higher prevalence of non-right-handedness in individuals with neurodevelopmental and neuropsychiatric conditions (Packheiser et al., 2025), including: attention deficit and hyperactivity disorder (Nastou et al., 2022), autism spectrum disorder (Markou et al., 2017), post-traumatic stress disorder (Borawski et al., 2023), and schizophrenia (Packheiser et al., 2025). Furthermore, atypical footedness has also been regarded as a better predictor of schizotypy than mixed-handedness (Tran et al., 2015). These findings show how most clinical studies have traditionally focused on handedness, missing the potential contribution of other lateral preference dimensions.

The segregation approach invites a multidimensional evaluation of lateral profiles, as atypical patterns of lateral preference in more than one dimension may occur. For instance, if NRH is such an important marker for neuropsychological conditions, atypical organization of other lateral preference dimensions can also occur at a higher rate at these conditions – with the potential to be a marker for screening patients (Ocklenburg et al., 2024; Packheiser et al., 2025). According to the segregation bias model (Gerrits, 2024), such multi-domain deviations from typical segregation may correlate with less efficient interhemispheric processing or reduced cognitive performance. Thus, integrating segregation-based assessments could aid early detection of neurodevelopmental risk and support more nuanced neurocognitive profiling, which can be implemented in clinical and research practice with the addition of questionnaires.

In the sports field, congruence between dimensions could be an advantage in certain modalities. In shooting and archery, for instance, having eyedness aligned with handedness facilitates biomechanical positioning, as the aiming eye is closer to the shooting hand (Moreno et al., 2022; Moretto et al., 2018). On the other hand, there has been evidence that crossed-eye preference (i.e., eyedness contrary to handedness) is more frequent in professional tennis and golf players (Moreno et al., 2022). It could be that having the preferred eye closer to the target or the moving ball provides an advantage from the motor control standpoint. However, performance measurements from experimental studies in these areas are not directly taken, being usually assessed based on the average number of wins or the athletes' rank (Moreno et al., 2022; Runswick et al., 2022). Therefore, it is not clear whether this organization of lateral preference provides a clear advantage or not in terms of performance. For team sports (e.g., soccer, basketball, handball), the relationship between these dimensions might not be so clear, as athletes are not allowed to use both upper and lower limbs for ball interactions in these modalities. Hence, its applicability in these contexts might be less relevant.

5. Limitations

Our investigation is not without limitations. Our data of comparison between age groups is not able to confirm developmental aspects, as participants were only measured once and not accompanied throughout their lifetime. Additionally, measures of performance are necessary to test if atypical patterns in the motor-sensory domains could actually be translated into disadvantages in certain types of motor tasks. Furthermore, even though LHs are represented in their expected proportion in our sample (i.e., around 10 %), it could be that analyzing a larger amount of LHs would produce different outcomes. This remains to be tested.

6. Conclusions

Our data on sensory-motor laterality dimensions partially fits the segregation bias model proposed by Gerrits (2024). The main predictions are observed, as NRHs showed a higher prevalence of atypical patterns of functional segregation, even though the exact percentage values from the model differ from the data observed. However, we highlight that the initially developed model accounted for handedness, language, and spatial bias, not the functions measured here. With that in mind, we believe the model holds for its applications and predictions, providing a strong basis to fundament future research and better model hemispheric segregation phenotypes variability. Young adults showed more deviations as compared to the other age groups, but the distribution of phenotypes for functional segregation patterns considering the sensory-motor laterality dimensions assessed in the present research did not significantly vary between sexes.

CRediT authorship contribution statement

Alexandre Jehan Marcori: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Victor Hugo Alves Okazaki:** Writing – review & editing, Supervision, Software, Methodology, Investigation, Data curation, Conceptualization. **Sebastian Ocklenburg:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization.

Disclosure statement

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2025.109327.

Data availability statement

The data supporting this research can be obtained with the corresponding author AJM upon reasonable request.

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