Handedness Modulates Spatial Attention – Insights From Individual Variations In Lateralization Of Cognitive Functions

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Abstract

Increased left-handedness and atypical lateralization in individuals with neurodevelopmental and psychiatric disorders point to a deep yet unresolved connection between handedness, hemispheric asymmetry, and normal brain functioning. Most handedness-lateralization research has either excluded left-handers due to their higher variability, or failed to control the degree of handedness. The discrete categorization based on arbitrary criteria or cut-offs has made it challenging to address inter-individual variations in the lateralization of cognitive functions. In this study, capturing responses from across the handedness continuum in tasks of the divided visual half-field paradigm, we explored the lateralization patterns in different stages of visual processing of orientation, global-and-local, faces and words. We found that the degree of handedness significantly affects lateralization in all tasks except orientation. Notably, even though the direction of hemispheric preference did reverse in left-handers for visuospatial attention like in global-local processing, the same was not for word and face processing. Our results substantially evidence that handedness differentially influences the lateralization of visual processes. The observed relationship between the dominant hand and global-local processing significantly points to the action-dependent modulation of visual attention. We conclude that the degree of left-handedness is potentially a critical factor in lateralization, and a continuum approach would be beneficial to control for the individual variations in laterality research.

Keywords: Handedness; Hemispheric Asymmetry; Action; Face and Word processing; Global-local processing; Visual attention; Individual Variation.

Introduction

One of the most fundamental characteristics of the brain is the structural and functional specialization of its hemispheres (Ocklenburg & Gunturkun, 2012). Hemispheric lateralization generally refers to the superior processing capacity of one hemisphere over the other in performing specific tasks. Studies over the years have found vital cognitive processes to be processed more efficiently in the hemisphere where the functions are lateralized (Corballis, 2019).

Language and visuospatial processes are the most studied cognitive functions in the lateralization literature. The left hemisphere (LH) is dominant for overt speech production, word processing, processing phonemic information, and syntactic information (Seghier & Price, 2011; Gutierrez-Sigut, 2015). Similarly, the right hemisphere (RH) has been found to be superior for various non-verbal tasks such as processing visuospatial, face, and emotion-based information (de Schotten et al., 2011; Godfrey & Grimshaw, 2016).

Atypical lateralization generally refers to the deviations from the typical patterns of brain functions and organization seen in right-handed individuals (Knecht et al., 2000). Left-handedness has long been associated with a higher prevalence of atypical lateralization of language (90-95% of right-handers but only about 70-75% of left-handers have left lateralization of language, Knecht et al., 2000; Mazoyer et al., 2014). However, studies on the association between handedness and spatial lateralization have rarely been studied in literature and are inconsistent. While some research indicates that right-hemispheric spatial dominance is relatively evenly distributed in right- and left-handers, albeit to varying degrees (Flöel et al., 2005; Powell et al., 2012), other studies show that the right hemisphere controls spatial tasks in right-handers while there is no hemispheric preference in left-handers (Vogel et al., 2003). Neuropsychiatric disorders like Schizophrenia, ASD etc., show altered hemispheric lateralization (Asai et al., 2009; Jouravlev et al., 2020). Interestingly, the likes of Brandler & Paracchini (2014) have noted how these neuroatypical populations have higher incidences of left-handers. The three-way interaction in handedness, hemispheric asymmetry and behavior suggests that handedness and lateralization are indispensable in addressing individual variations and brain functioning. Thus, research studies have strengthened the evidence for the strong relationship between handedness and its influence on the lateralization of cognitive functions.

Problems with handedness-lateralization studies

Since the majority of the population is right-handers, there are very few lateralization studies that focus on left-handedness. Thus, as O'Regan & Serrien (2018) point out, we have a very limited understanding of lateralization patterns in left-handers compared to right-handers. Furthermore, most handedness-lateralization studies suffer from the exclusion of left-handers due to their higher variability (Van der Haegen & Brysbaert, 2018). However, even the right-handers included in these studies are not entirely strong right-handers either, as they have been seen to exhibit some left-hand preferences (Beaton et al., 2021), thus suggesting the degree of handedness could end up being a possible confound in these studies. Moreover, most studies addressing the handedness-lateralization question tend to categorize people just into binary (left or right-handers) or triadic (left, right, ambidextrous) groups based on arbitrary handedness score cut-offs. However, any such approach of discrete classification, when applied on a whole continuum, would evidently fail to account for the entire range or degree of handedness and individual variations in lateralization of the examined cognitive functions, thereby possibly leading to the inconsistent findings of the effect of handedness on lateralization. Hence, to adequately examine this, capturing the entire handedness spectrum, and controlling for the degree of handedness, seems of utmost necessity. However, in our limited review, we could find no relevant study that has appropriately attempted to capture this continuum and its effects to study lateralization in healthy individuals.

Visual field asymmetries in the visual hierarchy

Our visual cortex has been found to process information hierarchically, with early visual areas extracting and processing the most simple visual features, which are further refined in the later stages of vision (Kamkar et al., 2018). One of the early aspects to get processed is the spatial frequency of visual input (Kauffmann et al., 2014). Low spatial frequency (LSF) information is the broad, global features, such as the overall shape and texture of the image, while high spatial frequency (HSF) refers to the fine, local details, such as edges, texture etc. The right visual field advantage (i.e., left hemisphere specialization) for local processing and the left visual field advantage (i.e., right hemisphere specialization) for global processing have been widely reported (Brederoo, 2019). Studies like Flevaris & Robertson, 2016 etc. have also noted how global-local lateralization (LH bias for processing HSF and RH bias for LSF) is strongly interlinked with the neural mechanisms of visual processing and attention. Even though no evidence has been found for lateralization of SF in the early stages of visual processing, seminal studies like Ivry & Robertson (1998) and Andresen & Marsolek (2005) modelled how relative SF processing may emerge in the later stages with their principles of selective tuning of spatial frequency bands. According to their double filtering by frequency theory, both hemispheres process SF information and only in later stages of perception does the specialization of SF happen. Thus, the observed lateralization of higher-order visual processing reflects an underlying specialization for relatively HSF in the LH and relatively LSF in the RH.

Studies have found that higher-level word and face processing in the typical right-handed population is lateralized to the left and right hemispheres, respectively (Dundas et al., 2013). Furthermore, these studies have also noted how removing LSF content from images of faces significantly altered face recognition; similarly, word processing was altered when the HSF information was separated (Goffaux & Rossion, 2006; Ossowski & Behrmann, 2015). Recent work like that of Brederoo et al., 2020 on varied visual field asymmetries have also observed RH lateralization for Face, global form, LSF processing, and spatial attention, and LH lateralization for processing visual word or local features. They conclude that the left and right lateralization of the word and face processing may be influenced by the underlying lateralization of LSF and HSF in RH and LH, respectively. Thus, one can also hypothesize that lateralization of high-level cognitive functions reflects the underlying patterns of low-level relative spatial frequency processing as lateralized to the left and right hemispheres.

Left-handedness and lateralized vision

Visual field asymmetry studies with left-handers are generally rare in the literature and limited to language, Face and spatial attention tasks. During face processing, Frässle et al., 2016 found enhanced recruitment of the left Fusiform Face Area (FFA) in left-handers compared to right-handers. While many studies suggest reduced language lateralization in left-handers, language is said to be left-lateralized irrespective of handedness (Serrien & Sovijrvi-Spap, 2015). Within our review, Goodarzi et al., 2005 have been the rare study that has investigated the lateralization of global local process in the left-handers and has found that left-handed individuals do tend to deviate from the typical pattern of lateralization, with evidence of more specialization of the right hemisphere in processing local information and of the left hemisphere in processing global information. It remains, however, an undeniable gap that none of these studies controlled for the degree of handedness. Thus, a detailed study on lateralization of visual processes with consideration of the effects of a handedness continuum turns necessary.

Our Approach

Even after scores of studies on handedness and lateralization, we lack a general framework that accounts for the individual variability in handedness in the population and the associated atypical lateralization. In this study, we thus tested whether capturing the handedness continuum would be able to explain the variations in lateralization in tasks among individuals with increasing levels of complexity in the visual processing hierarchy. Towards this, we thereby studied the lateralization patterns of various processes, which are considered early (orientation) and late (word/face) stage visual processing, as well as visuospatial attention (global-local) tasks.

Experiment 1 (E1-orientation judgment) examined the lateralization of early visual processes towards orientations of gratings, while also assessing the effects of LSF and HSF on processing orientation. Experiment 2 (E2) looked at visual attention (global-local attention task). In Experiment 3 (E3- Face matching task) and Experiment 4 (E4- Word matching task), we tried to capture an even higher-level process in the visual hierarchy. Our aim is to see whether or how handedness modulates any of these processes.

Methods

Participants: 104 college students from Indian Institute of Technology Kanpur (IITK, n=62) and National Institute of Technology, Calicut, India (NITC, n=42) were recruited via campus surveys using a modified Edinburgh handedness inventory (Oldfield, 1971). The participants were selected after controlling for the degree of handedness, meaning the entire handedness continuum was captured for the final analysis. Before the experiment, LexTale scores were measured, and 2 participants scoring < 65% were removed to control for linguistic differences. The final analysis included 102 participants (age: 23.64 (3.17), 13 females) with handedness scores ranging from -1 to +1 (M= -0.06, SD =0.62) and uniformly distributed (Asymptotic two-sample Kolmogorov-Smirnov test: D (102) = 0.12, p = 0.480).

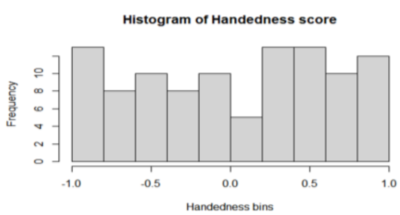

Figure 1: Distribution of handedness. Participants were sampled to ensure a uniform distribution.

General design: We used a divided visual half-field paradigm over four separate experiments (Figure 2), where different kinds of stimuli, depending on task, were presented to both sides of the visual field (presentation of bilateral stimulus on PC screen in a dark room) with a central arrow pointing towards the target. Trials in all four experimental blocks started with 500mS of the blank screen followed by 300mS of a fixation cross. The size of each stimuli image was 3° x 3° degrees, and the central arrow was 1° x 0.5°, together the entire frame extended to 9-10° of visual angle along the horizontal axis, ensuring foveal presentation. In word processing, words of length 4–5 letters were used and were displayed 3°/4° x 1°. This main stimuli screen always appeared for 150mS, followed by a response window of up to 2 seconds. Depending on the task, using both hands, participants had to press the 'z' and 'm' keys (with their index fingers) or the 'a' and 'k' keys (with their middle fingers) to respond to the target image. The bimanual responses were captured in order to remove any artifact that comes from the dominant hand. The average RT from left and right key presses was used in the analysis. The experiments were created on Psychopy builder and customized with code snippets. LexTale scores (Lemhöfer & Broersma, 2012) were measured as a proxy for linguistic proficiency.

Task and procedure: In E1, grating images with left and right orientations (inclined at -45° or 45° respectively) were used to study the lateralization of orientation. The grating frequency was also varied to check if relative SF processing is lateralized. On either side of the screen, participants were shown a left or right-oriented spatial grating from two sets of spatial frequencies (low SF: 0.5,0.6,0.7,0.8 and high SF: 5,6,7,8, all values in cycles per degree, *cpd*). Over 512 trials, participants judged the orientation of the target as pointed by the arrow and then responded by pressing with index fingers if gratings were perceived as right-oriented or both their middle fingers if they judged them to be left-oriented.

For E2, we used hierarchical image stimuli to assess global and local processing. Global shapes are made from local shape components– a bigger square (at the global level) made up of smaller squares (at the local level), or a bigger diamond made up of smaller diamonds. Similarly, a bigger square at the global level comprises smaller diamonds at the local level. Conversely, a diamond at the global level is made of smaller local squares. After the first fixation cross, a cue shape (a diamond or square with a size of the average of global and local shapes to avoid bias for either the global or local level) appeared for 300ms. The participant, following another fixation cross of 150ms, had to judge the level (global or local) at which the cue shape had appeared (for 150ms) in the target image on the screen.

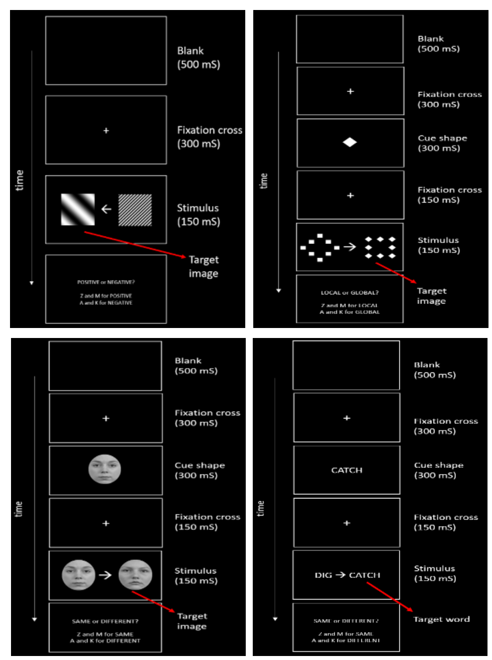

Figure 2: Instances of the four task conditions and corr key.
Top Left: E1- a left-oriented grating being pointed to Z&M
Top Right: E2- Cue shape is at local-level correct: Z&M
Bottom Left: E3- Cue face and Target do not match: A&K
Bottom Right: E4- Cue word and Target match: Z&M

Over 512 trials, they had to press with the index finger when they assessed the presence of the cue at a local level and with the middle-finger keys when assessed at a global level. Participants were asked to refrain from pressing any key when the target image did not have the cue shape.

In place of the cue shape, a cue face and cue word appeared at the center in E3 and E4 for 300 ms after the first fixation cross. For E3, randomized but gender-congruent pairings from a set of 10 male and ten female faces with neutral expressions from the Radboud faces dataset (Langner et al., 2010) were used as stimuli. Following the presentation of a cue face and another fixation of 150 ms, two face stimuli with a centered arrow were presented for 150 ms. The participant, over 256 trials and a 2-second response window, reported whether the target face, as pointed by the arrow, was the same as the cue.

In E4, the face stimuli were replaced with 60 words (4-5 letter length) controlled for concreteness, valence, arousal, and frequency using Brysbaert et al., 2014. Over 640 trials, two randomly selected and paired words were presented, and participants had to respond whether the cue word matched with the target or not. In both E3 and E4, they used index finger key presses to indicate match responses and middle finger presses for otherwise.

Analysis: We used a 3–SD cut-off on reaction times at the trial and population levels to capture maximum variation in our data. Correlation analysis was performed after cleaning out outliers at the trial and group levels. RT and accuracy were used as the independent variables. The laterality index (LI) was measured by subtracting the RT or accuracy values in the left (LVF) and right visual field (RVF). LVF-RVF > 0 indicated a preference for the left hemisphere (LH), whereas LVF-RVF < 0 showed a right hemisphere (RH) preference. LI was plotted as a function of the handedness score. Additionally, group level analyses were also performed by demarcating the handedness continuum into the generally left-handed (Hscore -1 to -0.33), mixed-handed (-0.33 to 0.33) and right-handed (0.33 to 1) groups.

Results

Across all the tasks, apart from E1- the orientation processing task, we found that the laterality indices exert a significant correlation relationship on handedness.

Lateralization at the handedness continuum

In E1, neither the laterality index of RT nor accuracy in positively (right) oriented or negatively (left) oriented gratings in LSF and HSF conditions were significantly correlated with the handedness continuum (all *p*s > 0.05).

In E2, the LI of both RT and accuracy of both global and local tasks were found to be significantly associated with the degree of handedness [Global RT: r(96) = -0.42, p=<0.001; Global accuracy: r(96) = 0.24, p=0.019; Local RT: r(96) = -0.33, p=<0.001; Local accuracy: r(96) = 0.24, p=0.016]. We also found a significant correlation even after combining global and local conditions by taking average as a proxy for hierarchical visual attention processing for both RT and accuracy [combined global-local average RT: r(96) = -0.41, p < .001; accuracy r(96) = 0.29, p = .005]. As observed throughout, accuracy was positively correlated, and RT was negatively correlated with handedness.

In the Face–matching (E3) task, LI of both accuracy and RT was significantly correlated with the handedness degree [Face RT: r(96) = -0.32, p=.001; Face accuracy: r(96) = -0.29, p=.003]. Again, RT was positively correlated with handedness, whereas accuracy was negatively correlated.

In the word-matching task (E4), LI of RT showed a significant negative correlation with handedness [Word RT: r(98) = -0.23, p=0.022]. No correlation with handedness was observed in LI of accuracy. Distributions are as in Fig3-Left.

Across E2, E3 and E4, RT and accuracy were significantly negatively correlated, [Global: r(96) = -0.47, p < 0.001; Local: r(96) = -0.34, p < 0.001; Face: r(96) = -0.87, p < 0.001; and Word: r(98) = -0.43, p < 0.001], reflecting an overarching RT-accuracy tradeoff in such visual processing.

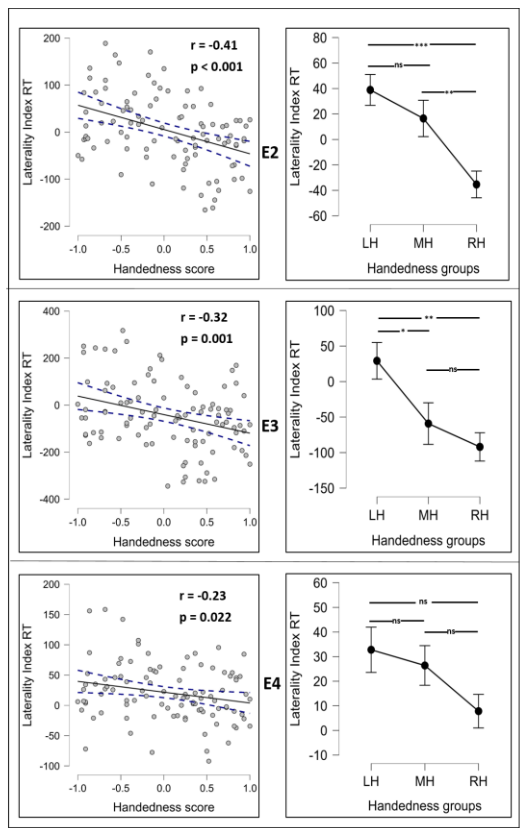

Figure 3: Left: Distribution of laterality indices across tasks on handedness continuum with r scores; Right: comparison of the responses from the discrete handedness groups

Lateralization in the handedness subgroups

To assess the nature of variation across responses from the different subgroups of the handedness spectrum, a 1-way

ANOVA was performed between laterality indices of RT and accuracy of responses and the handedness groups (left, mixed and right-handed) for all tasks. Lateralization of orientation and word processing showed no significant difference between the left, mixed and right-handers (all *p* values > 0.05). However, lateralization significantly differed between the groups in global-local and face processing.

In E2, one-way ANOVA revealed a significant difference in LI of the averaged global-local attention RT between handedness groups [F(2,95)= 10.669, p = <.001 η_p^2=0.183]. Post hoc analysis on revealed that left-handers (with LI of RT- mean=38ms SD=68) and right-handers (with LI of RT of mean=-35ms SD=65) [t=4.472, p_{holm}< 0.01, Cohen's d = 1.073] as well as mixed handers (LI of RT mean= 16ms SD=75) and right-handers [t=3.008, p_{holm}=0.007, Cohen's d= 0.749] significantly differed in lateralization of spatial attention, while the difference between mixed-hand and left-hand was insignificant (p=.214). Handedness was not observed to have a significant effect on accuracy in lateralized global-local attention [F(2,95) = 2.812, p = .065, η_p^2=0.056].

In the face-matching task (E3), one-way ANOVA revealed a significant effect of handedness groups in LI of RT and accuracy [Face RT: F(2,95) = 6.733, p = .002, η_p^2=0.124]; Face accuracy: F(2,95) = 6.784, p = .002, η_p^2=0.125]. Post-hoc analysis of LI-RT showed that between the left-handers (LI of RT mean= 29ms SD=143) and mixed-handers (LI of RT mean= -59ms SD=154), there was a significant difference [t = -2.428, p_{holm}= 0.034, Cohen's d = 0.633] as well between left and right-handers (with LI of RT at mean=-92ms SD=124) [t = 3.608, p_{holm}= 0.001, Cohen's d = 0.868]. The difference between mixed and right-handers was not significantly different (p_{holm}= 0.567).

In the word-matching task (E4), the one-way ANOVA did not reveal a significant effect of handedness in LI of RT and accuracy [Word RT: F(2,97)= 2.876, p= 0.061, η_p^2=0.056; Word accuracy: F(2,97)= 0.570, p= .567, η_p^2=0.012].

In global-local attention, left-handers' responses had LH preference (LI > 0), and right-handers with LI < 0 showed RH preference. Mixed-handers did not show any particular preference for either LH or RH (LI ~ 0). In face processing, right-handers and mixed-handers showed a preference for RH specialization. Left-handers were slightly left-lateralized (LI > 0). In the global-local, word and face tasks, LI of mixed-handers was consistently found to lie between left and right-handers, suggesting that the individual variations in the lateralization of these tasks vary along the handedness continuum.

Considering the handedness continuum, we observed a general trend towards RH lateralization of face processing and LH lateralization of words at the population level. However, the lateralization patterns of global-local attention shifted the hemispheres as the direction of handedness reversed (see Figure 4)

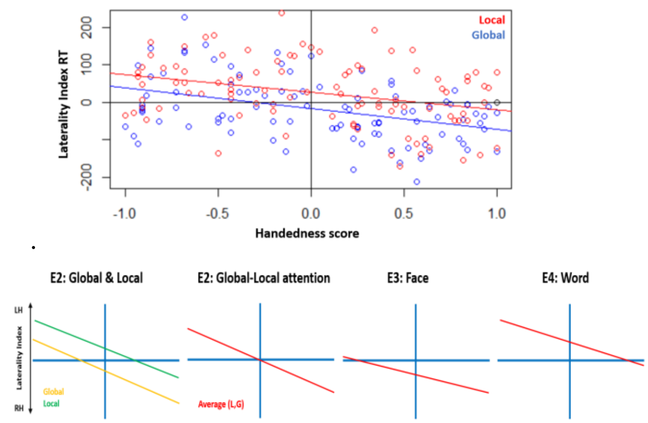

Figure 4: (a, b) Overlaying the global and local lateralization indices (LI-scores) gives the relative preferences of global and local processing across the handedness. (c) lateralization of spatial attention after average global-local processing (d) face (e) word processing

Discussion

This study looked at the lateralization patterns of orientation judgment, global-local processing, and word and face recognition along the handedness continuum. We found a significant association between hemispheric specialization and handedness in global-local, face, and word tasks but not in orientation judgment tasks. Consistently, we found that handedness influences the degree of lateralization across all these tasks. Interestingly, the direction of lateralization of global-local attention changed with the direction of handedness, suggesting the possibility that handedness and spatial attention, a lower-level feature (processed during the early stages of visual processing), could have an unexplored shared relationship.

In the orientation judgment task (E1), handedness did not show any effect on lateralization of orientation or SF processing. This is not surprising given that orientation and SF information are lower-level features and lateralization only emerges at an advanced stage of processing. The input asymmetry principle (Andresen & Marsolek, 2005) suggests that the first stage filtering of SF happens in both hemispheres, and no apparent preference is observed in the first stage. It is only later in processing that the hemispheres specialize in relatively HSF and LSF in the left and right hemispheres, respectively. Based on this, if the RH and LH preferentially process HSF and LSF, respectively, we had expected to observe lateralized spatial frequency processing. Since our task measured the effects of SF indirectly through the orientation of the grating, participants might not be engaging in processing relative SF information. It could be that participants are using LSF information of HSF gratings to judge its orientation. Thus, the effects of handedness on orientation and SF processing are inconclusive and require further investigations with better experimental designs.

When considering global-local features, based on existing literature (Goodarzi et al., 2005), one could hypothesize that right-handed participants would have RH lateralization for global–processing and a relative LH specialization for local processing. Contrary to this hypothesis, we found that both local and global processing show RH preference in right-handers (Fig 4a). Interestingly, left-handers showed an opposite pattern (i.e., RH preference for global and local processing). This observed reversal in the direction of lateralization of visual attention with the direction of handedness suggests that left-handedness and spatial attention are interlinked. This extends previous studies (O'Regan & Serrien 2018) that have also shown similar evidence of more atypical lateralization in the left-handers. Although our study did not directly inspect any cognitive rating tests or patient population, others have widely found evidence of abnormalities in integrating global-local level information and hindrances in attention in schizophrenia, ASD and ADHD (Coleman et al., 2009; Koldewyn et al., 2013; Booth & Happé, 2018). It is also intriguing to wonder if the observations of increased left-handedness incidence in these atypical populations (as seen in Brandler & Paracchini 2014, Hirnstein & Hudall 2014) is related to the underlying lateralization of spatial attention. The observed atypical lateralization of global-local attention in the left-handers and altered processing of global-local attention in the atypical populace (who also had elevated left-handedness) thereby reinforces support for possible claims that left-handedness and hemispheric asymmetry may be linked to each other and with cognition in general. Further research can investigate any causal mechanisms that may be binding the factors of handedness and lateralization to such cognitive functioning.

In face processing, our results indicated that handedness was significantly correlated with lateralization of the face. Looking at the handedness groups revealed that mixed and right-handers show right hemisphere preference. However, the left-handers were left-lateralized, aligning with the existing literature (Frässle et al. 2016). For word processing, we found that the handedness continuum significantly influences word lateralization. Yet, with our ANOVA, no significant effects of handedness groups were observed.

Nevertheless, comparing just the left and right-handers, we observed a stronger LH lateralization for word processing in the left-handers than in the right-handers. This supported the possibility of surface-level processing of the words, which would, in turn, depend on low spatial frequency information (Goffaux & Rossion, 2006). While we expected to see clear left lateralization of word processing irrespective of handedness, we observed that many right-handers showed right lateralization. Since the words were presented only for 150mS presentation time, it is possible that participants processed the words at the lexical level without evoking the phonological features of word processing (which are known to be left-lateralized Gutierrez-Sigut, 2015), thus showing weaker lateralization at the population level. Similarly, the stronger left preference for word processing in the left-handers than in the right-handers thus supports the possibility of the surface-level processing of words, which would thus depend on the processing of LSF information.

The role of the degree and direction of handedness in capturing individual variations

Since both the degree and the direction of lateralization of spatial attention change with handedness, one can infer, by extension, that both handedness and attention would also be deeply related. The emergence of such interrelatedness can be examined through our ontogenic traces. The consensus on the origins of variations in handedness is that it arises from the general hemispheric asymmetry during early embryonic development (Mitchell, 2018) and that this exact mechanism of neurodevelopmental variation paves the way for general hemispheric asymmetries. Thus, it is possible that the observed correlation of visuospatial attention with the degree and direction of handedness, as evident from our results, reflects an underlying asymmetric brain development during its early embryonic period. This then implies that neurodevelopmental variations may determine the degree of lateralization of low-level features as well as the degree of left-handedness at the individual level.

Since the lateralization of higher-level functions depends on the lateralization of lower-level features in the visual processing hierarchy, the individual variations captured by the handedness in higher-level word and face processing could be inferred as well to be emerging from the variations of the underlying lower-level features. Thus, it is essential to control for the degree of handedness as a proxy for low-level features and include left-handers in the lateralization studies to sufficiently address the questions and implications of the individual variations in lateralization and associated behavioral variations.

Overall, our results provide supporting evidence that handedness differentially influences the lateralization of lower-level visual attention and higher-level word and face processing. The change in the degree and direction of lateralization of spatial attention with that of handedness implies the possibility that action representation and spatial attention are inextricably interwoven. The current study provides significant evidence supporting the role of the degree and direction of handedness on lateralization patterns as exhibited in a myriad of cognitive tasks. Harnessing the continuum approach in further studies would benefit in exploring and explaining the inter-individual variations, as is seen in the lateralization literature. Improved experimental designs to capture the saliences behind relative spatial frequency processing could provide more insights into understanding handedness-lateralization and their further implications in cognition in the future.

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