AMERICAN PSYCHOLOGICAL ASSOCIATION
ibnec
Psychology & Neuroscience

ISSN: 1983-3288

2022, Vol. 15, No. 2, 89–104
https://doi.org/10.1037/pne0000269

Reciprocal or Independent Hemispheric Specializations: Evidence From Cerebral Dominance for Fluency, Faces, and Bodies in Right- and Left-Handers

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Objective: There are distinct cortical regions that respond preferentially to human faces and bodies. It is generally accepted that these face- and body-selective regions are lateralized to the right hemisphere, but unknown how frequently these biases occur or if they are lateralized in a complementary fashion to language processing. ***Method***: Functional magnetic resonance imaging (fMRI) was used to examine face and body lateralization in two samples of right-handers (*n*'s = 31 and 18) and left-handers (*n*'s = 43 and 24) with "typical", left hemisphere, language dominance to examine the frequency of these biases. Crucially, we also recruited individuals with "atypical," right hemisphere, language dominance (*n*'s = 17 and 10) to examine complementarity with language. ***Results***: Language typical right-handers had consistent population-level and average right-sided biases for face and body perception. Language typical left-handers had population-level biases for faces in Sample 2, but not Sample 1; and for bodies in Sample 1 but not Sample 2. Language typical left-handers were, on average, right-lateralized for faces in both samples, but right-lateralized for bodies in Sample 1 only. Language atypicals did not have a population-level bias for body or face perception, and were, on average, left-lateralized for faces in Sample 1, but not in Sample 2. Language atypicals were not lateralized for body perception. ***Conclusions***: These results add to the growing literature which suggests that many right hemisphere processes are not lateralized in a fully complementary fashion to language. Left-handers seem to have more varied lateralization patterns even when language dominance is controlled for.

Public Significance Statement
This research demonstrates differences in patterns of complementary brain processes across the hemispheres in left- and right-handers. We also show that the rare kind of brain dominance for language is not associated with specialization of body and face processing to the non-language hemisphere as a matter of routine. These data are important for models which claim unusual hemispheric dominance in individuals with neurodevelopmental conditions, as well as for our understanding of the nature of brain asymmetries in left-handed people.

This article was published Online First December 23, 2021.
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We have no known conflict of interest to disclose.
This work was supported by the Leverhulme Trust [grant number RPG-2019-102].
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Keywords: hemispheric lateralization, atypical language dominance, face perception, body perception, handedness

Supplemental materials: https://doi.org/10.1037/pne0000269.supp

Speculation about hemispheric specialization in the human brain predates contemporary neuroimaging by some distance. After the discoveries of language localization and left-hemispheric dominance by Broca, Dax, and Wernicke in the late 19th century, the idea of functional specialization in the cortex, within and between-hemispheres, became neurological canon (Hillis, 2007). As the majority of the 19th century aphasia cases were right-handed individuals, the association of language dominance and contralateral control of the writing hand was assumed (Benton, 1972; Eling, 1984; Goodglass & Quadfasel, 1954). Nevertheless, by the 1970s, a general consensus emerged from Wada testing of epileptics (e.g., Rasmussen & Milner, 1977), as well as group studies of aphasia in left- and right-handed patients with unilateral brain damage (e.g., Zangwill, 1967), confirming that roughly 70% of left-handers are lateralized in this "typical" left hemisphere fashion for speech and language, as are 90%–95% of right-handed individuals (Carey & Johnstone, 2014).

In sharp contrast, theories about functions that depend more on right hemisphere structures, such as face processing (Della Sala & Young, 2003; Kanwisher et al., 1997; Sergent et al., 1992) or visuospatial attention (Buxbaum, 2006; Holmes, 1918; Riddoch, 1935; Paterson & Zangwill, 1944) were much slower to develop. This literature became quite removed from the research on apraxia and aphasia, leaving a tendency for authors in either domain to refer to little more than right hemisphere dominance for attention (e.g., Blankenburg et al., 2010; Petersen & Posner, 2012), or left hemisphere dominance for speech/language (e.g., Friederici, 2017; or aspects of motor function; Geschwind, 1975; Kimura & Archibald, 1974). In neurology and neuropsychology, it is frequently assumed these two major classes of asymmetries "*anti-localize*" (i.e., if one function is over-represented in the left hemisphere, then the other will be over-represented in the right hemisphere), but there is limited evidence for or against this idea. For example, unlike several articles on unilateral brain damage and presence/absence of aphasia (reviewed in Carey & Johnstone, 2014), very few clinics or hospitals have published incidence data on neglect or prosopagnosia using standardized tests in the same individuals, recording both handedness (however specified) and side of lesion. A few early studies (e.g., Bryden et al., 1983) used multiple indices for visuospatial dysfunction in large patient groups, but these included measures of different dysfunctions (e.g., constructional apraxia), which can follow lesions of either cerebral hemisphere.

A limited number of neuroimaging studies have tackled questions of complementary specialization, and tend to be focused on language and visuospatial abilities (e.g., Ng et al., 2000; Powell et al., 2012) rather than face perception, the latter of which is implicated in recent models (see below). Nevertheless, attempts at comparing one or several functions in right- and left-handed groups are gradually becoming more common (Badzakova-Trajkov et al., 2010; Flöel et al., 2005; Johnstone et al., 2021; Mazoyer et al., 2016; Rosch et al., 2012; Van der Haegen et al., 2012; Whitehouse & Bishop, 2009; Woodhead et al., 2019, 2021). For instance, one of these experiments was designed to examine complementarity of hemispheric lateralization of attention and language (Cai et al., 2013). Individuals who were identified as right hemisphere dominant for verbal fluency in a previous experiment (Van der Haegen et al., 2011) were re-scanned using a landmark task requiring judgments of pre-bisected lines, known to depend more on right hemispheric mechanisms. Cai et al. (2013) found a near perfect complementarity of these two functions, in left-handed individuals with typical (left; 15 out of 16 individuals) and atypical (right; all 13 individuals) language dominance.

One caveat is that the authors selected individuals with very strong language dominance (discussed in Badzakova-Trajkov et al., 2016; Karlsson et al., 2019), where complementarity of function may be more likely. Nevertheless, a strength of the Cai et al. (2013) report is that it acknowledges the importance of the individuals with the rarer form of cerebral asymmetry for tests

of complementary hemispheric dominance(s). This group of individuals is hugely important, as data for language asymmetry, at the very least, is so skewed toward left hemispheric specialization in right-handed samples that many interesting questions regarding complementarity cannot be addressed by right-handers alone. *Any model of complementarity should apply in the same way to the rare individuals who are right-hemisphere dominant for speech and language*.

Large sample neuroimaging studies that measure multiple functions in the same individuals allow for comparison of pairs that depend on the right or the left hemisphere (Badzakova-Trajkov et al., 2010). Complementary specialization is the usual prediction; the lateralization of one function to one hemisphere causes, in some fashion, another function to lateralize to the opposite hemisphere (Bryden, 1990; Bryden et al., 1983). These functions may have been symmetrically located at an initial point, but growth or development of one system (often deemed to be language-related), has a causal role for the other function to lateralize in the opposite direction (Bradshaw & Nettleton, 1981). Many of these models are, in effect, "crowding" hypotheses, that suggest that functional specialization of some neural tissues in one hemisphere leaves "less brain" for the other function, which comes to depend on the other hemisphere.

Current variants of crowding hypotheses of left- and right-hemispheric function are almost exclusively focused on face processing, and their relegation to the right hemisphere as reading develops in foveal regions of occipitotemporal cortex in the left hemisphere (Behrmann & Plaut, 2015; Centanni et al., 2018; Dehaene et al., 2010; Plaut & Behrmann, 2011). As most people are (largely) innately left hemispheric (Carey & Johnstone, 2014; Holowka & Petitto, 2002; Rasmussen & Milner, 1977) for some of the auditory, somatosensory and motor aspects of speech perception/production, when reading training begins, it makes sense for linguistic systems to co-opt occipitotemporal regions in the same hemisphere. As a result, largely bilateral face processing gradually becomes more right hemispheric (although see Lochy et al., 2019, for a recent critique of the electrophysiological evidence in particular).

In contrast, the statistical hypothesis (Bryden, 1990; Bryden & Allard, 1981) assumes that whatever underlies the lateralization of one function is independent of that of another function and may reflect independent probabilistic biases. Each function has an independent statistical probability of being lateralized to the right or the left hemisphere, and the fact a population-level bias for language lateralized to the left hemisphere and, for example, face processing in the right hemisphere may arise, but reflect probabilities relating to independent causal sources.

In the current context, a first step in the evaluation of complementary hemispheric specialization requires estimating the frequency with which face and language hemispheric bias in groups that are lateralized in the more common pattern (i.e., left hemispheric for language, right hemispheric for faces) and quantifying the precision of that estimate. A second crucial step in such an evaluation is to collect data from individuals with the rarer types of asymmetry, in this instance right hemispheric dominance for language and left hemispheric dominance for faces. An important recent example of this approach is by Gerrits et al. (2019). These colleagues capitalized on a pool of left-handers with previously identified atypical (right hemispheric) language dominance, to examine asymmetry related to face and visual word recognition. Their sample included 12 left-handers with atypical dominance for language and 12 left-handers with typical (left hemispheric) dominance. In this sample, 75% of the language typically-lateralized individuals processed faced in the non-language hemisphere, but only 42% of individuals with atypical language dominance did so. In a second study, Gerrits, Verhelst, et al. (2020) examined hemispheric dominance for five different functions (language, praxis, emotional prosody, spatial attention, and face recognition) in a larger sample of left-handed individuals. In contrast to the earlier study, they found strong evidence for complementarity (ranging from 75% to 87%) for language typical and atypical participants for all functions, except for face perception in the language typical left-handers, who surprisingly did not have a population-level bias on the task.

The studies from Gerrits et al. (2019) and Gerrits, Verhelst, et al. (2020) are important for efforts of quantifying how asymmetries relate to one another. However, both studies lack right-handed "control" groups. Right-handed participants are crucial for teasing apart potential

handedness effects from potential language dominance effects (and are also important for relating handedness differences to genetic models, see below). There is some evidence that left-handers may be more variable in their brain dominance for right-hemisphere functions in general (Karlsson et al., 2019; Liu et al., 2009). The ideal experiment would, of course, also include a group of right-handed language atypical participants, but these individuals are rare (about 5%). Although our and other labs have started to search for these individuals, these efforts will take time.

Here, we use Functional magnetic resonance imaging (fMRI) to explore co- and anti-lateralization of three different functional asymmetries (language, face perception, body perception) in right- and left-handers with typical and atypical language dominance in two samples of participants. The data in Sample 2 was collected as part of a larger study effort to examine multiple asymmetries in large numbers of language typical and atypical participants, but gave us the opportunity to replicate in part, the findings of Sample 1.

Body perception was included as it has been associated with the right hemisphere (Downing et al., 2001). The lateralization of body selective activity is generally accepted in the body perception literature (it is common practice to only define and report data obtained from regions of interest in the right hemisphere, e.g., Peelen et al., 2009; Schwarzlose et al., 2005; Taylor et al., 2007), but not well characterized from an asymmetry perspective (although see Willems et al., 2010).

A verbal fluency task was also included to examine hemispheric dominance for language processing, to examine its' complementarity with these right hemisphere functions. The main goal of this project was to examine both the *breadth* (i.e., the frequency) of the asymmetry for face and body perception in right- and left-handers with known hemispheric dominance for speech/language, and its *depth* (i.e., magnitude). In other words, how many of the participants demonstrate right hemisphere dominance for face and body perception, and the size of the asymmetry. Most right- and left-handed participants with confirmed leftward asymmetry for language should be right hemispheric for these functions, for strong evidence of complete complementarity. Likewise, individuals with right hemisphere (atypical) language processing should show the reversed relationship and the breadth of asymmetry favoring their non-language dominant hemisphere should be similar in magnitude to that seen in language typical individuals. Furthermore, left-handed language typicals should show similar breadth and depth as the right-handed typicals if these functions are related to language, but not handedness per se.

Method

Participants

Sample 1

Ninety-three participants from the Bangor University community took part; 60 were left-handed (22 female), and 33 right-handed (21 female). Two participants (left-handed, one female and one male) were excluded from the final analysis due to excessive head movement (>4 mm). The left-handed participants had a mean age of 24.83 (SD = 7.55), and a mean Waterloo handedness questionnaire (WHQ; Steenhuis & Bryden, 1989: Ranging from −30 always left for each item, to +30 always right) score of −20.38 (SD = 13.31). The right-handed participants had a mean age of 26.09 (SD = 5.92) and a mean WHQ score of +28.13 (SD = 2.58). Data from these scans were subjected to a split-half reliability analysis in a previous article (Johnstone et al., 2020). This study was approved by the Bangor Psychology ethics committee.

Sample 2

Seventy-three participants from the Bangor University community took part in this study. Data from 21 participants (8 right-handed and 13 left-handed) who were included in Sample 1 were excluded from this analysis to make the sample independent. A total of 52 participants were included; 33 were left-handed (19 female), and 19 right-handed (15 female). The left-handed participants had a mean age of 23.91 (SD = 6.93), and a mean WHQ score of −20.75 (SD = 13.69). The right-handed participants had a mean age of 23.05 (SD = 4.64) and a mean WHQ score of +28.05 (SD = 2.01). This study was approved by the Bangor Psychology ethics committee.

Tasks

Verbal Fluency

A single letter verbal fluency paradigm was used in a blocked design. For Sample 1, the paradigm consisted of 14 experimental, 14 control blocks, and 30 rest blocks: Each with a duration of 15 s. In experimental blocks, participants were presented with a single letter in the middle of the screen which stayed on for the duration of the block. The letters used were those that begin the most words in English: T, A, S, H, W, I, O, B, M, F, C, L, D, P (as reported in the Natural Language Toolkit 3.0 - http://www.nltk.org/). Participants were instructed to think of as many words as they could which began with that letter when it was shown on screen. In control blocks, participants were shown one of two letter strings (RARA or LALA) and were instructed to covertly repeat these for as long as they were presented on the screen. A fixation cross was presented in the 30 rest blocks, and participants were instructed to relax and clear their minds. This experiment was presented across two runs, comprising seven experimental/control blocks respectively and 15 rest blocks per run. The letters were randomly presented in any order across these two runs.

The verbal fluency task for Sample 2 was identical to the one used for Sample 1, but with only one run of data collected. The seven different letters T, A, S, H, W, I, and O were used.

Face/Body Localizers

Brain activation for face- and body-related activation was obtained with a four-condition visual localizer (e.g., Peelen & Downing, 2005) in Sample 1. This involved viewing blocks of images from the stimulus categories: faces, bodies, chairs, and scenes. Participants completed two runs of this task, with two different fixed stimulus orders, which were counterbalanced across participants. Each localizer run consisted of 16 active blocks (four for each stimulus category) and 5 rest blocks where a central fixation point was shown on the screen. Each block lasted 16 s during which 16 images were displayed for 300 ms followed by a blank screen for 700 ms. Participants completed a one-back task, pressing a button if they saw a consecutive, repeated image. The hand participants held the button box in was counterbalanced within the right- and left-handed groups.

Two four-condition localizers were used to identify body- and face-selective brain areas for Sample 2. These were identical in implementation to the localizer used in Sample 1, but with different stimulus categories. The body localizer had images of hands, hand-held tools, human bodies without heads, and chairs; the face localizer images of faces with neutral expressions, faces with emotional expressions, butterflies, and flowers. Bodies were of 10 males and 10 females, and chairs were 20 various chairs in different styles. The neutral faces consisted of 10 male faces and 10 female faces from The Karolinska Directed Emotional Faces (KDEF) database (Lundqvist et al., 1998) with neutral facial expressions. The butterflies and flowers were both of largely symmetrical images depicting 20 unique variants of butterflies and flowers.

fMRI Data Acquisition

The scans were acquired in a Philips 3 Tesla Achieva magnetic resonance (MR) scanner at the Bangor Imaging Unit at Bangor University, using a 32-channel head coil. Functional images in Sample 1 were acquired with a T2-weighted gradient-echo echo-planar imaging (EPI) sequence, field of view (FOV) = 220 × 220, acquisition matrix = 96 × 96, 36 slices; acquired voxel size (mm) = 2.3 × 2.3 × 2.5, reconstructed voxel size (mm) = 2.3 × 2.3 × 2.5. Verbal fluency, repetition time (TR) = 2,500 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, consisted of two runs of 435 s each, and the face/body localizer (TR = 2000 ms, TE = 30 ms, FA = 90°) consisted of two runs of 332 s. Functional images for verbal fluency in Sample 2 were acquired with slightly different parameters: A T2-weighted gradient-echo single-shot EPI pulse sequence (SENSE, acceleration factor = 2); TR = 2,500 ms, TE = 30 ms, acquisition time = 435 s, FA = 83°, FOV = 240 × 240 × 105, acquisition matrix = 80 × 79 × 35; 35 slices (width = 3 mm, no gap); acquired voxel size (mm) = 3 × 3 × 3, reconstructed voxel size (mm) = 3 × 3 × 3. Functional images for the body and face localizers in Sample 2 were acquired with the following parameters: A T2-weighted gradient-echo single-shot EPI pulse sequence (SENSE, acceleration

factor = 2); TR = 2000 ms, TE = 30 ms, acquisition time = 336 s, FA = 77°, FOV = 240 × 240 × 105, acquisition matrix = 80 × 79 × 35; 35 slices (width = 3 mm, no gap); acquired voxel size (mm) = 3 × 3.04 × 3, reconstructed voxel size (mm) = 3 × 3 × 3. Fat suppression was implemented with spectral presaturation with inversion recovery (SPIR). The first five scans of each functional run were discarded before image acquisition to establish steady-state magnetization.

T1-weighted structural images were obtained with the following parameters: T1-weighted image acquisition using a multi echo, multi-shot turbo field echo pulse sequence, with a five echo average, TR = 12 ms, TE = 3.5 ms, acquisition time = 329 s, FA = 8°, FOV (mm) = 240 × 240 × 175, acquisition matrix = 80 × 79; 175 contiguous slices were acquired, voxel size (mm) = 1 × 1 × 2 (reconstructed voxel size = 1 mm^3).

fMRI Design and Analysis

All magnetic resonance imaging (MRI) data was pre-processed and analyzed using SPM12 (Wellcome Department of Cognitive Neurology, University College London, http://www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB R2015b 8.6 (Mathworks Inc., Sherborn, MA, USA). Anatomical images were manually aligned to the anterior and posterior commissure (AC-PC). The functional images were corrected for head motion (spatial realignment; trilinear interpolation) and realigned to the first (Sample 1) or last (Sample 2) functional volume of the session (the one closest to the anatomical scan). The functional scans were then coregistered to their anatomical scans and then normalized to standard Montreal Neurological Institute (MNI) space (3 mm isotropic voxels). Normalized data were then spatially smoothed using a Gaussian kernel of 6 mm full-width at half-maximum.

The general linear model was used to map the hemodynamic response curve onto each experimental condition using boxcar regressors. This boxcar function was then fitted to the time series at each voxel resulting in a weighted β-image. The fitted model was converted to a *t*-statistic image, comprising the statistical parametric map. The LI-toolbox plugin for SPM (Wilke & Lidzba, 2007; Wilke & Schmithorst, 2006) was used to assess hemispheric contribution for processing each of the three tasks. This toolbox allows for comparison of right and left hemispheres without commonly cited problems such as complications that arise from statistical outliers, threshold-dependent comparisons, or data sparsity (Wilke & Lidzba, 2007).

The toolbox employs a bootstrapping method whereby 20 equally-sized thresholds are calculated between 0 and the maximum *t*-value in the dataset. At each threshold, 100 bootstrapped samples (with a resampling ratio of $k = 0.25$) are taken at each threshold in each hemisphere. The 10,000 laterality index (LI) combinations are calculated from these samples for all surviving voxels on the left and right, with the standard (LI formula, LI = (R − L)/(R + L)), where a resulting positive score indicates more left hemisphere activity, and negative indicates more right. To avoid effects due to statistical outliers only the central 50% of data are kept. A final LI is calculated from all the LIs weighted to their corresponding threshold and provides an estimate of how lateralized a participant is for a given contrast.

Whole-brain LIs were calculated from the following contrasts: faces > scenes (Sample 1), neutral faces > flowers and butterflies (Sample 2), and bodies > chairs (Experiments 1 and 2). The cerebellum was excluded from the contrast fluency > letter string (Samples 1 and 2), as it is activated in some language tasks, including verbal fluency (e.g., Häberling et al., 2016; Schlösser et al., 1998). Cerebellar activation in language processing is contralateral to that of the cerebral cortex (e.g., Gelinas et al., 2014; Jansen et al., 2005).

Participant Classification and Statistical Analysis

Participants were first divided into three groups based on LI values for verbal fluency and based on hand preference. Zero was used as a cut-off for all tasks, thus each participant with an LI value of >0 were categorized as left hemisphere lateralized, and participants with LIs of <0 as right hemisphere lateralized. Language typical right-handers and language typical left-handers were separated into groups to examine for handedness differences independent of language dominance. The third group were the language atypically lateralized individuals. As language atypical right-handers are rare, this group included both right- and left-handed individuals.

Mean LI values were first compared against 0, using a one-sample *t*-test, to examine if the group,

on average, was significantly lateralized for the specified contrast. Differences in mean LI values for each of the non-language functions were assessed using Kruskal–Wallis tests comparing the three language/handedness groups. If there is no complementarity, then differences defined by language processing and handedness should have no bearing on how asymmetrical anyone is for any of these functions.

To examine if there was a statistical majority of individuals with dominance in one hemisphere over the other (i.e., the breadth of asymmetry), the proportion of individuals with right and left hemisphere processing was compared against 50% using a binomial test. Furthermore, z-tests were used to examine proportional differences in "typical" processing between the three language/handedness groups for all tasks. In other words, proportions of right hemisphere processing in the two language typical groups were compared with proportions of left hemisphere processing in the language atypical group. The z-test between the language typically lateralized groups and the language atypically lateralized group were two-tailed, as the proportions were assumed to be similar if complementarity of functions exists. The examination of proportional differences between language typical right-handers and language typical left-handers was two-tailed for the same reason. There was no reason to suspect that one group would be more lateralized than the other in terms of proportions. Lastly, we examine the different patterns of lateralization that are found across the two samples as a whole, and in how many individuals they are found.

Results

Sample 1

All tasks were found to be significantly lateralized in the sample as a whole; verbal fluency to the left hemisphere ($M = +.39$, $SD = .53$), $t(90) = 6.91$, $p < .001$, and face perception ($M = -.19$, $SD = .45$), $t(90) = -3.95$, $p < .001$ and body perception ($M = -.27$, $SD = .39$), $t(90) = -6.57$, $p < .001$, to the right hemisphere.

Participants were grouped according to handedness and language dominance. Three groups were created: Language typical (left hemisphere lateralized) right-handers ($n = 31$), language typical left-handers ($n = 43$) and language atypical (right hemisphere lateralized) individuals ($n = 17$, 2 right-handers and 15 left-handers). Average LI values are illustrated in Figure 1 and Table 1. All three groups were, on average, significantly lateralized for verbal fluency as assessed with a one sample t-test against 0 (see Table 1). There was no difference in the depth of fluency LIs between the groups, compared using absolute values ($p = .193$).

Face Perception

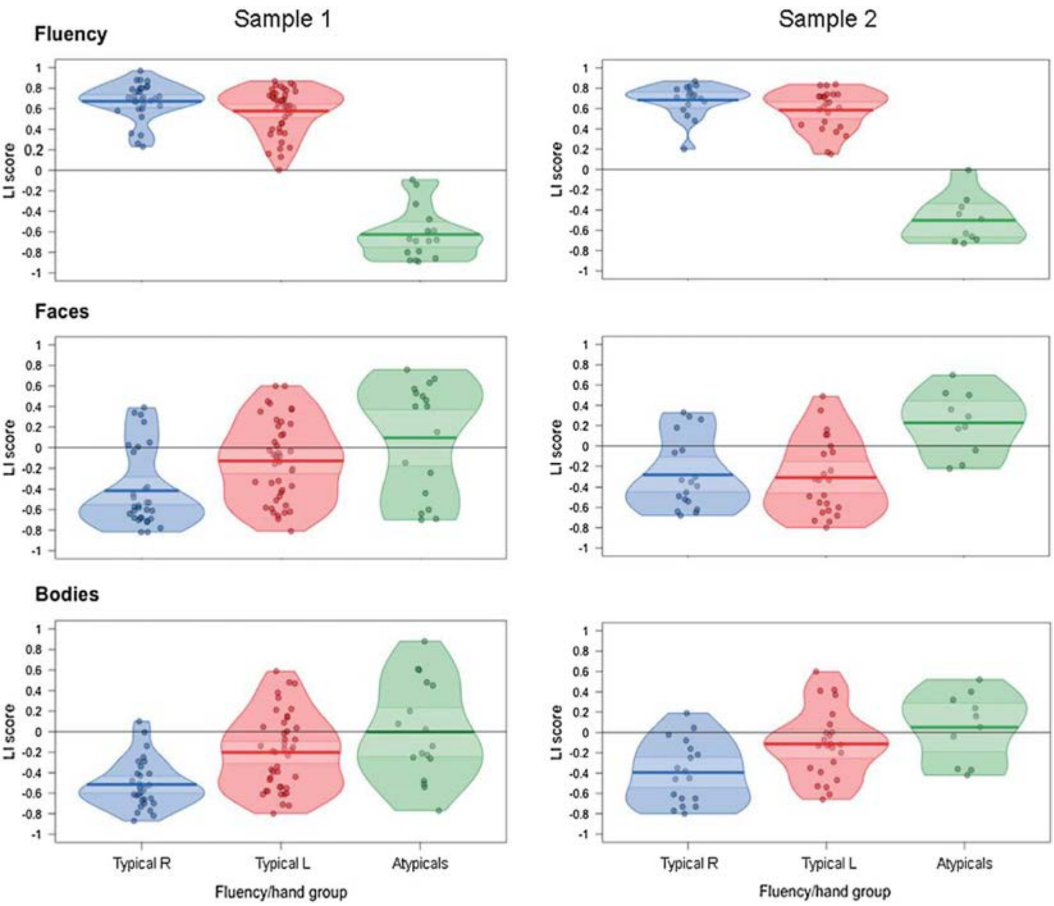
A Kruskal–Wallis test revealed a significant difference in LI values between the groups, $H(2) = 14.84$, $p = .001$ Pairwise comparisons revealed statistically significant between-group differences in the median face LI scores for language typical right-handers ($Mdn = -.57$) and language typical left-handers ($Mdn = -.11$; $p = .009$, $r = .34$), language typical right-handers and language atypicals ($Mdn = .40$; $p = .001$, $r = .51$), but not for language typical left-handers and language atypicals ($p = .581$).

The proportion of individuals with typical hemispheric processing in each group can be seen in Table 2 and were compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.77, 95% CI's .60, .89) was significantly higher, $p = .003$. The proportion of right hemisphere processing in language typical left-handers (.65, 95% CI's .50, .78; $p = .066$) or language atypicals (.59, 95% CI's .36, .78; $p = .629$) was not significantly higher. A z-test compared if there were differences in the number of participants with right hemisphere dominance in language typical right-handers (24/31) and language typical left-handers (28/43), and was not significant, $z = 1.14$, $p = .254$). To examine if there was a difference in the complementary patterns found for faces in the three groups, z-tests between proportion of right hemisphere processing in the language typical groups and left hemisphere processing in the language atypical group was compared. The proportion of complementarity in language typical right-handers was not significantly higher than the language atypicals (10/17), $z = 1.36$, $p = .174$, neither was the difference in language typical left-handers as compared to language atypicals $z = 0.46$, $p = .646$.

Body Perception

LI values for each group can be seen in Figure 1 and Table 1. A Kruskal–Wallis test revealed a

Figure 1
Pirate Plots Showing Distributions of Individual LI Values for Each fMRI Measure in Sample 1 and 2



Note. Pirate plots showing distributions of individual LI values for each language-defined group in Sample 1 (Left panel; language typical right-handers in blue, $n = 31$; language typical left-handers in red, $n = 43$; language atypicals in green, $n = 17$) for each of the three fMRI measures (verbal fluency, faces, and bodies) and Sample 2 (Right panel; language typical right-handers in blue, $n = 18$; language typical left-handers in red, $n = 24$; language atypicals in green, $n = 10$) for each of the three fMRI measures (verbal fluency, faces, and bodies) in Sample 2. The bold line indicates the mean and the lighter highlighted area the 95% CIs. All participants in the groups fall above and below the zero line in the verbal fluency graphs as this is how the groups were defined.

significant difference in LI values between the groups, $H(2) = 20.99$, $p < .001$. Pairwise comparisons revealed statistically significant between-group differences in the median face LI scores for language typical right-handers ($Mdn = -.56$) and language typical left-handers ($Mdn = -.19$), $p = .001$, $r = .43$, language typical right-handers and language atypicals ($Mdn = -.14$) was significant, $p < .001$, $r = .59$, but not language typical left-handers and language atypicals ($p = .612$).

The proportion of individuals with *typical* hemispheric processing in each group can be seen in Table 2 and was compared against .50. The proportion of right hemisphere processing in language typical right-handers (.97, 95% CIs .84, .99) was significantly higher, $p < .001$. The proportion of right hemisphere processing in language typical left-handers (.70, 95% CIs .55, .81) was significantly higher, $p = .014$. The proportion of left hemisphere processing in language atypicals of .47, 95% CIs [.26, .69] was not significantly different, $p = 1$. There was a significant difference in the proportion of individuals who processed bodies in the right hemisphere

Table 1

Sample Sizes, Mean laterality index (LI) Values, Standard Deviations, and t*-Values From One Sample t-Tests for Each Function (Fluency, Faces, Bodies) and Group in Samples 1 and 2*

Group		Fluency LI			Face LI			Body LI		
		M	*SD*	*t*	*M*	*SD*	*t*	*M*	*SD*	*t*
Sample 1	*n*									
Typical RH	31	+0.67	0.18	21.10***	−0.42	0.37	−6.19***	−0.52	0.23	−12.46***
Typical LH	43	+0.58	0.22	17.28***	−0.13	0.39	−2.25*	−0.20	0.36	−3.65**
Atypicals	17	−0.63	0.24	−10.56***	+0.09	0.54	0.72	−0.00	0.47	−0.04
Sample 2	*n*									
Typical RH	18	+0.68	0.16	18.31***	−0.28	0.35	−3.39*	−0.39	0.31	−5.45***
Typical LH	24	+0.58	0.20	14.41***	−0.31	0.37	−4.08***	−0.11	0.34	−1.64
Atypicals	10	−0.50	0.23	−6.88***	+0.23	0.31	2.34*	+0.05	0.34	0.47

Note. RH = Right-handers; LH = Left-handers. Degrees of freedom = $n - 1$.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

between language typical right-handers (30/31) and language typical left-handers (30/43), $z = 2.93$, $p = .003$, 95% CI of the difference (−0.27) did not overlap with zero [−0.42, −0.10]. There was a significant difference in complementarity of function between language typical right-handers and language atypicals (8/17), $z = 4.06$, $p < .001$, 95% CI of the difference (−0.50) did not overlap with zero [−0.71, −0.24]. There was no significant difference between language typical left-handers and language atypicals, $z = 1.64$, $p = .101$.

Sample 2

Again, all tasks were significantly lateralized in the sample as a whole; verbal fluency to the left hemisphere ($M = +.41$, $SD = .49$), $t(51) = 6.04$, $p < .001$, and face perception ($M = -.19$, $SD = .40$), $t(51) = -3.47$, $p = .001$, and body perception ($M = -.18$, $SD = .36$), $t(51) = -3.55$, $p = .001$, to the right hemisphere. The sample consisted of 18 language typical right-handers, 24 language typical left-handers, and 10 language atypicals (9 left-handed and 1 right-handed). Average LI values, standard deviations, and one-sample *t*-tests against 0 can be seen in Table 1. There was a difference in median LI values between the group, $H(2) = 6.63$, $p = .036$, and this was found between the language typical right-handers ($Mdn = 0.73$) and language atypicals ($Mdn = 0.56$ $p = .041$, $r = .47$), but not language typical right-handers and language typical left-handers ($Mdn = 0.64$; $p = .230$), or language typical left-handers and language atypicals ($p = .788$).

Face Perception

A Kruskal–Wallis test revealed a significant difference in LI values between the groups, $H(2) = 13.21$, $p = .001$. Pairwise comparisons

Table 2

Complementarity Patterns for Face and Body Processing With Language Found in Samples 1 and 2 and Significance Values for Binomial Tests Against 50%

Group	Face dominance			Body dominance		
	Right	Left	*p*	Right	Left	*p*
Sample 1						
Typical RH	24 (77%)	7 (23%)	.003	30 (97%)	1 (3%)	<.001
Typical LH	28 (65%)	15 (35%)	.066	30 (70%)	13 (30%)	.014
Atypicals	10 (59%)	7 (41%)	.629	8 (47%)	9 (53%)	1
Sample 2						
Typical RH	14 (78%)	4 (22%)	.031	16 (89%)	2 (11%)	.001
Typical LH	19 (79%)	5 (21%)	.007	17 (71%)	7 (29%)	.064
Atypical	3 (30%)	7 (70%)	.344	4 (40%)	6 (60%)	.754

Note. RH = Right-handers; LH = Left-handers.

adjusted for multiple comparisons revealed statistically significant between-group differences in the median face LI scores for language typical right-handers (*Mdn* = −.37) and language atypicals (*Mdn* = .24; $p = .006$, $r = .59$), language typical left-handers (*Mdn* = −.33) and language atypicals ($p = .001$, $r = .60$), but not language typical right-handers and language typical left-handers ($p = 1$).

The proportion of individuals with complementary hemispheric processing in each group can be seen in Table 2 and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.78, 95% CI's .55, .91) was significantly higher, $p = .031$. The proportion of right hemisphere processing in language typical left-handers (.79, 95% CI's .60, .91) was significantly higher, $p = .007$. The proportion of left hemisphere processing in language atypicals *of* .70, 95% CI's [.40, .90] was not significantly different, $p = .344$.

Z-tests were used to compare if there were differences in complementarity processing in the different groups. There was no significant difference between language typical right-handers (14/18), and language typical left-handers (19/24, $p = .913$). The proportion of language typical right-handed participants with a right hemisphere dominance was not significantly different to the left hemisphere processing in the language atypicals (7/10), $p = .648$. The proportion of right hemisphere processing in language typical left-handers was also not significantly different compared to language atypicals ($p = .564$).

Body Perception

LI values for each group can be seen in Figure 1, right panel and Table 1. A Kruskal–Wallis test revealed a significant difference in LI values between the groups, $H(2) = 10.47$, $p = .005$. Pairwise comparisons adjusted for multiple comparisons revealed statistically significant between-group differences in the median face LI scores for language typical right-handers (*Mdn* = −.42) and language typical left-handers (*Mdn* = −.13; $p = .048$, $r = .37$), language typical right-handers and language atypicals (*Mdn* = +.11; $p = .008$, $r = .57$), but not for language typical left-handers and language atypicals ($p = .734$).

The proportion of individuals with typical hemispheric processing in each group can be seen in Table 2 and was compared against .50 using binomial tests. The proportion of right hemisphere processing in language typical right-handers (.89, 95% CIs .67, .97) was significantly higher, $p = .001$. The proportion of right hemisphere processing in language typical left-handers (.71, 95% CIs .51, .85) was not significantly higher, $p = .064$. The proportion of left hemisphere processing in language atypicals (.60, 95% CIs .31, .83) was not significantly different, $p = .754$. *Z*-tests were used to compare the number of participants with complementary patterns in the different groups. There was no significant difference in the proportion of individuals who processed bodies in the right hemisphere between language typical right-handers (16/18) and language typical left-handers (17/24), $p = .157$. There was no significant difference between language typical right-handers and language atypicals (6/10 = .60), $p = .074$, or between language typical left-handers and language atypicals, $p = .540$.

Hemispheric Patterns of Lateralization in Individuals

The different combinations of hemispheric patterns found for verbal fluency, faces, and bodies, were investigated for all individuals in Samples 1 and 2 combined. The different patterns found in the two datasets can be seen in Table 3. The "traditional" pattern of hemispheric dominance (with language in the left hemisphere and the other asymmetries in the right hemisphere) is also the most common pattern, with 74 of participants (64% of all language typical participants) exhibiting this pattern. The second most common pattern, found in 19 individuals is with language and faces processed in the left hemisphere, and

Table 3
Patterns of Lateralization Found for Individuals in Samples 1 and 2 Combined

Verbal fluency	Faces	Bodies	Percentage (*n*)
L	R	R	52% (74)
L	R	L	8% (11)
L	L	R	13% (19)
L	L	L	8% (12)
R	L	L	8% (12)
R	L	R	4% (5)
R	R	L	1% (2)
R	R	R	6% (8)

Note. L = Left hemisphere; R = Right hemisphere.

bodies in the right hemisphere. Amongst language atypical individuals, the reversed "anti-localizing" asymmetry was also seen most frequently (in 12 individuals, 44% of all language atypicals). A z-test comparing the proportion of language typical and language atypical participants with these "traditional," assumed, patterns (i.e., .64 vs. .44) found no significant difference ($p = .056$). In total, all possible eight different combinations of asymmetry patterns were seen in this dataset.

Discussion

The aim was to examine the lateralization patterns of language, body perception and face perception in both left-handers and right-handers. To this aim we investigated lateralization of body and face perception in three groups: Language typical right-handed; language typical left-handed; and language atypical individuals. Of specific interest was the breadth (i.e., the proportion) of right hemisphere asymmetry in the language dominance groups, subdivided by handedness for language typicals. We specifically aimed to recruit individuals likely to have language dominance in the right hemisphere to examine rates of complementarity in right- and left-handers with typical and atypical language dominance. This inclusion meant that we focused on recruiting large numbers of strongly left-handed individuals, as they are more likely to exhibit atypical language dominance (Knecht et al., 2000).

A summary of the depth and breadth of biases for each of the three groups in both samples can be seen in Table 4. For face processing, typical right-handers had population-level breadth to the right hemisphere in both samples. Typical left-handers and atypicals did not have population-level breadth of face processing in Sample 1, and this was also the case for atypicals in Sample 2. Language typical right-handers and left-handers were, on average, right lateralized in both samples. The language atypical group was, on average, not lateralized in Sample 1 but left-lateralized in Sample 2.

Although the atypical group in Sample 1 was, on average, not lateralized for face processing, Figure 1 shows that there seems to be two clusters of participants, one left-lateralized and one right-lateralized, resulting in a no-asymmetry average. This suggests that face processing is still lateralized to the right or the left hemisphere in the majority of individuals. The LIs in the subgroups are similarly sized, even in individuals lateralized to the same hemisphere that is dominant for language. Altogether, these data suggest that face processing does not always lateralize to the non-language dominant hemisphere.

It can be deduced from the supplementary data in Badzakova-Trajkov et al. (2010) that a reduced number of language typical left-handers (77%) as compared to language typical right-handers (96%) were right hemisphere dominant for faces in their study. In their small sample of language atypicals, only 44% (4 out of 9) showed a complementary relationship, which is similar to that seen in Sample 1. Gerrits et al. (2019) also found that approximately 70% of their language typical left-handers processed faces in the right hemisphere, but similarly reduced to 40% in the language atypical sample. In contrast, Gerrits,

Table 4

A Summary of Significant Depth and Breadth of LI Values for the Three Different Language and Handedness Defined Groups in Samples 1 and 2

Type of bias	Sample	Language typical RH	Language typical LH	Language atypicals
Face processing				
Population-level breadth of bias?	1	✓	×	×
	2	✓	✓	×
Group-level depth of bias?	1	✓	✓	×
	2	✓	✓	✓
Body processing				
Population-level breadth of bias?	1	✓	✓	×
	2	✓	×	×
Group-level depth of bias?	1	✓	✓	×
	2	✓	×	×

Note. RH = Right-handers; LH = Left-handers.

Verhelst, et al. (2020) found that their left-handed language atypical sample showed higher rates of complementarity as compared to the language typical left-handers (75% complementarity in language atypicals vs. 56% in language typicals). Similarly, the language atypical group in the current Sample 2 showed high rates of complementarity (70%), although this was not as high as the rates seen for language typical left-handers (79%). The inconsistency seen for left-handers in the current samples, and across these studies, may suggest that they, *regardless of language dominance group*, are more variable for other lateralized processes such as face perception.

One important detail to note about the data in the present study is that all three groups were matched in terms of mean lateralization for verbal fluency in Sample 1 (although there was a difference between language typical right-handers and language atypicals in Sample 2). There was no difference in the depth of LI values for language typical left-handers and language typical right-handers. Language atypical participants did not show reduced depth of asymmetry when compared to language typical participants. That is, their laterality indices did not tend toward bilaterality as compared with the language typical group, and the depth of the asymmetry was at least equivalent to that of language typical left-handers. This "symmetry" for language processing means that any differences between the groups on other measures cannot easily be explained by different degrees of language specialization.

These results do not fully support current crowding hypotheses that specifically theorize that face processing and language processing are linked (Behrmann & Plaut, 2015; Dehaene et al., 2010). Of course, it should be noted that these results may also depend on the tasks used. The current incarnations of the crowding hypotheses between faces and language are about reading and asymmetry in the so-called visual word form area (vWFA). One caveat to the present analysis is that we used a verbal fluency task to estimate language dominance (as have several other laboratories, e.g., Badzakova-Trajkov et al., 2010; Gerrits, Verhelst, et al., 2020). We describe the reliability and validity of this measure elsewhere (Johnstone et al., 2020). Arguably it might be more stringent to measure asymmetries in the vWFA for letters and words, for direct comparison with faces. Attempts of this sort have been made by our colleagues in Ghent. Van der Haegen et al. (2012) find a surprisingly poor match in concurrence of hemispheric dominance within the same hemisphere between lexical decision LIs from the temporal lobes and verbal fluency LIs from the frontal lobes (63% language atypicals and 81% language typicals, hemispheric dominance as defined by the verbal fluency task, all left-handed). Gerrits et al. (2019) found an even lower congruency of verbal fluency and vWFA; only in 58% of their language typicals and 67% of language atypical left-handers (language typicality defined by verbal fluency). Surprisingly, these colleagues do not compare congruency of face asymmetry and vWFA asymmetry in their typical and atypical groups.

Language typical right-handers were, on average, right lateralized for body perception. Language typical left-handers were right lateralized in Sample 1 but not Sample 2. Language atypicals were not lateralized, on average. A large proportion (97% and 89%, respectively) of right-handers had more activation in the non-language hemisphere for body perception, and this was statistically higher than 50%. Language atypicals (53% and 60%) did not have a significant breadth for body processing, but language typical left-handers had a population-level bias in Sample 1 (70%) but not in Sample 2 (71%). This pattern suggests the intriguing possibility of handedness moderating the effect of body asymmetry. This possibility is further substantiated by the fact that language typical right-handers had consistently stronger right hemisphere LI values as compared to language typical left-handers and language atypicals.

This weakened asymmetry in body processing in left-handers is consistent with the results from Willems et al. (2010), who found that such participants were bilateral on average when measuring activation in the extrastriate body area (EBA), in comparison to right-handers who were right lateralized, as in the present study. Willems et al. (2010) did, however, also find that fusiform face area (FFA) was not lateralized, on average, in their sample of left-handed participants. Although FFA was not specifically targeted in the present study, left-handers were, on average, right-lateralized for the whole-brain activation pattern. Bukowski et al. (2013) also found that the FFA was activated bilaterally for their left-handed sample, but that the activation was overall right hemispheric when comparing the whole brain.

Of course, one limitation is that the sample sizes here are small for proportional analyses and

is particularly true considering the skewed nature of the data. The small sample size is reflected in the large confidence intervals that accompanies each proportional difference. Nonetheless, by accumulating data from more participants, this proportional approach is an extremely useful analysis for determining constructs/processes that really differentiate right- and left-handers (Carey & Johnstone, 2014; Karlsson et al., 2019). When right- and left-handed participants are compared, reduced asymmetries in the left-handers are usually found (e.g., Karlsson et al., 2019; Willems et al., 2010). Taking breadth into account will help to disentangle the underlying cause of a mean difference (i.e., is it driven by a small subgroup of the left handers who show the atypical cerebral asymmetry or are they less lateralized as compared to their right-handed counterparts? Karlsson et al., 2019).

In this study a cut-off of zero is used, rather than a band around zero labelled by many investigators as "bilateral". The boundaries for classification of no dominance are difficult to justify and to date are not well agreed upon in the literature. In fact, test–retest with fMRI LI data is rare. Therefore, it is difficult to know how stable these LI values are from session to session. Jansen et al. (2006) found that if a bilateral category was used (±.2), participants who were classified as bilateral by one calculation were often not by a different calculation of LIs. Test–retest for participants with LIs in this range were not reproducible (in terms of dominant hemisphere) in a second session. It would perhaps be more appropriate to classify participants in more data-driven ways. The boundaries for categorical misclassification rates could be defined by using data to decide an "uncertainty of lateralization" interval (Carey & Karlsson, 2019). In other words, identify how often individuals with single session LI values of, for example, ±0.1 would be misclassified in a second session or run.

Overall, these results add to the growing literature that does not fully support complementarity of functions when both language typical and language atypical participants are included. The strongest support for complementarity of face and body processing with language processing in the current dataset came from the group of language typically lateralized right-handers. Interestingly, the highest rates of complementarity in language typical right-handers alone was seen for body perception, a lateralized function rarely discussed in the cerebral asymmetries literature. Rates of right hemisphere processing in language typical left-handers were significantly reduced for bodies specifically. Again, these results suggest that left-handers are more variable in their lateralization patterns in a way that is independent from language dominance.

These kinds of data might be important for evaluating models of individuals with fluctuating asymmetry. Ideas have been proposed in the handedness literature suggest that fluctuating asymmetry is much more common in left-handed individuals (e.g., Annett, 2002; McManus, 1999). The extension of these accounts to underlying cerebral asymmetries could be fruitful. By cataloguing multiple brain asymmetries in large numbers of individuals, the most common phenotype(s) of cerebral patterns might be identifiable. According to this kind of model, some subset of individuals have handedness and different cerebral asymmetries randomly determined (subject to crowding constraints at some of the more extreme ends of the random distribution).

In conclusion, our results and other recent reports in the literature (Badzakova-Trajkov et al., 2010; Gerrits et al., 2019), suggest that ideas of complementarity of function need revisiting in the unfortunate labor-intensive manner that these studies require. The effects of handedness versus lateralization typicality can be teased apart from one another, but such studies need to go even further than just enriching samples with left-handers. They need to include left- and right-handers with typical and atypical dominance for the functions in question. Finding atypical participants, in particular, is a challenge that to date is mainly met with sheer sample size. Our lab and others (e.g., Gerrits, De Clercq, et al., 2020) are working on ways to simplify the search for these elusive, but nevertheless, fascinating individuals.

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Received December 5, 2020
Revision received April 6, 2021
Accepted July 5, 2021 ■