Cerebral Lateralization of Face-Selective and Body-Selective Visual Areas Depends on Handedness

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The left-hemisphere dominance for language is a core example of the functional specialization of the cerebral hemispheres. The degree of left-hemisphere dominance for language depends on hand preference: Whereas the majority of right-handers show left-hemispheric language lateralization, this number is reduced in left-handers. Here, we assessed whether handedness analogously has an influence upon lateralization in the visual system. Using functional magnetic resonance imaging, we localized 4 more or less specialized extrastriate areas in left- and right-handers, namely fusiform face area (FFA), extrastriate body area (EBA), fusiform body area (FBA), and human motion area (human middle temporal [hMT]). We found that lateralization of FFA and EBA depends on handedness: These areas were right lateralized in right-handers but not in left-handers. A similar tendency was observed in FBA but not in hMT. We conclude that the relationship between handedness and hemispheric lateralization extends to functionally lateralized parts of visual cortex, indicating a general coupling between cerebral lateralization and handedness. Our findings indicate that hemispheric specialization is not fixed but can vary considerably across individuals even in areas engaged relatively early in the visual system.

Keywords: bodies, faces, fMRI, handedness, visual

Introduction

The functional specialization of the 2 hemispheres is one of the most long-standing and core issues in cognitive neuroscience. Hemispheric specialization has been reported for a wide domain of cognitive functions, including attention, emotion, motor control, and language (e.g., Bryden 1982; Corballis 1983; Geschwind and Galaburda 1987; Hellige 1993; Hugdahl and Davidson 1994; Ivry and Robertson 1998; Toga and Thompson 2003; Dien 2008, 2009; Brancucci et al. 2009). Perhaps the most robust and most intensively investigated functional hemispheric specialization is the left-hemisphere dominance for language (e.g., Knecht, Deppe, et al. 2000). The degree of this dominance depends on handedness: Whereas 96% of right-handers has left-hemisphere language dominance, this number is decreased to 73% in left-handers (Knecht, Drager, et al. 2000).

Here, we investigate whether handedness is similarly related to the lateralization of visual cortical areas. One candidate region is the fusiform face area (FFA), which is generally right lateralized in right-handers (Kanwisher et al. 1997; Yovel et al. 2008; Dien 2009). It has been suggested that the right-hemisphere lateralization of face processing is independent of handedness (Hamilton and Vermeire 1988), but solid data from human neuroimaging are lacking (Kanwisher et al. 1997 anecdotally reported 2 left-handed subjects with apparent left-hemisphere lateralization of FFA). We investigated the func-

tional lateralization of several extrastriate visual areas involved in processing faces and bodies in left- and right-handed participants. If handedness has an influence on lateralization of these areas, it would be evidence that handedness and functional hemispheric lateralization are more strongly related than previously assumed (e.g., Hamilton and Vermeire 1988; see below) and that hemispheric specialization is rather variable across individuals.

A considerable body of evidence suggests that there is functional lateralization in the visual system. There is a behavioral bias to better remember and perceive faces shortly presented to the left visual field (mainly processed by the right hemisphere; e.g., Heller and Levy 1981). Moreover, participants consistently judge the emotion expressed by a face consisting of a happy and a neutral half in accordance with the part of the face presented in the left visual field (Levy et al. 1983a, 1983; for review and discussion, see Corballis 1983; Rhodes 1985; Sergent 1985; Sergent et al. 1992; Hellige 1993). In line with this, there is a correlation between the number of activated voxels in right FFA and the degree to which individual participants show a bias to better remember the left visual field part of chimeric faces (Yovel et al. 2008).

In a by now classical paper, Hamilton and Vermeire (1988) argued that the right-hemisphere bias for face processing is independent of handedness given that it was also observed in macaque monkeys (presumably without hand preference; Hamilton and Vermeire 1988; cf. Pinsk et al. 2005; Parr et al. 2009). On the contrary, behavioral work suggests that left-handers may not have a left-hemifield bias for faces (Gilbert and Bakan 1973; Levy et al. 1983; Hoptman and Levy 1988; Luh et al. 1994), but the evidence is mixed (e.g., Borod et al. 1990) and neural evidence is lacking. Here, we assessed whether handedness influences lateralization of 4 extrastriate visual areas in the healthy human brain.

Using functional magnetic resonance imaging, we measured cerebral activity in healthy, strongly left- or right-handed individuals while they observed pictures of faces, bodies or chairs, or watched moving and static dots. These stimuli allowed us to assess the influence of handedness upon FFA (Kanwisher et al. 1997; Kanwisher and Yovel 2006), fusiform body area (FBA; Peelen and Downing 2005, 2007), extrastriate body area (EBA; Downing et al. 2001), and human motion area MT (human middle temporal (hMT); Zeki et al. 1991; Tootell et al. 1995; Dumoulin et al. 2000). The localization of multiple visual areas allowed us to test whether the effect of handedness on lateralization is specific to one or to several of these areas.

If there are no lateralization differences in size or activation level of extrastriate regions, this would be in line with the conjecture by Hamilton and Vermeire (1988) that the right-

hemisphere advantage for, for instance, face processing is a property of the right hemisphere not influenced by handedness. Alternatively, it could be that left-handers show less lateralization as compared with right-handers. This would be evidence that functionally specific areas in left-handers' brains are less lateralized and that this extends beyond, for instance, language dominance or the motor system. It would also show that cerebral lateralization in the visual system is not fixed but can vary considerably between individuals.

Materials and Methods

Participants
We tested 32 healthy participants with no known history of neurological problems, dyslexia or other language-related problems, and with normal or corrected-to-normal vision, all of whom gave informed consent in accordance with the declaration of Helsinki. Half of the participants were left-handed (N = 16, 12 females, mean age: 23.4 years, range: 19–32 years, adapted Dutch version of Edinburgh Handedness Inventory [EHI] score [Oldfield 1971; Van Strien 1992]: mean = −94.3, standard deviation [SD] = 8.7, range: −82 to −100, mode = −100), and half were right-handed (N = 16, 12 females, mean age: 22.6 years, range: 19–27 years, EHI score: mean = 95.5, SD = 8.1, range: 82-100, mode = 100). The groups did not differ in age ($|t_{30}|$ < 1) or in absolute EHI value ($|t_{30}|$ < 1). The local ethics committee approved the study.

Materials
Stimuli consisted of colored pictures of faces, headless bodies, and chairs (Downing et al. 2006). Forty pictures per category were presented. Gender of the faces and bodies was equally divided across male and female. For the hMT localizer, moving or static dots were presented across the whole visual field.

Experimental Procedure
Pictures were presented (using "Presentation" software, version 10.2, www.nbs.com) in blocks of 18 pictures, intermingled with rest blocks in which a white fixation cross was presented against a black background. Each picture was presented for 350 ms, with a 500-ms intertrial interval, which means that an experimental block lasted 15.3 s. Rest blocks lasted 15 s. Six blocks per experimental condition and 7 rest blocks were presented (25 blocks in total, run lasted 8 min). Pictures subtended 9.5 × 9.5 cm (6.8° × 6.8° visual angle, viewing distance = 80 cm) and were presented from outside of the scanner room onto a screen visible through a mirror above the eyes of the participant. Participants were instructed to closely monitor the presented pictures and to press a button as quickly as possible with the right index finger when they observed a repetition of a picture within one block. Such repetitions occurred 2 times per block. For the hMT localizer, participants were required to fixate a fixation cross in the middle of the screen, with no explicit task instruction. Blocks consisted of moving dots, static dots, or fixation cross only (rest blocks). Moving or static dots were presented across the whole screen (45 × 33 cm; 31° × 23° visual angle, viewing distance = 80 cm). There were 6 blocks of each condition (motion, no motion, and rest), which lasted 15 s each.

Image Acquisition and Analysis
Echo-planar images covering the whole brain were acquired with an 8-channel head coil on a Siemens MR system with 3-T magnetic field strength (time repetition = 2060 ms; time echo = 30 ms; flip angle = 85°, 31 transversal slices; voxel size = 3.5 × 3.5 × 3 mm, 0.5-mm gap between slices). Analysis was performed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). Preprocessing involved realignment through rigid-body registration to correct for head motion, slice timing correction to the onset of the first slice, normalization to Montreal Neurological Institute (MNI) space, interpolation of voxel sizes to 2 × 2 × 2 mm, and spatial smoothing (8-mm full width at half maximum kernel). First-level analysis involved a multiple regression

analysis with boxcar regressors for faces, bodies, chairs, and rest blocks. Responses (button presses) were modeled separately using stick functions. For the hMT localizer data, the statistical model involved boxcar regressors for motion, no motion, and rest.

Magnetic resonance disturbances due to small head movements were accounted for by a series of nuisance regressors, namely the linear and exponential changes in the scan-by-scan estimated head motion, scan-by-scan average signals from outside the brain, and cerebrospinal fluid (Verhagen et al. 2006). Head motion never exceeded 3 mm or 3 degrees.

FFA, FBA, EBA, and hMT were defined for each participant separately, following the same procedure as employed previously (e.g., Downing et al. 2006; Yovel et al. 2008). That is, in each subject, voxels were identified that responded more strongly to faces as compared with chairs (FFA), to bodies as compared with chairs (FBA and EBA), or to motion as compared with no motion (hMT) at P < 0.05 uncorrected, in confined search regions with 9-mm ranges in all directions (x, y, z) around local maxima from previous literature (FFA and FBA: [MNI: x, y, z] [−40, −56, −15] and [40, −56, −15] taken from Downing et al. 2006; EBA: [−46, −72, −5] and [46, −72, −5] taken from Downing et al. 2006; hMT: [−47, −76, 2] and [44, −67, 0] taken from Dumoulin et al. 2000). When necessary, local maxima originally reported in Talairach space (Downing et al. 2006) were converted to MNI space using the transform described by Brett (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach).

Repeated measures analysis of variance was performed on the number of activated voxels as well as on the mean contrast values in each of these regions, with factors Hemisphere (left, right) and Group (left-handers, right-handers). If handedness influences the degree of lateralization, we expect a Hemisphere × Group interaction. If the lateralization preference for a given function (e.g., face processing) does not depend upon handedness, we expect a main effect of Hemisphere but no interaction. Follow-up planned within-group comparisons (2-sided t-tests) were performed to test for lateralization effects in each group in isolation. For technical reasons, no hMT localizer was conducted in one left-handed participant. This missing value was not replaced in the analysis.

Explorative whole-brain random effects analysis was performed for Faces > Chairs, Bodies > Chairs, and Motion > No Motion in each group separately. Correction for multiple comparisons was implemented by thresholding maps at P < 0.001 at the voxel level and subsequently taking the cluster extent into account to arrive at P < 0.05 corrected (Poline et al. 1997).

Results

Whole-Brain Analysis
The whole-brain analysis was explorative in the sense that we specifically focused on 4 extrastriate regions in a priori defined regions of interest (see below). For completeness, we report the results of the whole-brain analysis in the Supplementary Materials available online.

Region of Interest Analyses

FFA
There was a statistically significant Hemisphere × Group interaction for the number of activated voxels in FFA ($F_{1,30}$ = 4.80, mean squared error (MSE) = 358.52, P = 0.036), with left-handers showing more face-responsive voxels in left than right fusiform cortex and right-handers showing the reverse pattern of more face-responsive voxels in right than left fusiform cortex (Figs 1A and 2A; Table 1). Follow-up within-group comparisons showed that the lateralization was significantly different in right-handers (left vs. right: t_{15} = −2.96, P = 0.009) but not in left-handers (left vs. right: $|t_{15}|$ < 1; Fig. 1A).

No significant Hemisphere × Group interaction effect was present in the contrast values for the Faces > Chairs contrast in
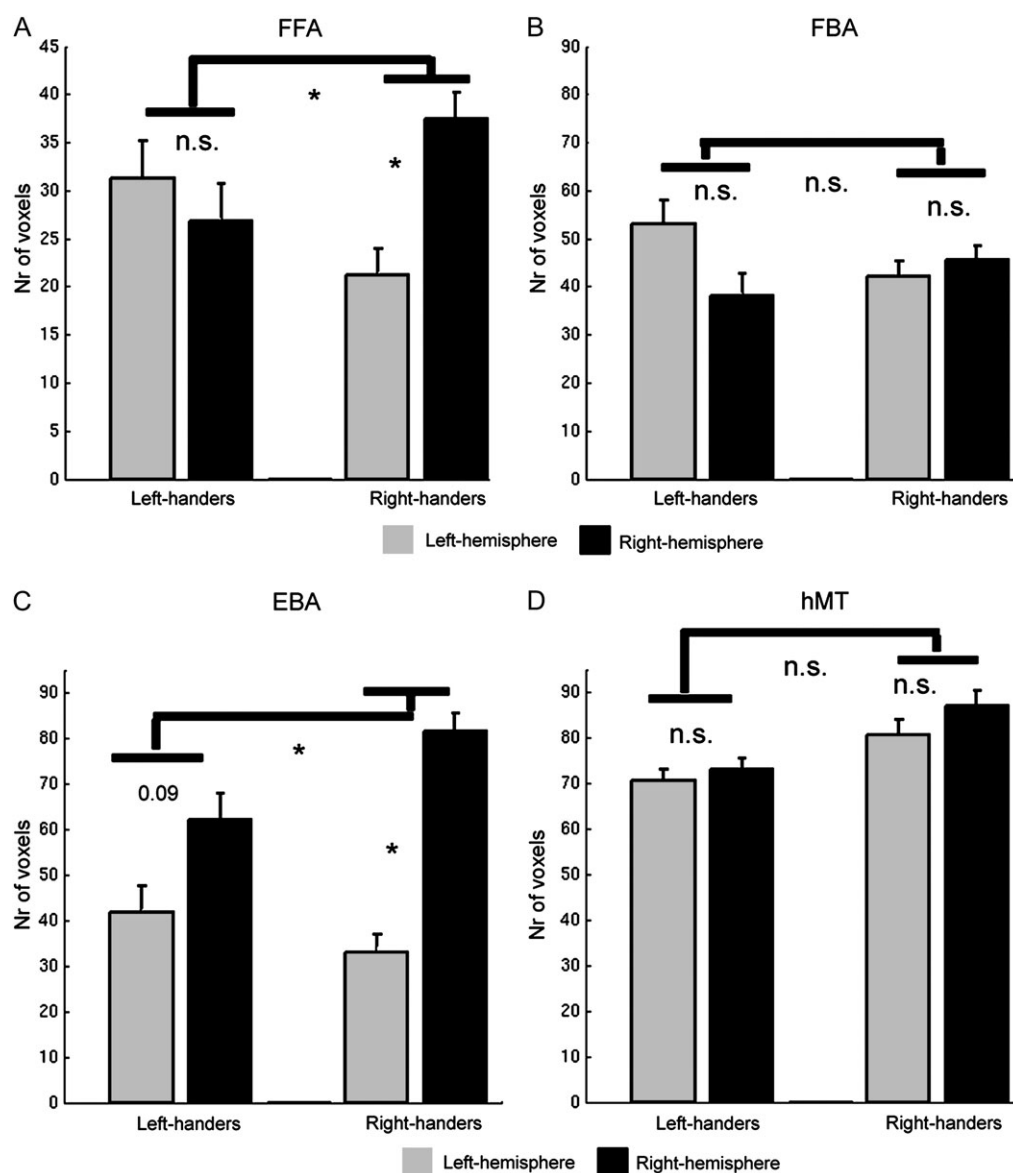
Figure 1. Number of voxels responsive to relevant contrasts in subject-specific ROIs in FFA (A), FBA (B), EBA (C), and hMT (D). For FFA, all voxels responsive to Faces > Chairs (at $P < 0.05$) in left- and right-hemispheric search areas were determined. For FBA and EBA, the relevant contrast was Bodies > Chairs and for hMT Motion > No Motion. The results showed a significant Hemisphere × Group interaction in FFA and EBA but not in FBA and hMT. Moreover, there were within-group differences in right-handers in FFA and EBA. In both regions, more voxels were activated in the right as compared with the left hemisphere. Note the difference in scale on the y-axis for FFA. Asterisks indicate statistical significance at the $P < 0.05$ level.

these areas ($F_{1,30} = 1.06$, MSE = 0.062, $P = 0.31$; Table 2). Planned within-group comparisons showed that there was a hemispheric difference in right-handers (left vs. right: $t_{15} = -2.10$, $P = 0.053$) but not in left-handers ($|t_{15}| < 1$). The latter results may be biased given that within the same subject the 2 regions of interest (left and right) differed in size. That is, including more voxels means that a more reliable estimate of the mean contrast value can be obtained. To correct for this, we computed mean contrast values for the complete a priori region of interest for left and right FFA (the whole 9 × 9 × 9 cubical region of interest defined based on previous research; see Materials and Methods). This analysis did reveal a significant Hemisphere × Group interaction (Table 3; $F_{1,30} = 8.83$, MSE = 0.08, $P = 0.006$). Similar to the interaction in the number of activated voxels reported above, this interaction was mainly

driven by the right-handed participants (right-handers, left vs. right: $t_{15} = -2.89$, $P = 0.011$; left-handers, left vs. right: $t_{15} = 1.36$, $P = 0.195$). A potential bias in the analysis may be that the a priori search regions were based on previously reported coordinates in right-handers (Downing et al. 2006). However, essentially the same results were obtained when taking the maximally activated coordinates from the whole-brain analysis in fusiform gyrus for each group as the center coordinate of our search region (number of voxels: Hemisphere × Group [$F_{1,30} = 3.73$, MSE = 836.94, $P = 0.063$]; mean contrast value: Hemisphere × Group [$F_{1,30} = 5.01$, MSE = 0.046, $P = 0.033$]).

FBA

FBA showed a similar pattern of response in terms of number of activated voxels as FFA, with left-handers activating more voxels
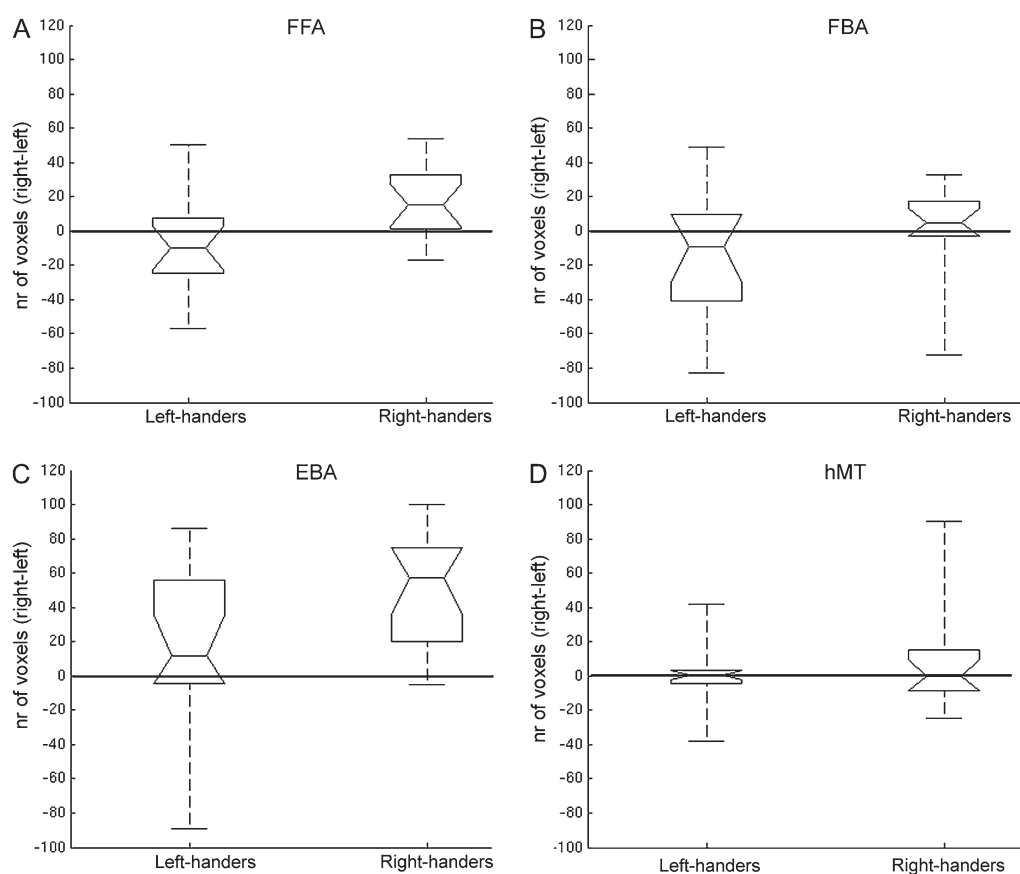
Figure 2. Box plots of the difference in number of activated voxels in left- and right-hemisphere subject-specific ROIs. The box plots show the median (middle line), and upper and lower quartile values (box ends), and the whiskers indicate the range of scores (lower and upper extremes; McGill et al. 1978). Positive values indicate a larger amount of voxels activated in the right hemisphere as compared with the left hemisphere (difference score is right minus left). The plots illustrate that the spread of interhemispheric differences is much bigger in FFA (A) and EBA (C) in left- as compared with right-handers.

Table 1

Statistical analysis of differences in number of voxels in 4 extrastriate regions

Region	F	df	MSE	P	η^2_p
FFA					
Hemisphere × Group	4.80	1, 30	358.52	**0.036**	0.138
Hemisphere	1.57	1, 30	358.52	0.22	0.005
Group	<1	1, 30	1046.07	NS	<0.001
FBA					
Hemisphere × Group	2.69	1, 30	498.9	0.11	0.082
Hemisphere	1.12	1, 30	498.9	0.30	0.036
Group	<1	1, 30	1608.9	NS	0.001
EBA					
Hemisphere × Group	4.25	1, 30	757.28	**0.048**	0.124
Hemisphere	25.24	1, 30	757.28	**<0.001**	0.457
Group	<1	1, 30	1681.23	NS	0.008
hMT					
Hemisphere × Group	<1	1, 29	300.29	NS	0.032
Hemisphere	<1	1, 29	300.29	NS	0.007
Group	1.48	1, 29	1479.92	0.23	0.049

Note: Repeated measures analysis of variance was performed with factors Hemisphere (left, right) and Group (left-handers, right-handers). The dependent variable was the number of voxels activated to relevant contrasts in a priori defined regions of interest determined for each participant separately. Relevant contrasts were Faces > Chairs (FFA), Bodies > Chairs (FBA and EBA), and Motion > No Motion (hMT). In short, in FFA and EBA, there was a Hemisphere × Group interaction, which was not present for hMT and did not reach statistical significance for FBA ($P = 0.11$). For a visualization of the results, see Figure 1. Bold typeface indicates significance at the $P < 0.05$ level. Greenhouse–Geisser correction for violation of sphericity assumption was applied when appropriate, but original degrees of freedom (df) are reported. We report η^2_p as a measure of effect size. NS, not significant.

in the left hemisphere and right-handers activating more voxels in the right hemisphere (Figs 1B and 2B). The Hemisphere × Group interaction was not statistically significant however ($F_{1,30} = 2.69$, MSE = 498.9, $P = 0.11$; Table 1). Planned within-group comparisons showed no significant lateralization differences neither for right-handers (left vs. right: $|t_{15}| < 1$) nor for left-handers (left vs. right: $t_{15} = 1.61$, $P = 0.13$).

This was similarly the case for the mean contrast values from these voxels (Hemisphere × Group: $F_{1,30} = 2.49$, MSE = 0.019, $P = 0.13$; right-handers, left vs. right: $t_{15} = -1.97$, $P = 0.067$; left-handers, left vs. right: $|t_{15}| < 1$; Table 2). However, taking the mean of contrast values of the whole FBA search region did reveal a crossover interaction ($F_{1,30} = 6.41$, MSE = 0.022, $P = 0.017$; Table 3), which was driven by left-handers activating FBA more strongly in the left as compared with the right hemisphere (left-handers, left vs. right: $t_{15} = 2.62$, $P = 0.019$; right-handers, left vs. right: $|t_{15}| < 1$).

EBA

A Hemisphere × Group interaction was found for the number of voxels in left and right EBA ($F_{1,30} = 4.25$, MSE = 757.28, $P = 0.048$; Table 1). The pattern of results was however different than for FFA: Both left- and right-handers showed more activated voxels in right as compared with left EBA, but this lateralization was less in left-handers (Figs 1C and 2C). Follow-up within-group comparisons showed a significant right-hemisphere lateralization in right-handers (left vs. right:

Table 2

Statistical analysis of differences in activation levels (mean contrast values) in 4 extrastriate regions when taking only sensitive voxels from an a priori search region

Region	F	df	MSE	P	η^2_p
FFA					
Hemisphere × Group	1.064	1, 30	0.062	0.31	0.034
Hemisphere	3.57	1, 30	0.062	0.069	0.106
Group	<1	1, 30	0.070	NS	0.001
FBA					
Hemisphere × Group	2.494	1, 30	0.019	0.125	0.077
Hemisphere	1.851	1, 30	0.019	0.184	0.058
Group	<1	1, 30	0.062	NS	0.022
EBA					
Hemisphere × Group	4.94	1, 30	0.047	**0.034**	0.141
Hemisphere	14.02	1, 30	0.047	**0.001**	0.319
Group	<1	1, 30	0.092	NS	<0.001
hMT					
Hemisphere × Group	<1	1, 29	0.031	NS	<0.001
Hemisphere	<1	1, 29	0.031	NS	0.026
Group	1.48	1, 29	0.205	0.233	0.049

Note: Repeated measures analysis of variance was performed with factors Hemisphere (left, right) and Group (left-handers, right-handers). Relevant contrasts were Faces > Chairs (FFA), Bodies > Chairs (FBA and EBA), and Motion > No Motion (hMT). In short, in EBA, there was a Hemisphere × Group interaction, which was not present in the other regions. Bold typeface indicates significance at the $P < 0.05$ level. Greenhouse–Geisser correction for violation of sphericity assumption was applied when appropriate, but original degrees of freedom (df) are reported. We report η^2_p as a measure of effect size. NS, not significant.

Table 3

Results when taking mean activation levels (mean contrast values) from whole a priori defined search region in both hemispheres

Region	F	df	MSE	P	η^2_p
FFA					
Hemisphere × Group	8.83	1, 30	0.08	**0.006**	0.23
Hemisphere	<1	1, 30	0.08	NS	0.032
Group	<1	1, 30	0.09	NS	0.009
FBA					
Hemisphere × Group	6.41	1, 30	0.022	**0.017**	0.176
Hemisphere	1.458	1, 30	0.022	0.237	0.046
Group	<1	1, 30	0.095	NS	0.001
EBA					
Hemisphere × Group	6.73	1, 30	0.070	**0.015**	0.183
Hemisphere	23.77	1, 30	0.070	**<0.001**	0.442
Group	<1	1, 30	0.161	NS	0.003
hMT					
Hemisphere × Group	<1	1, 29	0.039	NS	0.011
Hemisphere	<1	1, 29	0.039	NS	<0.001
Group	1.36	1, 29	0.258	0.253	0.045

Note: We added this as an extra analysis next to taking sensitive voxels per participants per hemisphere (Table 2). That analysis could have been biased given that ROIs on both hemisphere were of unequal size. In the present analysis, ROIs were of equal size since we took all voxels from the a priori defined search regions. The pattern of results is the same as for the number of voxels (Table 1), showing Hemisphere × Group interactions in FFA, FBA, and EBA. Bold typeface indicates significance at the $P < 0.05$ level. Greenhouse–Geisser correction for violation of sphericity assumption was applied when appropriate, but original degrees of freedom (df) are reported. We report η^2_p as a measure of effect size. NS, not significant.

$t_{15} = -6.13$, $P < 0.001$) and a trend to such an effect in left-handers ($t_{15} = -1.81$, $P = 0.089$).

A similar pattern of response was observed in the mean contrast values for the Body > Chairs contrast, both in the subject-specific ROIs (Table 2; Hemisphere × Group interaction: $F_{1,30} = 4.94$, MSE = 0.047, $P = 0.034$; right-handers, left vs. right: $t_{15} = -4.26$, $P = 0.001$; left-handers, left vs. right: $t_{15} = -1.07$, $P = 0.30$) as well as when taking all voxels from the EBA region (Table 3; Hemisphere × Group interaction: $F_{1,30} = 6.73$, MSE = 0.070, $P = 0.015$; right-handers, left vs. right: $t_{15} = -5.25$, $P < 0.001$; left-handers, left vs. right: $t_{15} = -1.62$, $P = 0.13$).

hMT

No differential lateralization was observed for the number of voxels in hMT (Figs 1D and 2D; Table 1; Hemisphere × Group interaction: $F < 1$), nor was there a main effect of Hemisphere or Group (Table 1; Hemisphere: $F < 1$; Group: $F_{1,29} = 1.48$, MSE = 1479.92, $P = 0.23$). Planned within-group comparisons revealed that in none of the groups more voxels were activated in either hemisphere (right-handers: $|t_{15}| < 1$; left-handers: $|t_{14}| < 1$). For the contrast values, there similarly was no interaction, neither in the subject-specific ROIs ($F < 1$; Table 2) nor when taking all voxels into account ($F < 1$; Table 3). Similarly, there were no within-group differences in the strength of activation in the left as compared with the right hMT (all $|t| < 1$).

Summary of Results

We found a Hemisphere × Group interaction both in terms of size (number of activated voxels) as well as in terms of activation strength (contrast values) for FFA and EBA. In FFA, right-handers activated more voxels in the right as compared with the left hemisphere, confirming previous work (Yovel et al. 2008). Left-handers showed no statistically reliable lateralization. There were more activated voxels and a stronger response in right as compared with left EBA in both groups, but the lateralization was only reliably present in right-handers. Finally, for FBA, we observed a significant Hemisphere × Group interaction for one of the measures we used (mean contrast values across whole search region), which was driven by left-handers activating left FBA more strongly than right FBA. No lateralization and no group differences in lateralization were observed in hMT.

Discussion

In this study, we investigated whether hand preference influences the degree of lateralization in 4 extrastriate visual areas. We observed an influence of handedness on the amount of lateralization of FFA and EBA. This was the case in terms of number of activated voxels as well as in terms of activation levels. In both cases, a right-hemisphere bias was present in right-handers, whereas no hemispheric bias was present in left-handed participants. That is, right-handers activated face- and body-related areas to a larger and stronger extent in the right- as compared with the left hemisphere. No such difference was present in left-handers. Hence, lateralization of functional specialization in the visual system does depend on handedness, and functional cerebral specialization seems more flexible than previously thought (cf. Hamilton and Vermeire 1988). In FBA, a handedness-dependent difference in activation strength was observed in one of the dependent measures that were used. Human motion area MT (hMT) was not functionally lateralized in either group. Hence, the group differences were restricted to functionally lateralized areas and did not extend to nonlateralized areas.

The relationship between handedness and cerebral lateralization of the language and motor systems is well established (Bryden 1982; Corballis 1983, 1998; Geschwind and Galaburda 1987; Hellige 1993; Kim et al. 1993; Ivry and Robertson 1998; Knecht et al. 2000; Kloppel et al. 2007; Rocca et al. 2008; Willems and Hagoort 2009; Willems et al. 2009, 2009). The handedness–language lateralization link has been claimed to be special, reflecting a common evolutionary basis (Corballis 1998). Here,

we show that there also is an influence of handedness upon lateralization of functionally specific areas in extrastriate cortex. We want to point out that our data do not refute the evolutionary scenario sketched by Corballis (1998, 2003, 2009). However, we do show that the handedness–language link is supplemented (at least) with a relationship between handedness and lateralization of parts of the visual system.

Handedness arises from a complex interplay between genetic, developmental, and cultural influences (Annett 1973, 2002; Bryden 1982; Corballis 1983; McManus 1985, 2002; McManus and Hartigan 2007; Llaurens et al. 2009; for recent analyses, see Medland et al. 2009; Vuoksimaa et al. 2009), and it seems unlikely that left- and right-handers' differential motor behavior would influence neural lateralization of visual areas. Previous studies suggest a genetic influence upon functional cortical specialization: For instance, Polk et al. (2007) showed that responses in FFA are more similar in monozygotic as compared with dizygotic twins (Polk et al. 2007). In line with this, Sugita (2008) showed that monkeys raised without visual input to faces showed a looking preference for face stimuli as compared with other visual stimuli. In general, lateralization of cognitive functions can be thought of as an evolutionary strategy to use cortical tissue efficiently in the sense that lateralization to one hemisphere "frees up" space on the other hemisphere (Levy 1988). The lateralization of parts of the visual system (in right-handers) can likewise be regarded as an efficient way of using cortical tissue. Lateralization in left-handers may be altogether different, raising the question of what the advantage of less lateralization could have been in evolutionary terms (for a recent overview of evolutionary scenarios associated with left-handedness, see Llaurens et al. 2009).

Our data show that the amount of lateralization in the visual system is not fixed but can differ among individuals, depending upon their hand preference. Current theories of hemispheric specialization are mostly cast in terms of local versus global processing and high versus low-frequency processing/filtering (for overview, see Hellige 1993; Ivry and Robertson 1998). None of these proposals explicitly predicts a difference in cerebral lateralization in the visual system of left- and right-handers, and the current results can hence not be used to argue in favor or against them. Our findings, however, do open the exciting possibility of validating some of the claims made by theories on hemispheric specialization by studying left- and right-handed individuals to see whether they differ on core variables suggested to be hemisphere-specific (e.g., processing of visual and auditory frequency).

Finally, it should be noted that our participant group contained more female than male participants (12 females and 4 males in both groups). Given that an influence of gender on cerebral lateralization has been suggested (but is not agreed upon, see Hellige 1993), this somewhat limits generalizability of our results to the full population. We want to stress though that the female–male ratio was the same in both left- and right-handed participant groups and that a gender difference can thus not explain the lateralization effects that we found. It is up to future research to investigate whether and how handedness and gender interact in terms of cerebral lateralization.

Conclusion

We found that functionally specific areas in extrastriate cortex are differentially lateralized in left-handers as compared with right-handers. Whereas right-handers show larger and stronger activation to faces and bodies in right FFA and right EBA, left-handers show no such interhemispheric differences. This effect was observed to a lesser degree in FBA and was absent in human motion area (hMT). We conclude that handedness has an effect upon brain lateralization of areas in the visual system and thus that this lateralization varies across individuals.

Supplementary Material

Supplementary material can be found at http://www.cercor.oxfordjournals.org/.

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