Neuropsychologia 93 (2016) 394–406

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

The association between hemispheric specialization for language production and for spatial attention depends on left-hand preference strength

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ARTICLE INFO

Article history:
Received 18 June 2015
Received in revised form
16 October 2015
Accepted 23 November 2015
Available online 25 November 2015

Keywords:
Cerebral asymmetry
Handedness
Cognitive function
Pseudoneglect

ABSTRACT

Cerebral lateralization for language production and spatial attention and their relationships with manual preference strength (MPS) were assessed in a sample of 293 healthy volunteers, including 151 left-handers, using fMRI during covert sentence production (PROD) and line bisection judgment (LBJ) tasks, as compared to high- and low-level reference tasks. At the group level, we found the expected complementary hemispheric specialization (HS) with leftward asymmetries for PROD within frontal and temporal regions and rightward asymmetries for LBJ within frontal and posterior occipito–parieto-temporal regions. Individual hemispheric (HLI) and regional (frontal and occipital) lateralization indices (LI) were then calculated on the activation maps for PROD and LBJ. We found a correlation between the degree of rightward cerebral asymmetry and the leftward behavioral attentional bias recorded during LBJ task. This correlation was found when LBJ-LI was computed over the hemispheres, in the frontal lobes, but not in the occipital lobes. We then investigated whether language production and spatial attention cerebral lateralization relate to each other, and whether manual preference was a variable that impacted the complementary HS of these functions. No correlation was found between spatial and language LIs in the majority of our sample of participants, including right-handers with a strong right-hand preference (sRH, $n=97$) and mixed-handers (MH, $n=97$), indicating that these functions lateralized independently. By contrast, in the group of left-handers with a strong left-hand preference (sLH, $n=99$), a negative correlation was found between language and spatial lateralization. This negative correlation was found when LBJ-LI and PROD-LI were computed over the hemispheres, in the frontal lobes and between the occipital lobes for LBJ and the frontal lobes for PROD. These findings underline the importance to include sLH in the study sample to reveal the underlying mechanisms of complementary HS.

1. Introduction

Hemispheric specialization (HS) is a fundamental principle in the functional organization of the human brain (Hervé et al., 2013). In more than 90% of humans, the left hemisphere is specialized for language and the motor control of their dominant hand, whereas the right hemisphere is more dedicated to the control of visuospatial skills including spatial attention. This complementary hemispheric pattern between the language and spatial domain prevailing in the population probably results from evolutionary adaptive processes and selection pressure (Hopkins and Cantalupo, 2008; Hutsler et al., 2002). Different mechanisms have been suggested to account for HS, most of them emphasizing a major role of the corpus callosum in the development and maintenance of hemispheric asymmetry. For example, Gazzaniga (2000) suggested that once considering the corpus callosum as the great communication link, a pre-existing system (i.e, perceptual function) could be jettisoned as new functions (language) developed in one hemisphere, while the other hemisphere could continue to perform the previous functions for both half-brains (Gazzaniga, 2000). Thus, it allowed the development of new competences by saving brain space through reduced redundancy.

Two questions remain largely unresolved: how do the lateralized functions of the two hemispheres relate and what is the nature (biologic, genetic and/or environmental) of the

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.11.018
0028-3932/

mechanisms underlying cerebral asymmetries. Bryden proposed two accounts for the way in which the functions of the two hemispheres are related to one another (Bryden, 1990; Bryden et al., 1983). The first one called *causal* complementarity considers that the division of functions between hemispheres is causally related, with right hemisphere dominance for spatial functions as a consequence of left-hemispheric involvement with language. In that case, causal complementarity predicts that people who show left-hemisphere lateralization for a verbal task should show right-hemisphere lateralization for spatial tasks, and those few who show right-hemisphere lateralization for verbal tasks should also show left-hemisphere effects for spatial ones (mirror-reversed lateralization). In the literature, the causal hypothesis has been evaluated either by looking for by negative correlations between the degree of lateralization of verbal and spatial tasks (Badzakova-Trajkov et al., 2010; Cai et al., 2013; Whitehouse and Bishop, 2009) or by searching whether the functions always dissociate between hemispheres (Flöel et al., 2001). The second account of complementarity is called *statistical* or *independent* complementarity and considers that the asymmetries of language and visuospatial functions are independently determined. Although a bias for language to be left-lateralized and visuospatial skills to be right-lateralized does exit in the population, it would simply reflect probabilities relating to independent underlying mechanisms. The independent complementarity predicts the existence of all possible patterns of HS (albeit in different proportions) for language and spatial functions and an absence of correlation between verbal and nonverbal asymmetries, since the atypical lateralization of one function has no consequence for the lateralization of the other functions. In that case, language and spatial functions can be specialized within the same hemisphere (Flöel et al., 2005).

Until recently, the majority of studies favored an independent complementary HS of language and spatial functions. Using the functional Transcranial Doppler ultrasound (fTCD) imaging technique, several studies reported the existence of almost all combinations of cerebral lateralizations for verbal and spatial functions at the individual level (Flöel et al., 2005, 2001; Powell et al., 2012; Whitehouse and Bishop, 2009), speaking against the prediction of the causal account. Moreover, an absence of negative correlation between language and spatial lateralization has been observed in right-handed participants (Dorst et al., 2008; Lust et al., 2011; Rosch et al., 2012). Opposite results have been obtained by Badzakova-Trajkov et al. (2010) with functional magnetic resonance imaging (fMRI)-based indices of regional asymmetry in a sample of 155 participants including 48 left-handers (Badzakova-Trajkov et al., 2010). They evidenced negative correlations between left frontal-lobe asymmetry for word generation and both right temporal-lobe asymmetry for face processing and right parietal lobe asymmetry for visuospatial landmark task, supporting a causal relationship between the regional specialization of language, and face processing / spatial attention functions. More recently, Cai et al. (2013) specifically investigated the lateralization of spatial attention in participants with atypical right-lateralized speech dominance (Cai et al., 2013). They found that the 13 left-handers who showed atypical right-hemispheric lateralization of the inferior frontal area during a word generation task presented a leftward lateralization for spatial attention in a parietal region. By contrast, among the 16 left-handers typical for language lateralization, all but one were right-lateralized for spatial attention. The authors concluded that, in left-handers, both lateralizations are dependent, and that the spatial function also lateralize atypically when language is atypically represented.

Interestingly, these recent fMRI studies that demonstrated a relation between language and spatial lateralization all included an important number of left-handers. Manual preference could be a factor that impacts the complementary HS of language and spatial functions. Badzakova-Trajkov et al. (2010) indeed showed that handedness is associated with frontal-lobe asymmetry during word production, but not with parietal-lobe asymmetry during landmark task (Badzakova-Trajkov et al., 2010). Moreover, we recently demonstrated that the rare category of right dominant individuals for language, corresponding to 0.6% of the general population, is composed exclusively of strong left-handers (Mazoyer et al., 2014). The proportion of left-handers included in the studies could be a major component explaining the contradictory results present in the literature. One hypothesis stemming from these observations would be that the left-handed population may obey to different rules of complementary HS in comparison with right-handers.

To test this hypothesis, we investigated how lateralized functions such as language production and spatial attention relate to each other in a large cohort of 293 healthy participants. To address the effect of manual preference on complementary HS, this cohort included 152 left-handers to cover the spectrum of cerebral lateralization and to maximize the chances of including atypical cerebral lateralizations (Cai and Van der Haegen, 2015; Willems et al., 2014). Manual preference was evaluated with a modified version of the Edinburgh questionnaire (Mazoyer et al., 2014; Oldfield, 1971). To take into account both the strength and the direction of manual preference as recommended by some authors (Corballis 2009; Ocklenburg et al., 2014a), the population was divided in three groups of strong left-, strong right-, and mixed-handed participants. Language lateralization was assessed with a covert sentence production task (Mazoyer et al., 2014) while spatial attention lateralization was assessed with a line bisection judgment, a modified version of the landmark task. These two tasks are considered as experimental paradigms suited to measure language (Dym et al., 2011) and spatial attention (Jansen et al., 2004) dominances, respectively.

2. Methods and Materials

2.1. Participants

Two hundred and ninety three healthy volunteers (151 men, 142 women; age, 18–57 y; mean age, 25.2 y, S.D.= 6.4 y) participated to the study. All were recruited within the framework of the BIL&GIN, a multimodal imaging/psychometric/genetic database specifically designed for studying the structural and functional neural correlates of cerebral lateralization (Mazoyer et al., 2015). Note that these 293 participants were included in the study of Mazoyer et al. (2014). Among the 293 subjects, 142 declared themselves as right-hander (RH, 70 women, 72 men) and 151 as left-hander (LH, 72 women, 79 men). The mean level of education was 15.5 years $\pm$ 2.3 y (range: 11–20) that corresponded to approximately 3 years of education after the French baccalaureate. The local ethics committee (CCPRB Basse-Normandie) approved the experimental protocol. The participants provided written, informed consent and received compensation for their participation. All participants were free of brain abnormalities, as assessed via inspection of their structural T1-MRI scans by a neuroradiologist. All had normal or corrected-to-normal vision.

2.2. Manual preference strength (MPS)

MPS was quantified using the score at Edinburgh Handedness Inventory (Oldfield 1971), a series of 10 items dealing with subject-preferred hand for manipulating objects and tools. In the present study, we only used 9 of these 10 items, dropping the “broom” item since very few young people had enough familiarity with this tool. MPS values ranged from -100 for strong left-