



## Editorial

## The neural bases of hemispheric specialization



## 1. Introduction

Hemispheric specialization (HS) is a fundamental large-scale feature of brain organization, but its underpinnings are still unknown. Since the pioneering observations of Marc Dax and Paul Broca, the left hemisphere dominance is factually assumed for language processing and the control of the right hand, which are the most studied manifestation of HS at the behavioral and functional level. The fact that the left hemisphere controls both language and the right hand, preferred by more than 90% of healthy adults, led neurologists of the 19th century to call it the ‘dominant hemisphere’. HS concerns most brain functions as demonstrated by split-brain studies that have revealed the specific functional properties of each hemisphere in terms of cognitive processing and the split of functions between them (Gazzaniga, 2000). To explain HS and to characterize its spatio-temporal properties, many models have been put forward in the literature. Nearly 50 years ago, Semmes (1968) suggested in *Neuropsychologia* that HS results from a qualitative difference in elementary functions representation in each hemisphere: focal representation in the left hemisphere that favors integration of similar units and hence specialization for behaviors which demand fine sensorimotor control such as speech, versus diffuse representation in the right hemisphere that leads to integration of dissimilar units and hence specialization for behavior requiring multimodal coordination such as spatial attention (Semmes, 1968). Since then, thousands of papers have been published in the aim to thoroughly explain and model the origin, development, and the where, when and what of HS. To contribute to this rich literature, this special issue of *Neuropsychologia* includes a collection of 17 papers that represent a snapshot on some of the current issues in the search for the origin of HS, and the understanding of its structural and functional properties in relation with normal and pathological cognitive processing.

Before succinctly summarizing the main findings of those 17 papers, we need to tentatively define what we mean by HS. First, we must acknowledge that we are dealing with a dynamic and multifaceted biological property of the brain that emerges across different spatio-temporal scales. It usually equates with the asymmetric processing of sensory, affective and cognitive information (Bryan, 1982), with significant dependency on task type, performance and difficulty. Although the two hemispheres are in continual communication with each other mainly through corpus callosum fibers, *relative* differences between the left and right hemisphere have extensively been reported in numerous studies and described under different terms, including hemispheric specialization, brain lateralization, brain asymmetry, division of labor, hemispheric cooperation, laterality, hemispheric dominance, and many other terms. Those terms, previously introduced as *post-hoc* explanations, do not necessarily mean the same thing, which makes the exact mechanisms of HS difficult to depict (see critique in Efron (1990)). However, one can argue that the definition of HS has evolved over time and also across disciplines, i.e. (1) an association between a specific deficit and focal damage to a given hemisphere as in early neuropsychological studies and also in recent lesion-symptom mapping studies, (2) a specific property of a given hemisphere as assessed by split-brain investigations and further explored as left-right performance asymmetry under different experimental manipulations as in behavioral studies in particular using divided-fields experimental set-up, or (3) a left-right difference in brain structure and function as in recent neuroimaging studies, with this left-right asymmetry equating with differences between roughly homotopic cortical areas connected through the corpus callosum. A definition of HS that transcends specific disciplines should thus take into account the many features of asymmetric processing in the brain. For instance, the exponential growth in the number of neuroimaging studies has added another dimension that needs to be taken into account when it comes to the definition of HS, that is the manifestation of HS at the system/network level. Here, we adopt the following definition (cf. (Hervé et al., 2013)): HS reflects the hosting by a given hemisphere of specialized networks that have specific functional properties and interact inter-hemispherically in a way that optimizes brain processing.

Early work suggested that what shapes and constrains functional brain lateralization is the inherent regional asymmetry in brain structure (Galaburda et al., 1978). However, these early studies could not directly test anatomo-functional relationships and their conclusions were based on the idea that brain leftward asymmetries are directly related to left hemisphere dominance for language with sometimes contradictory results. For example, depending on the language task, the asymmetry of the planum temporale is either positively correlated or not with functional asymmetries (Josse et al., 2006). In any case, structural asymmetries explain only a small fraction of HS variance (Josse et al., 2009), and alone cannot explain the dynamic context-dependent nature of functional lateralization when anatomy is held constant; see example in Seghier et al. (2011).

An alternative classic explanation attributes HS to differences in the functional properties of each hemisphere, with stronger bias for verbal, analytical, and high-frequency processing in the left hemisphere versus stronger bias for visuospatial, configurative and low-frequency processing in the right hemisphere (Dien, 2009). Within this frame, some have suggested that the *raison d'être* of lateralized hemispheric functions is to enhance processing efficiency in different cognitive tasks (Gotts et al., 2013; Rogers et al., 2004). However, even if there is evidence of higher performances in lateralized individuals as compared to those with low lateralization (Gotts et al., 2013; Mellet et al., 2014; Rogers et al., 2004), the size of effect

remains small and the exact mechanisms behind the emergence of such lateralized patterns are still not fully understood (Banich and Weissman, 2000; Beaumont, 1997; Seghier and Price, 2011). Perhaps most importantly, HS is regulated by the dynamic flow of interhemispheric interactions (Bryden and Bulman-Fleming, 1994; Chiarello and Maxfield, 1996) and by the balance between within- and between-hemisphere interactions (Allen, 1983; Ocklenburg et al., 2016). For instance, recent work has suggested that the left and right hemispheres have qualitatively different biases in how they dynamically interact with one another: left regions interact more strongly within the same hemisphere, whereas right regions interact more strongly with both hemispheres during language processing (Vigneau et al., 2011), as well as when considering asymmetries in intrinsic connectivity (Gotts et al., 2013). All these factors may potentially contribute to the emergence of HS.

It is important to stress that HS, as a phenomenon, may emerge at different levels, from the molecular to the behavioral level (Francks, 2015; Sun and Walsh, 2006); here, we are mainly concerned with its emergence at the mesoscopic and macroscopic level at which neuroimaging techniques can operate, using functional Magnetic Resonance Imaging (fMRI), Diffusion Tensor Imaging (DTI), Electroencephalography (EEG), Magnetoencephalography (MEG), and Transcranial Magnetic Stimulation (TMS). In the following of the Wada test, as the gold standard procedure for individual HS rating, neuroimaging allowed brain asymmetries to be mapped noninvasively at high definition in both patients and healthy participants, including recently the search for markers of HS with intrinsic connectivity and the (co-)investigation of lateralized functions other than language such as emotion, face, praxis, or attention. The 17 papers that are part of this special issue addressed different topics in HS with different techniques, but can be grouped into the following main questions of interest: (1) developmental, phylogenetic and genetic origins of HS; (2) regional asymmetries in brain structure; (3) inter-hemispheric interactions; (4) how task-related functional connectivity can shape functional lateralization, and how intrinsic connectivity influences task-related HS; (5) the impact of sensory and cognitive factors on HS; and (6) the question of handedness and its contribution to inter-individual variability in HS.

## 2. Phylogenetic, developmental, and genetic origins of HS

The question of the origins of HS is timely and open, and the present issue includes three articles tackling this question by the exploration of primate behavior, the analyses of the development of language-hand lateralization and the search for a genetic origin of atypical handedness. An emerging domain of interest concerns the search for associations between behavior and anatomo-functional asymmetries in nonhuman primates, with an emphasis on inter-species homology in lateralization. When characterizing lateralization across species, some authors have suggested that the left hemisphere has become specialized for control of well-established patterns of behavior, performed under familiar environmental circumstances, while the right hemisphere has become specialized for detecting and responding to unexpected stimuli in the environment (MacNeilage et al., 2009). This also has many ramifications for the origin of language, given that HS is a key feature of language organization (Corballis, 2014).

It has been hypothesized that brain size impact (i.e. inverse relationship) on brain asymmetry within and between species. Hopkins and colleagues investigated this hypothesis in a sample of chimpanzees by looking at correlation between the asymmetry in the planum temporale and many callosal metrics, including the surface area of the corpus callosum, streamline count as measured from diffusion tensor imaging, fractional anisotropy values and the ratio in the number of fibers to surface area. In male but not female chimpanzees, larger asymmetries in the planum temporale were found in chimpanzees with smaller callosal surface areas, fewer streamlines and a smaller ratio of fibers to surface area. This suggested that the relationship between regional brain asymmetry and the morphology of the corpus callosum is sex-dependent.

Cochet reviewed the developmental aspects of the setting of manual, language and spatial lateralization and argued that handedness, as commonly measured by the lateralization of grasping or objects manipulation, has weak relationships with the development of language unlike communicative gestures. It is important to stress that these two aspects of hand lateralization measures develop independently before the age of 3. The author questioned the causal nature of the statistical link existing between left hemisphere specialization for language and right hand preference for unimanual daily activities. Her review also pointed towards the need to extend developmental studies on HS to other domains other than language and stressed the need to include visuospatial attention in order to have a comprehensive understanding of the development of HS.

Research on the genetic origins of HS is still an ongoing endeavor and it concerns both language and hand lateralization. Because recent genome-wide association scans did not detect any gene polymorphism with substantial effect on handedness, Kavaklioglu and colleagues searched for genes involved in non-right-handedness based on the investigation of a large Pakistani family of 89 members (6 generations) rich in left-handers. They carried out exome sequencing in 17 family members but did not find any clear candidate genomic region to be involved in handedness. They concluded that the genetic contribution to handedness in this family is likely to have a complex etiology.

## 3. HS and brain structural asymmetries

Before the discovery by Norman Geschwind that there is a larger leftward planum temporale on the supratemporal plane (Geschwind and Levitsky, 1968), the brain was considered symmetrical. Actually, a torsion of the brain, named the Yakovlian Torque, makes both hemispheres anatomically dissimilar (review in Toga and Thompson (2003)), but the implications of anatomical dissimilarities on brain function are very complex to predict (Ocklenburg et al., 2016). For instance, when investigating the anatomical variability of the lateral frontal lobe in healthy right-handers, the anterior horizontal of the Sylvian fissure was found to be absent in some subjects (Juch et al., 2005) but this anatomical variety had no or little impact on behavior. This is because there are many-to-one structure-function mappings in the brain (Noppeney et al., 2004), which means that multiple structural subsystems can support the same brain functions. Perhaps most importantly, brain structures change with age, learning and exercise, which suggests that the relative degrees of structural left-right asymmetries are not static but could change with time. In this Special Issue, two studies have investigated the different regional features of structural asymmetries that are complementary in terms of resolution (vertex-wise and ROI-based) and consistent in terms of the question tackled since both works investigated the key issue of the relationships between asymmetries of cortical thickness and asymmetries of cortical surface area. A third study assessed the impact of hippocampal asymmetry on memory processing.

Maingault and colleagues looked at different surface-based morphometry measures of brain structure in a large cohort of 250 healthy adults selected among 452 subjects as those having a typical lateralization for language as measured during language production task with fMRI. This selection of participants with left-lateralized language representations allowed the authors to reduce potential variability in structural asymmetries associated with variation in functional language lateralization. Vertex-wise asymmetries were obtained with respect to cortical thickness, cortical surface area, and sulcal depth. When assessing the relationships between these measures across all participants, the authors revealed a strong

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