Neuropsychologia 93 (2016) 386–393

Contents lists available at ScienceDirect

Neuropsychologia

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

Complementarity or independence of hemispheric specializations? A brief review

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ARTICLE INFO

Article history:
Received 29 September 2015
Received in revised form
16 December 2015
Accepted 18 December 2015
Available online 19 December 2015

Keywords:
Hemispheric asymmetry
Laterality
Complementarity
Neuroimaging
Language
Spatial
Face
Genetic
Handedness

ABSTRACT

The current review investigates the question of the relationship of different hemispheric specializations. Hemispheric specializations are the result of the seemingly distinctive ability of the left and right hemisphere to specialize in different cognitive functions. The review focuses on the concept of complementarity whereby the lateralization of one function predicts the asymmetric processing of another one. The complementarity of hemispheric specializations presents an interesting dilemma as the literature evidence is outwardly mixed. The causal and statistical hypotheses attempt to account for the observed findings, with support for both hypotheses. However, most of the evidence appears to align with the statistical pattern of complementarity. Converging lines of evidence suggest that there are multiple independent biases that play a role in how these functional cerebral asymmetries are organized in the human brain. Some of the functional and evolutionary implications of the existence of complementarity of hemispheric specializations are also briefly discussed.

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1. Introduction

Ever since Paul Broca's discovery of language impairments after left hemisphere lesions, the concept of hemispheric specialization, whereby one hemisphere is superior compared to the other in processing a certain cognitive function, has received much attention (Josse and Tzourio-Mazoyer, 2004; Bryden, 1982). Interestingly though, not all individuals adhere to this pattern with a minority reversing or negating the asymmetry. In terms of language dominance, a relationship with handedness, which can be considered a different form of hemispheric specialization, has been well documented, with about 95% of right-handers having left-hemispheric specialization compared to about 70% of left-handers (e.g., Badzakova-Trajkov et al., 2010a, 2010b; Rasmussen and Milner, 1977). The right hemisphere is considered to play a bigger role in a variety of non-verbal abilities, including spatial abilities, face recognition, and emotional expression (Hellige, 1996; Duecker et al., 2013; Thoma et al., 2014; Bourne, 2008; Onal-Hartmann et al., 2012). Right-hemisphere specialization for these functions is well established but is not as striking or clear-cut. Only about 76% of right-handed males and 59% of right-handed females are right-hemisphere dominant for spatial ability (Bryden et al., 1983), based on the incidence of spatial disorders following unilateral brain lesions, which is considerably lower than the over 90% population bias found for language functions.

Hemispheric specialization has been studied extensively using a variety of approaches: unilateral brain lesions, split-brain patients, intraoperative brain stimulation, behavioral methods, and more recently, neuroimaging methods. Using a variety of methods is important as hemispheric specialization can be viewed as an underlying principle of how the human brain is organized. More recently, resting-state functional Magnetic Resonance Imaging (fMRI) studies, which measure the correlation between spontaneous activation patterns of brain regions, provide an opportunity to explore the potential underlying organization of resting-state networks that may provide the framework of functional hemispheric asymmetries in the brain. This is feasible given resting-state networks consist of anatomically separated, but functionally linked, brain regions that show a high level of ongoing functional connectivity during rest (van den Heuvel and Hulshoff Pol, 2010).

It is believed that hemispheric specialization allows increasing the speed and efficacy of information processing (e.g., Levy, 1969). Conversely, deviations of hemispheric specialization have been linked to a variety of different disorders and phenomena such as reading disability, schizophrenia, stuttering, gender-related differences in spatial ability, infantile autism, and developmental language difficulties (Bryden, 1982; Herbert et al., 2002; Kleinhans et al., 2008; Crow et al., 1989; Whitehouse and Bishop, 2008). Most

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.12.018
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significantly, perhaps, hemispheric specialization is thought to contribute to the evolution of human language as well as providing an axis for the specialization of cortical systems beyond language (Liu et al., 2009).

Although hemispheric specialization has been widely documented in a variety of cognitive domains, research investigating the relationship between functional cerebral asymmetries has been less forthcoming or conclusive. The question remains as to whether the localization of one function to a certain hemisphere predicts the localization of another function to the opposite hemisphere, a phenomenon termed complementarity. Complementarity of functional cerebral asymmetries can be likened to a "diagonal laterality" mechanism whereby asymmetry to the left in one part of the brain is accompanied by asymmetry to the right in another part of the brain (Wood et al., 1991). For the purposes of this review, we are interested in cases where different functions are in opposite hemispheres, and are therefore complementary in the sense that specialization in one hemisphere is complemented by another specialization in the other hemisphere. The assumption of complementarity of functional cerebral asymmetries is generally assumed, yet left- and right-hemisphere cognitive functions are commonly assessed in isolation, with little attention to the relationship in the degree and direction of lateralization within individuals (Badzakova-Trajkov et al., 2010a, 2010b; Harms and Elias, 2014).

In this review, we evaluate whether complementarity of functions exists and the patterns of complementarity commonly observed. We present the main hypotheses on the complementarity of hemispheric specializations, with evidence for each hypothesis presented and evaluated to see which hypothesis best fits the data. Finally, a brief discussion around the implications of complementarity of functional cerebral asymmetries and some concluding remarks on the topic are put forward.

2. Literature review

2.1. Complementarity of functional cerebral asymmetries

Complete hemispheric specialization is questionable, given that both hemispheres usually contribute to complex and multifaceted cognitive domains. It is very typical that both hemispheres have some ability to perform the same task, with one hemisphere usually doing so more effectively than the other (Hellige, 1993). This is evident in neuroimaging research where brain activity is generally observed across both hemispheres even for tasks that commonly exhibit clear hemispheric dominance (e.g., Badzakova-Trajkov et al., 2010a, 2010b). In addition, research shows that we must be cautious in attributing dominance to one hemisphere for cognitive domains that are complex and multifaceted. For example, despite the overwhelming evidence for left-hemisphere dominance for language processing, there is extensive evidence of the importance of the right-hemisphere in processing pragmatic aspects of language (as reviewed by Hellige, 1993). Language processing in the two hemispheres is parallel in the sense that each performs its own computation on information at every level of processing (Beeman and Chiarello, 1998). Furthermore, according to Beeman and Chiarello (1998), the left-hemisphere language processing is characterised as relatively fine coding, resulting in sharp activation patterns and categorical representations whereas right-hemisphere language processing is characterized as relatively coarse coding, resulting in diffuse activation patterns and analogical representations. This leads one to think that the hemispheres may play somewhat complementary roles in the intact brain (Hellige, 1993) given the nature of their contributions. More recently, according to Hickok and Poeppel (2007), the cortical organization of speech processing is characterised by a dorsal stream that is responsible for language production and is left-hemisphere dominant versus a ventral stream that is bilaterally organized and is responsible for comprehension. The complementarity of the hemispheres in the processing of information for a complex cognitive domain such as language may represent an underlying hemispheric organization that lends itself to complementarity not only within a cognitive domain but also across cognitive domains. The wide variety of cognitive systems asymmetrically organized in the human brain further highlight the importance of understanding how and why this asymmetry occurs (Ocklenburg et al., 2014).

The idea of complementarity involves the study of more than one asymmetrically distributed cognitive function with usually one favouring the left- and the other one the right-hemisphere. Despite the abundance of research on the lateralization of functions, only few assess the relationship between them in the same sample, and these usually involve language as a left-hemispheric function and spatial processing as a right-hemispheric function. Therefore, the main question is whether being left-lateralized for one function implies being right-lateralized for another. If so, a correlation between these functional asymmetries can be observed.

2.2. Causal or statistical pattern of complementarity

Two hypotheses as to the nature of complementarity are commonly distinguished, a causal hypothesis and a statistical hypothesis. A brief introduction of the two main hypotheses will be presented next before reviewing the key evidence in the next section.

In the causal pattern of complementarity (Bryden, 1990; Bryden et al., 1983), the asymmetrical lateralization of one function pushes the other function to the opposite hemisphere. As this pattern predicts that two complementary functions should be opposite in lateralization, a *negative correlation* in the direction and degree of lateralization between the two can be observed (Harms and Elias, 2014). As reviewed in Andresen and Marsolek (2005), this theory (cf. Bradshaw and Nettleton, 1981) posits that although subsystems in the two hemispheres may be nearly symmetric at an initial time point, the growth of an asymmetry for one subsystem plays a causal role in the development of the opposite asymmetry for a complementary subsystem. Potential mechanisms for such a causal effect have been put forward. For example, the "snowball" mechanism (Hellige, 1993) suggests that a small number of "seed" asymmetric subsystems must be in place (possibly innate in nature). Interactions are more effective among subsystems in the same hemisphere, so tuning of a subsystem, through practice and training, is more influenced by within-hemisphere subsystems than by across-hemisphere subsystems. Eventually, such tuning should have the effect that asymmetries similar in nature to the seed asymmetries will be found in the other subsystems as well (i.e., asymmetries "snowball" from seed subsystems to other subsystems).

Another explanation comes from the notion of homotopic callosal inhibition (Cook, 1984). According to this, the homotopic areas of the hemispheres mutually inhibit each other. In addition, adjacent areas within one hemisphere mutually inhibit one another. If an area in one hemisphere is inhibited, two things happen: 1) the surrounding area in that hemisphere is activated; and 2) the activated area inhibits its homotopic area in the other hemisphere. The outcome from this is that different hemispheres become dominant for the different processes performed in closely contiguous neural areas (of one hemisphere) and hence for complementary functions (i.e., become dominant for two different ways of processing information in the same general homotopic brain regions).

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