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The influence of handedness on hemispheric representation of tools: A survey

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ABSTRACT

An important debate exists in contemporary cognitive neuroscience about the innate or experience-dependent origin of the brain representation of conceptual categories. The 'domains of knowledge' hypothesis maintains that innate factors subsume the categorical organization at the brain level of animals, plant life and artefacts. On the other hand, the 'sensory-motor model of conceptual knowledge' and the embodied cognition theory attribute this categorical organization to experience-dependent factors. I tried to clarify this issue by surveying the influence that handedness could have on the lateralization of tools representation in the inferior fronto-parietal and posterior middle temporal cortices of the left hemisphere. The underlying assumption was that, if this lateralization results from innate mechanisms, then handedness should not influence this hemispheric asymmetry. If, on the other hand, this lateralization is due to the motor and somatosensory experiences made with the right dominant hand during the manipulation of tools and other artefacts, then this asymmetry should be inverted or strongly attenuated in left-handers. Results of the review strongly suggest that manual experience acquired during tool manipulation can influence the hemispheric representation of tools and other artefacts. They also suggest, however, that handedness-related embodiment is not fixed, but influenced by personal motor experiences (such as those made by left-handers who have been forced to use their right hand) and by social visual experiences (such as the fact that, living in a right-handed world, left-handers see more people in their environment who use the right rather than the left hand) during tool manipulation.

1. Introduction

An important topic in contemporary debates about the brain representation of conceptual categories (and in particular of biological and artefact categories) concerns their innate or experience-dependent nature (see Gainotti, 2015 for survey). Both innate and experiential models acknowledge that categories are subsumed by networks of brain structures processing the basic features on which the different categories are based (e.g. Bressler, 1995; Bressler & Menon, 2010; Bressler & Tognoli, 2006; Caramazza & Mahon, 2006; Gainotti, 2000, 2006, 2013; Gainotti, Silveri, Daniele, & Giustolisi, 1995; Gainotti, Silveri, & Marra, 2009; Kourtzi & Connor, 2011; Mahon & Caramazza, 2009, 2011; McIntosh, 2000; Gainotti et al., 2013). These models also acknowledge (giving a different stress to this fact) that various perceptual, motor and encyclopaedic sources of knowledge have different weights in the construction of different categories. However, one of these models, the 'domains of knowledge' hypothesis, (Capitani, Laiacona, Mahon, & Caramazza, 2003; Caramazza, 1998; Caramazza & Mahon, 2003, 2006; Caramazza & Shelton, 1998; Mahon & Caramazza, 2009, 2011), maintains that innate factors subsume the categorical organization at the brain level of animals, plant life and artefacts representations, because natural selection produced specialized neural circuits for these categories, which have an important and specific role in human survival (Caramazza & Mahon, 2003). On the contrary, the second theoretical model, the 'sensory-motor model of conceptual knowledge' (Chao, Haxby, & Martin, 1999; Chao & Martin, 2000; Gainotti, 2000, 2005; Gainotti et al., 1995; Martin, 2007; Martin & Chao, 2001; Martin, Ungerleider, & Haxby, 2000; Saffran & Schwartz, 1994), attributes to experience-dependent factors the construction of the corresponding neural networks. For instance, both models acknowledge that the anterior parts of the right and left temporal lobes (ATLs) play a fundamental role in the representation of biological entities, whereas the left inferior fronto-parietal cortices

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and the posterior middle temporal gyrus play a critical role in the representation of tools and other manmade objects. However, the 'distributed domain-specific hypothesis' (Mahon and Caramazza (2011), argues that innately determined patterns of connectivity mediate the integration of visual information with other kinds of perceptual data at the level of the ATLs, giving rise to the representation of biological categories, whereas motor-relevant information (processed by the inferior fronto-parietal cortices) is integrated with motion visual information (processed by the posterior middle temporal gyrus), building a network appropriate for tools and other artefacts. On the contrary, the 'sensory-motor model of conceptual knowledge' maintains that the representations of living beings in the right and left ATLs and of tools and other manmade objects in the left fronto-parieto-temporal cortices, are constructed, according to Hebbian correlation learning (Hebb, 1949) mechanisms, integrating the sources of knowledge more relevant for the construction of these categories.

Largely overlapping with the sensory-motor model of conceptual knowledge and also based on experience-dependent factors is the embodied cognition theory (Barsalou, 1999; Barsalou, Kyle Simmons, Barbey, & Wilson, 2003; Casasanto, 2009; Gallese & Lakoff, 2005), which maintains: (a) that what happens in our body strongly influences our cognition; (b) that our conceptual representations are based on the retrieval of information stored in sensory and motor areas and (c) that the conceptual processing of tools involves the retrieval or simulation of the movements associated with tool usage. A definite choice between 'innate' and 'experience dependent' factors is obviously difficult, because both mechanisms certainly intervene in the functional brain organization and it is often impossible to say whether learning results in long-term changes in neural connections or optimizes the readout signals in predetermined structures. There is, however, an aspect of the brain network subsuming the representation of tools and other manmade objects for which different predictions can be made on the basis of 'inborn' and 'experience dependent' models. This aspect concerns the well documented (e.g. Boronat et al., 2005; Buxbaum & Kalénine, 2010; Buxbaum & Saffran, 2002; Chao & Martin, 2000; Gainotti, 2000, 2013; Garcea, Almeida, & Mahon, 2012; Johnson-Frey, 2004; Kellenbach, Brett, & Patterson, 2003; Martin, 2007; Noppeney, Josephs, Kiebel, Friston, & Price, 2005) left laterality of mechanisms playing a critical role in the representation of artefacts (which contrasts with the bilateral representation of biological categories) and the influence of handedness on this left lateralization. As a matter of fact, if the bilateral representation of living entities in the right and left ATLs might be due to the fact that visual and other perceptual inputs (namely their major sources of knowledge) are bilaterally represented, more difficult could be to understand why tools and other artefacts are left lateralized. It is, indeed, possible to assume that, if this laterality results from innate mechanisms, then handedness should not influence this lateralization, because hand preference has been attributed to a complex interplay of genetic, anatomical, hormonal, developmental and cultural factors. Just to mention some of the theories that have been advanced on this subject, some genetic theories, such as those of McManus and Bryden (1991), of Annett (1985, 2000) and of Corballis (2009), assume that there is a genetic "right-shift factor" that disposes individuals to be right-handed and left-cerebrally dominant for language, but that individuals lacking this factor are subjected to random influences. According to this model, left-handers could belong to this latter group, along with a proportion of right handers. This raises the possibility that the "right-shift gene" innately fixes cerebral asymmetries, but that in its absence the asymmetries are more subject to experiential influences. According to other authors (e.g. Liu, Stufflebeam, Sepulcrea, Heddena, & Buckner, 2009), the situation may be even more complex, because 4 separate factors, each accounting for significant variation across subjects and associated with brain systems involved in vision, internal thought, attention, and language could be put in evidence. Liu et al. (2009) also claim that hand dominance could differentially affects brain asymmetry across the 4 factors. Bishop (2013), on the other hand, has suggested that cerebral asymmetry for language is dependent on experience, and not on genetic influences, whereas Stout and Chaminade (2012) have hypothesized that language itself evolved from tool manufacture. Much more simple than the predictions that can be made on the basis of these controversial models, and in particular of the genetic ones, are the predictions that can be made on the basis of the 'experience dependent' models. As a matter of fact, if left laterality results from the motor and somato-sensory experiences made during the manipulation with the dominant hand of tools and other artefacts, then this lateralization should be inverted or strongly attenuated in left-handers. The aim of the present review will, therefore, consist in surveying the available literature to check if handedness modulates the hemispheric representation of tools and other artefacts. In my search through the literature I used the keyword 'handedness' in association with 'tools representation'; 'left fronto-parietal areas'; and 'tool use pantomimes'. I did not use the more general terms 'apraxia', 'ideo-motor apraxia' or 'ideational apraxia' for two main reasons. The first is that, to explore the subject that had motivated this survey, activation studies were more appropriate than anatomo-clinical investigations. The second is that apraxia can be due to many different mechanisms (Buxbaum, 2001; Heilman, Maher, Greenwald, & Rothi, 1997; Heilman, Rothi, & Valenstein, 1982; Buxbaum & Kalénine, 2010; Goldenberg, 2014; Gross & Grossman, 2008) and I deemed that the keyword 'tool use pantomimes' more specifically pointed to a tool use representation.

2. Early investigations relevant to the issue of the cortical organization of tool related networks in left-handers

In spite of the methodological considerations made at the end of the last section and concerning the use of the terms 'apraxia', 'ideo-motor apraxia' or 'ideational apraxia' as keywords for my search through the literature, I must acknowledge that the first studies that have examined some aspects of tool use in left-handers have concerned left-handed patients exhibiting some form of apraxia. In particular, two of these case studies, reported by Poeck and Lehmkuhl (1980) and by Ochipa, Rothi, and Heilman (1989) described left-handed patients who exhibited ideational apraxia after sustaining damage to the right hemisphere. The inability of these patients to use tools could not be explained by: (a) a motor production deficit (ideomotor apraxia), because they made content errors and were impaired both on transitive and on intransitive actions or (b) by language comprehension deficit, because they could name tools and point to tools on command. These were the first observations which suggested that knowledge, related to tool use could be lateralized to the right hemisphere in a left-hander, mirroring what happens in right-handers. Other instances of left-handed patients exhibiting some form of apraxia after damage to the right hemisphere have been reported by Poeck and Kerschensteiner (1971), Heilman, Coyle, Gonyea, and Geschwind (1973), Valenstein and Heilman (1979), and Archibald (1987). All these papers could support the hypothesis of a link between handedness and hemispheric representations of tools, but will not be taken analytically into account here because they did not meet the criteria suggesting a right hemisphere tools representation presented by the case studies, reported by Poeck and Lehmkuhl (1980) and by Ochipa et al. (1989).