Neuroscience and Biobehavioral Reviews 64 (2016) 421–437

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review article

# On the neurocognitive origins of human tool use : A critical review of neuroimaging data

Emanuelle Reynaud[a,1], Mathieu Lesourd[a,1], Jordan Navarro[a,1], François Osiurak[a,b,*,1]

[a] Laboratoire d'Etude des Mécanismes Cognitifs (EA 3082), Université de Lyon, France
[b] Institut Universitaire de France, Paris, France

ARTICLE INFO

*Article history:*
Received 6 November 2015
Received in revised form 4 March 2016
Accepted 9 March 2016
Available online 11 March 2016

*Keywords:*
Inferior parietal cortex
Manipulation knowledge
Mechanical knowledge
Meta-analysis
NeuroImaging
Tool use

ABSTRACT

Since more than a century, neuropsychological models have assumed that the left inferior parietal cortex is central to tool use by storing manipulation knowledge (the manipulation-based approach). Interestingly, recent neuropsychological evidence indicates that the left inferior parietal cortex might rather support the ability to reason about physical object properties (the reasoning-based approach). Historically, these two approaches have been developed from data obtained in left brain-damaged patients. This review is the first one to (1) give an overview of the two aforementioned approaches and (2) reanalyze functional neuroimaging data of the past decade to examine their predictions. Globally, we demonstrate that the left inferior parietal cortex is involved in the understanding of tool-use actions, providing support for the reasoning-based approach. We also discuss the functional involvement of the different regions of the tool-use brain network (left supramarginal gyrus, left intraparietal sulcus, left posterior temporal cortex). Our findings open promising avenues for future research on the neurocognitive basis of human tool use.

**Contents**

---

[*] Corresponding author.
*E-mail address:* Francois.Osiurak@univ-lyon2.fr (F. Osiurak).
[1] Laboratoire d'Etude des Mécanismes Cognitifs EA 3082, Institut de Psychologie, 5 Avenue Pierre Mendès-France, 69676 Bron Cedex, France.

http://dx.doi.org/10.1016/j.neubiorev.2016.03.009
0149-7634/© 2016 Elsevier Ltd. All rights reserved.

## 1. Introduction

Since the appearance of symbolic reasoning (e.g., language skills) in human lineage, Man has largely overlooked the physical reasoning skills involved in tool use. A good illustration of this lack of attention is the implicit hierarchy of intellectual work over manual work, as if tool use did not require any kind of specific intelligence or reasoning. This belief is also deeply ingrained in the minds of scholars and scientists alike. For instance, since more than a century, neuropsychological models have assumed that knowledge about manipulation is central to tool use (the *manipulation*-based approach). This knowledge is supposed to be stored within the left inferior parietal lobe (IPL). By contrast, a more recent perspective, initiated by Goldenberg in the 2000's, assumes that, to use tools, people reason about the physical object properties in order to generate mechanical actions (the *reasoning*-based approach). This reasoning would be supported by mechanical knowledge located in the left IPL. Historically, these two approaches have been developed from data obtained in left brain-damaged patients. The goal of the present review is to examine their validity by reanalyzing functional neuroimaging studies of the past decade. To anticipate our conclusions, we demonstrate that the left IPL is clearly involved in the understanding of tool-use actions, providing support for the reasoning-based approach. From our findings, we shall also discuss the functional involvement of the different regions of the tool-use brain network.

Tool use is considered by many to be a hallmark of complex cognitive adaptations (Beck, 1980; Johnson-Frey, 2004). So, understanding the neurocognitive bases of human tool use can provide fundamental insights into the evolution of human lineage. More than a century after the publication of *Descent of Man* by Darwin in 1871, the issue of the origins of human cognition is still a matter of debate between proponents of continuity versus discontinuity theories of the evolution of human cognition. Both of them are not at odds with regard to the fact that differences exist between human and nonhuman tool use. Nevertheless, they differ greatly as to the interpretations they lend to these differences. Continuity theories consider that these differences are rather quantitative than qualitative, whereas discontinuity theories assume that at least some of them can be viewed as qualitative. We will begin by presenting these theories in order to help the reader to understand how, at an epistemological level, they have framed the manipulation-based and the reasoning-based approach to human tool use. We would also like to add one caveat. Particularly, the interpretations based on neuroimaging studies will be discussed parsimoniously all along the paper, notably to avoid circularity between them and the results obtained from the present meta-analysis. Rather, we decided to present how the manipulation-based and the reasoning-based approach have been developed mainly from the neuropsychological literature. In this context, neuroimaging data are considered as a good means to examine their validity.

### *1.1. The primate behind the Man: the primate prehension system*

Tool use was once considered to be one of the defining characteristics of the genus *Homo*, dating back 2.5 million years (Oakley, 1949; see Ambrose, 2001). The diversity of tool behavior in several nonhuman species including primates, birds, mammals, and even insects, has forced us to revise this assumption (for reviews, see Baber, 2003; Beck, 1980; Van Lawick-Goodall, 1970). In broad terms, tool use is not unique to humans. This conclusion might appear surprising given the subtle – and sometimes less subtle – differences that exist between human and nonhuman tool use (see below). Nevertheless, these differences can be masked by the way we define what is a tool. Tools are commonly defined as handheld physical objects that are manipulated in order to increase the user's sensorimotor capabilities (for a critical review about this definition, see Osiurak et al. 2010). This definition puts a heavy emphasis on manipulation and, as a result, can include a wide range of animal behaviors to the extent that there is manipulation. In this frame, it is true that some similarities do exist between nonhuman primates[1] and humans, particularly with regard to prehension skills.

Prehension skills are based on two basic components, namely, reaching (transportation of the hand to the object by the upper limb) and, more relevant to our concerns here, grasping (shaping the hand according to object size and orientation, and applying the correct grip force). Although the nonhuman primate brain is cytoarchitectonically quite different from ours, a significant body of evidence from neurophysiology has suggested considerable functional homologies between the human and the primate brain with regard to grasping (for reviews, see Johnson-Frey and Grafton, 2003; Rizzolatti and Matelli, 2003; Vingerhoets, 2014). In monkeys the anterior intraparietal area (AIP) in combination with area F5 is involved in the transformation of 3D properties of an object into appropriate finger formations and hand orientation for visually guided grasping movements (Jeannerod et al., 1995; see also Nelissen et al., 2011). Interestingly, it has been proposed that the anterior dorsal intraparietal sulcus (DIPSA) and the putative human homologue of AIP (phAIP) together represent the equivalent of monkey AIP. DIPSA corresponds to the more visual, posterior part of AIP and phAIP to its more somatosensory and motor, anterior part (see Orban et al., 2006; Vanduffel et al., 2014). Neuroimaging data also indicate that area phAIP is activated by observing a tool being grasped (Jacobs et al., 2010; Peeters et al., 2013). Different brain areas within the ventral premotor cortex (vPMC) and phAIP are also involved in the representations of different hand movements or handgrips (e.g., precision vs. power grips; Ehrsson et al., 2000, 2001; see also Dinstein et al., 2007; but for discussion see Sawamura et al., 2006).

---

[1] As mentioned, there is considerable evidence that some non-primate animals can also use tools. However, in the rest of the article, we shall focus only on the differences between human and nonhuman primates.