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**ON THE NEUROCOGNITIVE ORIGINS OF HUMAN TOOL USE**

**A CRITICAL REVIEW OF NEUROIMAGING DATA**

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### **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.

**Keywords:** Inferior Parietal Cortex; Manipulation Knowledge; Mechanical Knowledge; Meta-Analysis; NeuroImaging; Tool Use.

### 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<sup>1</sup> 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 cytoarchitecturally 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., 2009; 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).

To sum up, both human and nonhuman primates possess a primate prehension system involved in the elaboration of motor schemas (e.g., preshape, enclose, selection of the number of fingers) that would be potentially elicitable by the extraction of information about the object properties<sup>2</sup> (e.g., size, shape) (see also Arbib, 1985; Jeannerod et al., 1995). This system is both effector-specific and side-specific and, as a result, is distributed bilaterally (Vingerhoets, 2014). It is supposed to be the basis of non-tool-use actions, such as object transport, or even “simple tool use” as in nonhuman primates<sup>3</sup> (Orban and Caruana, 2014).

### *1.2. THE UNIQUENESS OF HUMAN TOOL USE*

The story could have ended here: Humans and nonhuman primates share a common neural network for prehension skills – including manipulative, motor schemas –, explaining why both can use tools. Nevertheless, beyond these similarities, it appears that human tool use differs from that known to occur in nonhumans in different ways. For instance, in nonhumans, tool use is incidental and rare in the wild (Beck, 1980; Byrne, 2004; Chappell and Kacelnik, 2002; Van Schaik et al., 1999). By contrast, humans spontaneously engage in object-object manipulations (McGrew, 1992) and employ a wide range of tools everyday and during all the life (Johnson-Frey, 2007), a feature that characterizes humans of all cultures through the ages (Leroi-Gourhan, 1971). In addition, only humans are able to use a tool to create another one (i.e., use of secondary tools; Gibson, 1993; McGrew, 1992, 1993; Toth and Schick, 1993). A substantial body of evidence also indicates serious limitations on the ability of nonhuman animals to solve tool-use situations that are relatively simple for humans (e.g., Povinelli, 2000;

Visalberghi and Limongelli, 1994) or to transfer the mechanical relationships they learn in one specific situation to other ones (Martin-Ordas et al., 2008; Penn et al., 2008). In short, even if humans are not unique in using tools, there is undoubtedly something unique about the way humans use tools.

Differences also exist at a neuroanatomical level. More specifically, it has been repeatedly assumed that in humans more ventral parts of the parietal cortex may play a central role in the skillful use of tools (Binkofski and Buxbaum, 2013; Buxbaum, 2001; Daprati and Sirigu, 2006; Johnson-Frey and Grafton, 2003; Rizzolatti and Matelli, 2003; Orban and Caruana, 2014; Vingerhoets, 2014). This system is lateralized to the left hemisphere and includes the left IPL, and particularly, the supramarginal gyrus (SMG), a new human brain area that does not exist in monkeys (Orban and Caruana, 2014; Peeters et al., 2009, 2013; Vingerhoets, 2014). In sum, not only humans possess specific behavioral characteristics, but there is also a uniquely human brain area that might be the basis for this specificity. The important issue is to understand the functional role of this area. This issue has raised considerable interest in the fields of neuropsychology and neuroimaging, leading to the formulation of two different approaches, which mirror the classical distinction between continuity and discontinuity theories of the evolution of human cognition.

### *1.3. CONTINUITY OR DISCONTINUITY?*

The theory of a continuity among species was initially formulated more than a century ago by Darwin (1871/1992) and Romanes (1883), the two founders of comparative psychology. They assumed that there is no qualitative difference or discontinuity between nonhuman and human minds. As Darwin claimed, “the difference, great as it is, certainly is one of degree and not of kind.” (Darwin 1871/1992, p. 445).



The core assumption is that in cases in which other species exhibit behavior similar to our own, similar cognitive causes are at work. This is the argument by analogy (see also Boesch, 2005; McGrew, 2005; Suddendorf and Whiten, 2001; Van Lawick-Goodall, 1970). To the question as to why human tool use appears to be not completely similar to that of nonhuman animals, the answers generally highlight the importance of environmental resources and pressures (e.g., prey, predators), which could have led humans to use tools more frequently for survival (Boesch and Tomasello, 1998; De Beaune, 2008; Wynn, 1993). It has also been hypothesized that differences between human and primate tool use may reflect hominin enhancements of pre-existing primate prehension systems (Ambrose, 2001; Marzke et al., 1992; Napier, 1956, 1960; Van Schaik et al., 1999). The manipulation-based approach is highly inspired by these theories, by formulating that in humans the left IPL is central to store sensorimotor knowledge about how to manipulate familiar tools skillfully (e.g., Buxbaum, 2001; Buxbaum and Kalénine, 2010; Thill et al., 2013; Van Elk et al., 2014). In a way, the left IPL would store the same kind of information as that contained in the primate prehension system (see above). Simply, the difference is that this knowledge is not dedicated to know how to grasp objects to move them, but rather to know how objects have to be grasped in order to use them as tools. In this approach, the main difference between nonhuman primate and human tool use is more one of *degree* than of kind.

Proponents of the discontinuity theory stress that the argument by analogy has unfortunately led many scientists to document the similarities and downplay the differences between human and primate behavior (Penn et al., 2008; Povinelli et al., 2000). They advocate that it is not because two behaviors are analogous that similar psychological causes are at work, and suggest that those differences are not quantitative but qualitative in that they are the consequences of psychological diversity (Penn et al.,

2008; Tomasello et al., 2005). Thus, it has been argued that humans alone are able to understand observable regularities of the environment in terms of unobservable causal forces (gravity, force, shape, mass; e.g., Penn et al., 2008; Povinelli, 2000). The reasoning-based approach is akin to these theories by stressing that in humans the left IPL is critical to store mechanical knowledge necessary to reason about how tools and objects have to be used in a purposeful way (Goldenberg, 2013; Osiurak, 2014c; Osiurak et al., 2010). The corollary is that this *kind* of reasoning would be unique to humans. In broad terms, the main difference between nonhuman primate and human tool use is rather one of kind than of degree. In the following lines, we shall present in more detail how the neuropsychological literature has documented these two approaches.

### *1.4. THE MANIPULATION-BASED APPROACH*

The common definition of tool use put a special emphasis on manual actions, as if the main problem the user faces when using a tool is to know how to manipulate it but not to reason about how the tool has to interact with the object. This way of addressing the problem of the neurocognitive bases of human tool use strongly reflects the folk psychology. Since centuries, people needing to use tools to carry out everyday activities have been described as doing manual work, as if there was no need to reason when using tools, contrary to intellectual work. This belief is also profoundly ingrained in the minds of psychologists and neuroscientists alike. For instance, since the first descriptions of brain-damaged patients with tool use disorders in the late 1800's, the difficulties to use tools have been included in the terminology of apraxia<sup>4</sup>, thereby suggesting that tool use disorders are first and foremost a matter of gesture. During the last 50 years, several neuropsychological models have been formulated, wherein tool use disorders have been described within a general architecture also useful for

explaining difficulties in producing symbolic gestures (e.g., waving goodbye) or imitating meaningless postures (e.g., putting the back of the hand on the front) (Buxbaum, 2001; Cubelli et al., 2000; Geschwind, 1965; Heilman et al., 1982; Heilman and Watson, 2008; Rothi et al., 1991; Roy and Square, 1985; but see also Binkofski and Buxbaum, 2013; Buxbaum and Kalénine, 2010; Thill et al., 2013; Van Elk et al., 2014).

In line with this approach, it has been posited that central to tool use is the storage of sensorimotor knowledge about tool manipulation (i.e., manipulation knowledge), also called visuo-kinesthetic engrams (Heilman et al., 1982), action lexicons (Rothi et al., 1991), motor engrams (Buxbaum, 2001) or motor programs for tool use skills (Johnson-Frey et al., 2005). This long-term knowledge is supposed to contain the main parameters of the gesture associated with the manipulation of a tool (e.g., the hand posture, the position of the hand in the space, the amplitude of the movement executed by elbow joints) so that it provides a processing advantage by avoiding that each gesture is reconstructed *de novo* with each use. As discussed, manipulation knowledge might be the basis for an additional prehension system, only present in humans and specifically devoted to tool use. This knowledge has been associated with the left IPL (Binkofski and Buxbaum, 2013; Buxbaum, 2001; Buxbaum and Kalénine, 2010; Daprati and Sirigu, 2006; Gainotti, 2013; Heilman et al., 1982; Johnson-Frey and Grafton, 2003; Rizzolatti and Matelli, 2003; Rothi et al., 1991; Van Elk et al., 2014). The manipulation knowledge hypothesis has also been repeatedly stressed to account for the activation of the left IPL in neuroimaging studies (e.g., Boronat et al., 2005; Buxbaum et al., 2006; Grèzes and Decety, 2002; Hermsdörfer et al., 2007; Imazu et al., 2007; Johnson-Frey et al., 2005; Kellenbach et al., 2003; Kroliczak and Frey, 2009; Rumiati et al., 2004; Vingerhoets, 2008; Vingerhoets et al., 2009). Importantly, manipulation knowledge is supposed to be associated only with the conventional use of familiar tools, because it is based on the

experience we have with those tools. So, this knowledge cannot be useful to use novel tools or familiar tools in a non-conventional way. Moreover, it encodes egocentric relationships, namely, relationships between the user (and particularly his/her hand) and a tool. The manipulation knowledge hypothesis has found resonance in recent years, with the growing interest in the embodied cognition approach, suggesting that knowledge is constituted by information represented within the motor and sensory systems (Barsalou, 2008; Borghi, 2004; Borghi et al., 2013; Pezzulo et al., 2013a, 2013b; Mizelle and Wheaton, 2010; Thill et al., 2013).

As mentioned just above, manipulation knowledge encodes egocentric relationships (i.e., user-tool). The corollary is that it cannot help people to know with which object or in which context a specific tool can be used (i.e., tool-object, allocentric relationships). The storage of long-term, allocentric relationships has been suggested to be specific to the ventral system (e.g., Goodale and Milner, 1992; Milner and Goodale, 2006). In line with this, it has been assumed that the left temporal lobe would be particularly involved in conceptual knowledge about tool function (e.g., Buxbaum, 2001; Thill et al., 2013; Van Elk et al., 2014; see also Hodges et al., 2000). However, the precise localization of the area concerned is still a matter of debate. Neuropsychological studies in patients with semantic dementia, herpetic encephalitis or left brain damage have indicated the involvement of anterior portions of the left temporal lobe (e.g., Bozeat et al., 2002; Buxbaum et al., 1997; Hodges et al., 1999, 2000; Goldenberg and Spatt, 2009; Lauro-Grotto et al., 1997; Silveri and Cicarrelli, 2009; Sirigu et al., 1991). Although some neuroimaging studies have corroborated these findings (e.g., Canessa et al., 2008), others have stressed the potential role of the left posterior temporal lobe (Ebisch et al., 2007; see also Hermsdörfer et al., 2007; Tsuda et al., 2009; Vingerhoets, 2008) or have

failed to obtain any significant neural correlates (Boronat et al., 2005; Kellenbach et al., 2003).

Contrary to manipulation knowledge, the study of function knowledge in the field of human tool use has received far less attention in recent years. This might be explained by compelling evidence that function knowledge and real tool use (i.e., the actual use of a tool with its corresponding object) can be impaired independently from each other (Bartolo et al., 2007; Bozeat et al., 2002; Buxbaum et al., 1997; Forde and Humphreys, 2000; Goldenberg and Spatt, 2009; Hodges et al., 2000; Lauro-Grotto et al., 1997; Negri et al., 2007; Osiurak et al., 2008, 2009, 2011; Silveri and Ciccarelli, 2009). Given that function knowledge is neither necessary, nor sufficient for tool use, the intriguing question is what is the role of this knowledge? It has been posited that even if function knowledge is not central to tool use, it can be useful when manipulation knowledge is impaired, as a means of compensation (the multiple-routes-for-action hypothesis; e.g., Buxbaum, 2001; Buxbaum et al., 1997; Sirigu et al., 1991). The opposite is also true in that impaired function knowledge might be compensated by intact manipulation knowledge.

Finally, the manipulation-based approach assumes the existence of a production system that involves bilateral dorsal structures (particularly both superior parietal lobes [SPL] and IPS) and is specialized for acquiring objects on the basis of visual information about object shape, size and location that is constantly updated in function of the positions of objects with respect to retina, eye, head, torso, limb and hand (Buxbaum and Kalénine, 2010; see also Binkofski and Buxbaum, 2013; Buxbaum, 2001; Buxbaum et al., 2000; Heilman et al., 1986; Thill et al., 2013; Van Elk et al., 2014). In a way, the production system is very close to the primate prehension system mentioned above. Like manipulation knowledge, the production system encodes egocentric

relationships between the tool and the agent. It is also thought to support non-tool-use actions. In addition, even if it does not contain any long-term information about tool-use skills, it can receive input from the left IPL in order to adapt the tool-use representation created from manipulation knowledge to the situational constraints.

### *1.5. THE REASONING-BASED APPROACH*

The critical role given to manipulation in tool use by the manipulation-based approach may appear quite surprising for developmental psychologists, for whom tool use is viewed as an instance of problem-solving situation supporting by mechanical reasoning skills (e.g., Beck et al., 2011; Mounoud, 1996). The same is true in the field of animal cognition, wherein animal tool users have been shown to fail to solve tool-use situations that are relatively simple for young children (see above; e.g., Povinelli, 2000; Visalberghi and Limongelli, 1994). In this field, too, reasoning is viewed as central to tool behavior (Penn et al., 2008; Penn and Povinelli, 2007; but see also Wolpert, 2003). The reasoning-based approach has been elaborated in line with this perspective, mainly in the light of studies in left brain-damaged patients with tool use disorders (Goldenberg, 2009, 2013; Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak, 2013, 2014a, 2014c; Osiurak et al., 2009, 2010, 2011, 2013). The Four Constraints theory (Osiurak, 2014c) and the dialectical theory of human tool use (Osiurak et al., 2010; see also Osiurak and Badets, in press) correspond to the most recent versions of this approach. Orban and Caruana (2014) recently proposed a more precise neural model of this approach. Globally, this approach is based on the core assumption that, in everyday life, people use tools to solve problems (e.g., preparing a meal). To do so, they have to use mechanical knowledge to reason about how to solve them.

The reasoning-based approach has been developed because of theoretical and empirical limitations inherent to the manipulation-based approach. First, the multiple-routes-for-action hypothesis associated with the manipulation-based approach is questionable (see Osiurak, 2014c; Osiurak et al., 2010, 2011). According to this hypothesis, a patient with impaired manipulation knowledge is still able to select and use tools appropriately because function knowledge can compensate. However, function knowledge is supposed to store information about allocentric relationships, but not about how to manipulate a tool skillfully (i.e., egocentric relationship). To solve this theoretical problem, the manipulation-based approach assumes that the production system can be in charge of adapting the movements from input from the left temporal cortex (i.e., function knowledge). If so, the issue is why the human brain possesses manipulation knowledge that is not necessary for tool use? Likewise, impaired function knowledge can be compensated by intact manipulation knowledge. But, manipulation knowledge only encodes user-tool, egocentric relationships and is not thought to contain information about how to select and use the appropriate tools and objects (i.e., allocentric relationships). In other words, even if the multiple-routes-for-action hypothesis may appear very attractive at first glance, it suffers from theoretical problems that question the functional roles associated with function knowledge and manipulation knowledge.

Second, a significant body of evidence has indicated a strong link in left brain-damaged patients between the ability to actually use tools and to solve mechanical problems<sup>5</sup> (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Hartmann et al., 2005; Jarry et al., 2013, 2015; Osiurak et al., 2009, 2013; for reviews see Goldenberg, 2013; Osiurak, 2014c). Given that mechanical problem solving tasks involve the use of novel tools, it can be hypothesized that they put a heavy demand on executive functions.

However, mechanical problem solving tasks are not impaired after frontal lobe lesions (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009) and are not correlated with performance on “executive” tasks (e.g., Tower of London; Hartmann et al., 2005; Jarry et al., 2013). In addition, patients with dysexecutive syndrome perform relatively well on these tasks as compared with healthy subjects (Goldenberg et al., 2007). Rather, neuropsychological evidence suggests that a common cognitive process is involved in any use situation, whatever tools are familiar or novel. This process could be supported by the left IPL (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009). Neuroimaging studies have corroborated this finding (Peeters et al., 2009, 2013; Vingerhoets et al., 2011; see also Fridman et al., 2006; Orban and Caruana, 2014).

The strong link between real tool use and mechanical problem solving is difficult to explain within the manipulation-based approach. Given that the tools used in mechanical problem solving tasks are novel, manipulation knowledge cannot be activated to determine how to manipulate them skillfully. Moreover, to solve mechanical problems, people have to form an allocentric representation of the tool solution (e.g., a hooking action involves the relationship between a hook and something that can be hooked; see Osiurak, 2013). Manipulation knowledge encodes egocentric relationships, so it cannot be employed to form this allocentric representation. Another possibility is that function knowledge is the common process underlying both real tool use and mechanical problem solving, notably because this kind of knowledge contains information about allocentric relationships. However, neuropsychological evidence demonstrates that function knowledge and mechanical problem solving skills can be disrupted independently (Goldenberg and Spatt, 2009; Hodges et al., 1999, 2000; Jarry et al., 2013, Lesourd et al., in press; Spatt et al., 2002), ruling out this possibility.



On the basis of these findings, it has been assumed that human tool use might be supported by the ability to reason about the physical object properties (Osiurak, 2014c; see also Goldenberg, 2013; Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak et al., 2010, 2011, 2013). This reasoning is based on mechanical knowledge (e.g., cutting, lever, percussion), which corresponds to abstract knowledge about physical principles and, as a result, encodes allocentric relationships. This knowledge is viewed as abstract for two reasons. First, there is no overlapping between the physical reality and the technical reality. The same physical matter (e.g., glass) can possess distinct properties (resistant, sharp, transparent, etc.). Conversely, distinct physical matters (plastic, wood, metal, etc.) can have the same property (e.g., resistant). Moreover, the same physical matter does not always offer the property appropriate for a given action. For example, the lead of a pencil is friable when applied to paper but not to leather. Second, if people stored the properties of a given tool or object (e.g., friability of the lead of a pencil) in an absolute way, then they would not be able to transfer the mechanical principles they learned in a given situation to another one. Yet, as mentioned above, one of the specificities of human tool use lies in the transfer ability (Leroi-Gourhan, 1971; Martin-Ordas et al., 2008; Penn et al., 2008). In addition, this knowledge is supposed to be contained within the left IPL (e.g., Goldenberg, 2009, 2013; Goldenberg and Spatt, 2009; Osiurak, 2014c; Osiurak and Lesourd, 2014) and particularly within the area PF of the SMG (Orban and Caruana, 2014; see also Caspers et al., 2006, 2008; see also below). This contrasts with the manipulation-based approach according to which the left IPL is associated with manipulation knowledge.

The reasoning-based approach also offers another interpretation of the role of function knowledge located within the left temporal cortex. As discussed, the manipulation-based approach suggests that function knowledge is useful only when

manipulation knowledge is impaired, as a means of compensation. In this view, no prediction is emitted about the idea that function knowledge may be differentially involved in real (i.e., the actual use of a tool with its corresponding object) versus single tool use (i.e., the use of a tool presented in isolation). By contrast, according to the reasoning-based approach, function knowledge might help people to organize the search in memory in order to get tools and objects that are not here now. When people engage in everyday activities, all the needed tools and objects are not at hand in the workspace, forcing them to get them either before or during the activity. In this view, Osiurak (2014c, see also Osiurak et al., 2008, 2010, 2011) proposed that real tool use is mainly supported by mechanical knowledge, as demonstrated by the strong link between real tool use and mechanical problem solving. Nevertheless, function knowledge might be particularly involved in single tool use. When people are presented with a tool in isolation, they have to form a representation of the examiner's expectations. Even though function knowledge is based on personal experience, it is also a vehicle for social knowledge given that daily life activities are culturally shared. Therefore, people can access information from function knowledge to represent the examiner's expectations and, as a consequence, identify the category to which the tool belongs as well as a potential usage and an object with which it can be used. In line with this, patients with a selective impairment of function knowledge should encounter difficulties to show the conventional use of familiar tools presented in isolation, leading them to use mechanical knowledge to infer potential uses from the surrounding environment. However, performance should be improved by the addition of the corresponding object because mechanical knowledge enables to infer a potential use. Neuropsychological evidence supports this view.

Osiurak et al. (2008, see also Sirigu et al., 1991) described a patient (MJC) with left temporal lobe lesions and bilateral frontal lobe lesions following a closed-head injury. She had a severe semantic impairment and met difficulties in single tool use tasks. Interestingly, MJC used the desk to demonstrate how to use the tools. For example, she used a screwdriver as a kind of gimlet, saying: "One can make a hole with it". The performance was normal when both the tool and its corresponding object were present (real tool use) as well as when she had to show how to use familiar tools in a non-conventional way. Other studies in patients with a selective impairment of function knowledge have corroborated this observation by documenting a strong relationship between function knowledge and single tool use as well as intact ability to use novel tools (e.g., Hodges et al., 2000; Silveri and Ciccarelli, 2009; Sirigu et al., 1991; Spatt et al., 2002; for a review, see Osiurak et al., 2011; see also Lesourd et al., in press).

The reasoning-based approach posits that the movements associated with manipulation are reconstructed de novo on the basis of (1) the mental simulation of the tool-use action generated by mechanical knowledge<sup>6</sup> and (2) on-line information about the physical environment and the position of the body in the space. This reconstruction would take place within the production system, a system very close to the aforementioned primate prehension system. So, the production system might be essentially supported by the IPS (phAIP and DIPSA; see Orban and Caruana, 2014). This perspective is very close to the one proposed by the manipulation-based approach. However, contrary to the manipulation-based approach, the production system is thought here as the only system that encodes egocentric relationships between the user and the tools and objects. Besides, Orban and Caruana (2014; see also Peeters et al., 2009, 2013) proposed that an anterior portion of the left SMG (aSMG) might play a critical role by integrating the information coming from phAIP (i.e., production system)

and from the area PF of the left SMG (i.e., mechanical knowledge). In this view, the left aSMG might send some biasing signals to phAIP to favor the selection of the handgrip (i.e., egocentric relationship) that best suits the correct use of the tool generated by mechanical knowledge (i.e., allocentric relationship).

### *1.6. OVERVIEW OF THE PRESENT STUDY*

A significant body of literature has demonstrated considerable functional homologies between the human and the primate brain with regard to prehension skills. These homologies can explain why both humans and nonhuman primates are able to manipulate objects and, as a result, to use tools. However, despite this similarity, human tool use appears to differ from nonhuman primate tool use in several respects (i.e., frequent use, wide repertoire of tools, use of secondary tools, and transfer abilities). These differences go along with the existence of evolutionary new neural substrates peculiar to humans within the left IPL/SMG. The manipulation-based approach claims that this area might be responsible for the storage of sensorimotor knowledge about tool manipulation, a perspective close to the continuity theory by considering that the main difference between human and nonhuman tool use is more one of degree than of kind. By contrast, for the reasoning-based approach, this area might be involved in the ability to reason about physical object properties on the basis of mechanical knowledge. This approach is more akin to the discontinuity theory by suggesting that the main difference is of kind rather than of degree.

As discussed so far, most of our understanding of the neurocognitive bases of human tool use has come from the studies of brain-damaged patients with tool use disorders. Although these studies have been fruitful to generate a certain number of theoretical proposals, they are generally insufficient to characterize with a great deal of

precision the neural substrate associated with tool use skills. Particularly, the role of the left IPL remains a matter of debate, notably because no less than seven cytoarchitectonic areas have been identified within this area. Five of them (PfoP, PFt, PF, PFm, and PFcm) are located approximately at the position of BA 40 on the SMG, the remaining two areas (PGa and PGp) approximately cover the region of BA 39 on the angular gyrus (Caspers et al., 2006, 2008; Zilles et al., 2002). As discussed by Orban and Caruana (2014), special attention has to be paid to PF (mechanical knowledge) as well as aSMG (integration area), which largely overlaps with cytoarchitectonic area PFt (Caspers et al., 2008; Peeters et al., 2013). Interestingly, many neuroimaging studies have been carried out on the topic in the last decade. So, even if no theoretical model of human tool use has been formulated on the sole basis of these studies, they offer a good opportunity to reach this level of precision.

To sum up, the goal of the present review is to examine the predictions derived from the manipulation-based and the reasoning-based approach by conducting a comprehensive meta-analysis on functional neuroimaging data, based on activation likelihood estimation (Eickhoff et al, 2012). Since the development of neuroimaging techniques and the subsequent increase in the number of functional imaging studies, the scientific community has been faced with the need to synthesize results from the literature. Therefore we aim to provide here an overview of previous experiments on the functional brain activity related to tool use. We wished to integrate functional neuroimaging results across a large number of selected studies through a quantitative meta-analytical approach. To do so, we used a coordinate-based meta-analysis (CBMA, Chein et al. 2002; Turkeltaub et al., 2002) with the aim of identifying anatomical locations where an effect can be observed consistently across experiments.

The numerous published neuroimaging studies concerning human tool use have employed a wide range of tasks and task comparisons, also called contrasts. These contrasts can be qualified as general or specific (see Binder et al., 2009). A general contrast is one between a condition that elicits cognitive processes involved in tool use and a “baseline” condition (e.g., performing a meaningless gesture). A specific contrast entails a comparison between two conditions involving tool-use cognitive processes (e.g., conditions with correct manipulation versus conditions with incorrect manipulation). In this review, we only included general contrasts, because the number of specific contrasts of the same kind was too low to run a meta-analysis. A critical criterion concerned the nature of the task. In this review, we included both use and non-use tasks. Use tasks correspond with tasks wherein participants have to imagine, plan or execute tool-use actions either with the object in hand (real use) or not (pantomime). In non-use tasks, participants are not asked to perform or even imagine tool-use actions. Nevertheless, they are confronted with tool stimuli and have to decide, for instance, whether the tool-use action shown is correct or not (complex observation) or simply observe the tool-use action while performing an *n*-back memory task (simple observation). We focused on data obtained with visual objects to avoid the involvement of language-related neural circuit. Thus, all the studies using words and silent reading were excluded from the analysis. Only two studies using words but not visual objects were included because the task was to determine whether the tools shared the same action, gesture or context. On the basis of these criteria, the general contrasts (hereafter referred to as conditions) included in the present meta-analysis were as follows.

The first category of conditions only concerned “non-use tasks”. We identified three sub-types for this first category.

- **Action.** The task focuses on the understanding of the action made by the tool with the object (allocentric relationship; e.g., Is it correct to use this pair of scissors to cut this sheet of paper? Bach et al., 2010). Here, no judgment has to be made on the appropriateness of the manipulation.

- **Gesture.** The task is to determine whether the manipulation is correct or not (egocentric relationship), without taking into account the action made by the tool with the object (e.g., Does this hand posture – for instance a pinch posture – matches the action goal – for instance, throwing a dart? Vingerhoets et al., 2013).

- **Context.** The task is to determine with which object or in which context a given tool can be used (allocentric relationship; e.g., Can these two tools – poultry shears and hand spiral beater – be used in the same context? Canessa et al., 2007).

The second category of conditions was based on the nature of the tools presented, whatever the task required (both use and non-use tasks). Two sub-types of conditions were concerned.

- **Familiar.** The task focuses on the conventional use of familiar tools (e.g., pantomiming the use of *a pair of scissors*; Vingerhoets et al., 2013).

- **Unfamiliar.** The task includes novel tools or familiar tools used in a non-conventional way (e.g., pantomiming the use of *screwdriver-like tool*; Vingerhoets et al., 2013).

Finally, the third category only included use tasks. Three sub-types could be identified.

- **Planning.** This corresponds to tasks wherein participants have to imagine using a tool or to a specific condition of the tasks where they have to plan a subsequent tool-use action (e.g., imagining both grasping and using a toothbrush; Vingerhoets et al., 2009).

- **Execution.** This corresponds to a specific condition of a task where participants execute the tool-use action (e.g., performing the real tool-use actions, such as using a hammer to pound a nail; Hermsdörfer et al., 2007).

- **Planning/Execution.** Here, the distinction between planning and execution is not made (e.g., transporting pins with chopsticks; Tsuda et al., 2009).

On the basis of these different categories of conditions, several predictions can be emitted from each approach that will be detailed in the following lines (**Table 1**).

< Insert Table 1 about here >

(1) The role of the left IPL diverges according to the two approaches. To explore this, we compared data from studies exploring how people judge the appropriateness of use gestures (GESTURE) versus how they understand the actions performed by tools (ACTION). The manipulation-based approach predicts that GESTURE conditions should show an activation of left IPL/SMG (e.g., Buxbaum, 2001; Buxbaum and Kalénine, 2010; Thill et al., 2013; Van Elk et al., 2014). By contrast, the reasoning-based approach predicts that the left IPL (particularly the area PF of SMG) should be only involved in ACTION conditions (e.g., Goldenberg, 2013; Orban and Caruana, 2014; Osiurak, 2014c). Moreover, the reasoning-based approach assumes that only the production system encodes tool-hand interaction (i.e., egocentric relationship). So, in line with this, this approach predicts that the IPS (Orban and Caruana, 2014) should be more involved in GESTURE conditions.

(2) The manipulation-based approach remains silent about the strong link between real tool use and mechanical problem solving. Consequently, it does not predict that FAMILIAR and UNFAMILIAR use of tools should involve different cerebral regions (e.g., Buxbaum, 2001; Van Elk et al, 2014). At best, it can be expected that both the left IPL (i.e., manipulation knowledge) and the left temporal cortex (i.e., function knowledge) are preferentially activated by FAMILIAR use as compared to UNFAMILIAR use. By contrast, the reasoning-based approach suggests that only left temporal lobe regions should be more involved in FAMILIAR use than in UNFAMILIAR use (e.g., Goldenberg, 2013; Osiurak, 2014c). This rationale is based on the idea that the left temporal lobe contains function knowledge that is of particular interest for familiar tools (see above). Moreover, the left IPL (particularly the area PF of SMG; see Orban and



Caruana, 2014) should be more activated in UNFAMILIAR use than in FAMILIAR use, because only mechanical knowledge is involved when people are confronted with unfamiliar use.

(3) Both the manipulation-based and the reasoning-based approach assume that, besides the areas supporting the production system (mainly the left IPS because the participants included were right-handed), the left IPL should be particularly involved in PLANNING tool-use actions, because manipulation knowledge or mechanical knowledge is thought to be the basis for the conception of intended actions. Interestingly, according to the reasoning-based approach, the left aSMG should be specifically activated in PLANNING because of its integrative role (Orban and Caruana, 2014). In addition, both approaches agree on that the production system should be engaged in EXECUTION.

## **2. METHODS**

### *2.1. SELECTION OF STUDIES*

Candidates for inclusion were initially identified using a search through the following databases: PubMed and PsycInfo. We restricted our search to studies published between January 2000 and February 2014. To narrow our search we used the logical conjunction of keywords: (“brain mapping” OR “functional magnetic resonance imaging” OR “fMRI” OR “positron emission tomography” OR “PET”) AND (“tool use” OR “object use” OR “tool manipulation” OR “object manipulation” OR “praxis” OR “tool recognition”). This search returned 302 studies at the date of 03/03/2014. We evaluated candidate papers for inclusion, according to a series of selection criteria:

- (1) Theoretical papers and reviews were excluded.
- (2) Papers must use functional magnetic resonance imaging or positron emission tomography as imaging modality.

- (3) They were comprised of neurologically healthy and adults participants.
- (4) Relevance of the tasks used in relation to our goal. As explained above, both use and non-use tasks were considered. Moreover, only studies using visual stimuli were included with the exception of two studies using words (see above).
- (5) Neuroimaging results must be based on whole-brain scanning. Regions of interest analyses were therefore excluded from our selection.
- (6) The complete list of activation peaks (i.e., foci) with their coordinates must be reported in a stereotactic space.
- (7) We selected only reported results corrected for multiple comparisons with a statistical significance threshold of  $p < 0.05$  or, for a small part of the selected results uncorrected data thresholded at  $p < 0.005$ . We did require that the same threshold be applied uniformly across the whole brain. Results derived from ROI (Region of Interest) or SVC (Small Volume Correction) analyses were excluded even if spatial coordinates were provided. Because our meta-analytic statistical tests assumed that foci were spatially randomly distributed across the whole brain under the  $H_0$  assumption, it was important to avoid experimenter-induced bias in the locations at which effects could be identified.

Two authors independently conducted the literature search, assessed the methodological quality of the included trials and screened the studies for the aforementioned inclusion criteria. In case of disagreement between the reviewers, consensus discussion resolved the conflict. This quality assessment resulted in 35 studies and 60 experiments fulfilling our criteria, involving a total of 916 participants (all right-handed) and 642 peaks of activation (participants that took part in more than

one experiment were only counted once). These studies are described in more detail in **Table A** (see **Supplementary Material**).

## *2.2. DATA ANALYSIS*

Our meta-analysis was conducted using the revised version (Eickhoff et al., 2009, 2012) of the activation likelihood estimation method (ALE; Turkeltaub et al., 2002), as implemented by the GingerALE 2.3 software (<http://www.brainmap.org/ale/>).

ALE is a coordinate-based method for pooling neuroimaging studies results. The objective of the ALE method is to reveal brain regions that are reliably activated across studies. Based on the stereotactic coordinates of activation peaks collected in each study included in the meta-analysis, this method estimates at each voxel the probability that an activation focus truly exists within that given voxel, under Gaussian assumptions on spatial uncertainty. The voxel-wise union of probabilities over all activation foci permits to create an ALE map. Clusters of significantly high ALE are the significantly overlapping clusters of activation, revealing a convergence across included imaging studies.

To perform this meta-analysis, coordinates of every significant activation peak for each included condition were collected. The meta-analysis was performed in the Talairach reference space (Talairach and Tournoux, 1988). Coordinates that were reported in the Montreal Neurological Institute (MNI) space were first converted to Talairach space using the *icbm2tal* transformation (Lancaster et al., 2007) implemented in the GingerALE software. For each included study and at each voxel, ALE computes the probability that an activation focus lies at this voxel location. To account for spatial uncertainty, foci are considered to be the centres of three-dimensional Gaussian probability density functions. Full widths at half maximum of 3D Gaussian functions

(FWHM) are dependent on the sample size: Studies with a larger sample size therefore have a stronger impact on the results.

The probability distributions of all foci in the considered experiment are combined in a Modelled Activation (MA) map. The union of all MA maps for all the experiments included in the meta-analysis allows computing an ALE score on a voxel-by-voxel basis. This score quantifies the likelihood of convergent activations at each voxel across all included studies. Significance tests are conducted by comparing the ALE scores with a null distribution obtained from the same number of randomly generated activation foci. At the condition level, all foci from a generic contrast are pooled together: The resulting non-parametric  $p$ -values are then thresholded at a false discovery rate (FDR) of  $p < 0.01$ , and only clusters of a minimum volume of  $500 \text{ mm}^3$  are reported. For specific contrasts between two conditions (subtraction analysis), ALE individual maps corresponding to each condition were thresholded at a level of  $p < 0.05$  (FDR corrected) as was the pooled map for both conditions. The contrast analysis was then performed on these maps and the results were reported with a  $p$ -value threshold set to  $p < 0.05$  and minimum cluster sizes set to  $200 \text{ mm}^3$  (Laird et al., 2005; Turkeltaub et al., 2012). The resulting thresholded ALE maps were visualized on fiducial and flat-map representations of a standardized brain atlas (PALS-B12: Population-Average, Surface- and Landmark-based human cortical atlas; Van Essen, 2005), using Caret, version 5.65 (<http://brainmap.wustl.edu/caret.html>; Van Essen and et al., 2001).

### **3. RESULTS**

#### *3.1. OVERVIEW*

We identified the “common tool-use circuit” as defined by the regions of overlap between all the studies included. The results of the meta-analysis conducted are given in

**Fig. 1.** They show that a set of brain regions of the left hemisphere was consistently recruited, namely, the IPL (PFt/aSMG, PF), the IPS (phAIP, DIPSA, medial dorsal intraparietal sulcus [DIPSM], ventral intraparietal sulcus [VIPS]), the posterior middle temporal gyrus (pMTG), the posterior inferior temporal cortex (pITC), the occipital cortex (LOC and MT cluster), the premotor cortex (vPMC and dPMC), the middle frontal cortex (BA46) and the pre- and post-central cortex (PreC, PostC). Activation also occurred in the right hemisphere (pMTG, vPMC). This tool-use circuit is largely consistent with previous findings obtained in right-handed participants (e.g., see Johnson-Frey, 2004; Lewis, 2006; Orban and Caruana, 2014).

< Insert Fig. 1 about here >

### *3.2. ACTION, GESTURE AND CONTEXT*

The first category of conditions concerned non-use tasks, wherein participants are confronted with tool stimuli without having to perform or imagine tool-use actions. Three types of tasks were identified, namely, ACTION, GESTURE and CONTEXT. The results of the meta-analyses conducted separately for each task are illustrated in **Fig. 2**. For ACTION, activation occurred only in the left hemisphere, in the IPL (PF), the vPMC and the middle frontal cortex (BA46; **Fig. 2a**). The left IPS (phAIP, DIPSA, DIPSM), the left pITC, and the left occipital cortex (BA19) were more robustly activated for GESTURE (**Fig. 2b**). Finally, the left occipital cortex (LOC, BA19) and the left frontal cortex (BA46, BA11) were more activated by CONTEXT (**Fig. 2c**).

< Insert Fig. 2 about here >

### 3.3. FAMILIAR AND UNFAMILIAR

The second category of conditions was based on the nature of the tools presented, whatever the task required. Two types of stimuli were identified, namely, FAMILIAR and UNFAMILIAR. The results of the meta-analyses conducted separately for each type of stimulus are displayed in **Fig. 3**. A left-lateralized brain network was recruited for FAMILIAR (**Fig. 3a**). A smaller, left-lateralized network was found for UNFAMILIAR, including the IPL (PF, PFm, PFt/aSMG), the IPS (phAIP, DIPSA), the premotor cortex (vPMC and dPMC) and the PreC (**Fig. 3b**).

Statistical comparisons were conducted to identify brain regions responding more reliably to one type of stimulus relative to the other (**Fig. 3**). Specifically, we found that the left temporal cortex (pMTG, posterior superior temporal gyrus [pSTG]), the left SPL, the left occipital cortex (MT cluster), and the left cingular gyrus (BA24) were more likely to be activated by FAMILIAR as compared to UNFAMILIAR (**Fig. 3c**). A left-lateralized network, including the IPL (PF, PFm, PFt/aSMG, BA39), the IPS (particularly phAIP), the premotor cortex (vPMC and dPMC) and the PreC was more reliably activated by UNFAMILIAR than FAMILIAR (**Fig. 3d**).

< Insert Fig. 3 about here >

### 3.4. PLANNING AND EXECUTION

The third category of conditions only concerned use tasks and included experiments wherein only planning/imaging (PLANNING), only execution (EXECUTION) or both planning and execution (PLANNING/EXECUTION) of tool-use actions were assessed. The results are given in **Fig. 4**. As can be seen, the left IPS (phAIP, DIPSA), the left premotor cortex (dPMC, vPMC) and the left PreC were more likely to be activated for

PLANNING (**Fig. 4a**). Concerning PLANNING/EXECUTION, the left IPL (PFt/aSMG), the IPS (DIPSA, VIPS), the left SPL, the left occipital cortex (MT cluster), the left premotor cortex (dPMC, vPMC), the left middle frontal cortex (BA46), the left PreC, and the left PostC were more reliably activated (**Fig. 4b**). Finally, the left IPL (PF), the left IPS (phAIP, DIPSA), the left pMTG, the left premotor cortex (dPMC, vPMC), the left middle frontal cortex (BA46), and the left PostC were preferentially recruited for EXECUTION (**Fig. 4c**).

< Insert Fig. 4 about here >

#### 4. DISCUSSION

The main goal of the present review is to shed a new light on the neurocognitive bases of human tool use. Two main approaches exist in the literature. The manipulation-based approach assumes that the storage of manipulation knowledge is central to tool use. This knowledge is supposed to be located within the left IPL. This approach is somewhat akin to continuity theory by suggesting that manipulation knowledge is of the same kind as motor schemas also presented in nonhuman primates within the primate prehension system. By contrast, the reasoning-based approach is close to discontinuity theories by positing that humans alone possess mechanical knowledge allowing them to reason about object physical properties. This knowledge is also supposed to be contained within the left IPL. In the present review, we tested the predictions derived from each approach by conducting a comprehensive meta-analysis on functional neuroimaging data. In the following lines, we will address each of these predictions in turn in the light of our results. Then, we shall discuss how our findings offer new insight into the understanding of the different neurocognitive processes involved in human tool use.

### *4.1. EXAMINATION OF THE PREDICTIONS*

#### ***4.1.1. Action, gesture, and context***

According to the manipulation-based approach, manipulation knowledge located in the left IPL supports the ability to know how to manipulate a tool correctly (egocentric relationship, GESTURE conditions) (Buxbaum, 2001; Binkofski and Buxbaum, 2013; Rothi et al., 1991; Van Elk et al., 2014). In line with this, preferential activation of the left IPL should be expected for GESTURE. This prediction is not confirmed by our results given that the left IPL/SMG (PF) was more likely to be activated by ACTION and the left IPS (phAIP, DIPSA, DIPSM) by GESTURE. Two possibilities can be proposed to reconcile this discrepancy. The first is that manipulation knowledge is located within the left IPL but is strongly involved in ACTION, but not GESTURE. This possibility is delicate given that the difficulties of judging the appropriateness of manipulation postures has been considered to be the hallmark of left brain-damaged patients with impaired manipulation knowledge (e.g., Buxbaum and Saffran, 2002; Buxbaum et al., 2003, 2005; Rothi et al., 1985, 1986, 1991). The second is that manipulation knowledge is located within the left IPS, but this possibility is also inconsistent with the manipulation-based approach. Indeed, the IPS is supposed to belong to the production system. This system is devoted to on-line motor control and is not thought to contain long-term information about tool-use skills (Buxbaum, 2001; Buxbaum and Kalénine, 2010). So, the activation of the left IPS in GESTURE conditions is at odds with the manipulation-based approach.

A related finding concerns the involvement of the left pITC in GESTURE. Based on results from left brain-damaged patients, Buxbaum et al. (2014) recently proposed that manipulation knowledge might be divided into two components. The first component



encodes specific information about kinematic features (e.g., amplitude and timing) and is stored within the left IPL, whereas the second contains information about postural features (e.g., hand or arm positioning) and is located within the left pMTG and pITC. In line with this, it might be suggested that the activation observed in the left pITC in GESTURE conditions demonstrates the existence of the postural component of manipulation knowledge. However, Buxbaum et al. (2014) did not suggest that some of the tasks generally used in GESTURE conditions are more likely to assess either the postural or the kinematic component of manipulation knowledge. Therefore, it can be posited that both the left IPL and the left pMTG/ITC should be activated in GESTURE conditions. As discussed, we did not find that the left IPL is particularly activated in these conditions, questioning the distinction drawn by Buxbaum et al. (2014) between postural and kinematic components. So, the intriguing issue is what is the role of the left pITC in the GESTURE conditions of the present study as well as in the tasks used by Buxbaum et al. (2014) with left brain-damaged patients. We will come back later to this point (see Section 4.2.2.)

Having said that, the question is now whether our findings confirm the predictions emitted by the reasoning-based approach. According to this approach (e.g., Goldenberg, 2013; Osiurak, 2014c; Osiurak et al., 2010), mechanical knowledge is stored in the left IPL and is central to understand how tools and objects work together (i.e., allocentric relationship). Orban and Caruana (2014) even suggested that the area PF of the left SMG might be critical for this kind of knowledge. This prediction is fully supported by the strong involvement of the left PF for ACTION. In addition, this approach suggests that the ability to carry out an appropriate hand posture is supported by the production system probably located within the IPS (see Orban and Caruana, 2014). The rationale is that only the production system is in charge of encoding tool-hand interactions (i.e.,

egocentric relationships). Our findings corroborated this prediction by indicating that the left IPS (phAIP, DIPSA, DIPSM) are preferentially involved in GESTURE. In sum, our results are relatively consistent with the reasoning-based approach by making a clear distinction between the processing of egocentric, tool-hand relationships (IPS) and the processing of allocentric, tool-object relationships (left ASMG/PF). A tricky point, nevertheless, is that this approach does not predict any involvement of the pITC in GESTURE conditions. As mentioned above, we will come back later to this point (see Section 4.2.2.).

Even if the manipulation-based and the reasoning-based approach differ as to the theoretical interpretation given to function knowledge, both of them assume that the left temporal cortex is the neural basis of this knowledge. Our results are however at odds with this prediction because no specific activation of the left temporal cortex was found in CONTEXT. This finding is in line with previous studies indicating that the neural basis of function knowledge is difficult to locate with neuroimaging (e.g., Boronat et al., 2005; Kellenbach et al., 2003). This contrasts with lesion studies that have repeatedly shown that patients with damage to the left temporal cortex have impaired function knowledge. Perhaps, the activations observed in neuroimaging studies such as those reported here are epiphenomenal or supportive rather than critical (for a somewhat similar argument, see Buxbaum et al., 2014). Note that activation of the left LOC was observed in CONTEXT. This result is somewhat consistent with Orban and Caruana (2014) who suggested that function knowledge might be supported by both the left PMTG and LOC. Nevertheless, their model posits that the left LOCT but not the left LOCa and LOCo would be associated with function knowledge. By contrast, our findings seem to show activation of the left LOCa and LOCo, but not of the left LOCT (**Fig. 2c**). In sum, future

research is clearly needed to specify the specific location of function knowledge in the human brain.

### ***4.1.2. Familiar and unfamiliar***

The manipulation-based approach considers that both manipulation knowledge and function knowledge are useful for determining how familiar tools have to be used. It has even been suggested that manipulation knowledge might be activated automatically (i.e., without any intention) from the mere observation of a familiar tool (e.g., Buxbaum and Kalénine, 2010; Thill et al., 2013). Therefore, it should be expected that the cerebral regions underlying both manipulation knowledge and function knowledge (i.e., the left IPL and the left temporal cortex, respectively) are preferentially activated by the visual observation of familiar use as compared to unfamiliar use. Our findings are partially at odds with these predictions given that we observed that only the pMTG and the pSTG are activated for FAMILIAR (see FAMILIAR > UNFAMILIAR). In addition, we found that the left IPL (PF, PFm, PFt/aSMG) is more reliably involved in UNFAMILIAR (see UNFAMILIAR > FAMILIAR). One way of interpreting this finding is that unfamiliar tool use is based on manipulation knowledge, but not on function knowledge. However, manipulation knowledge is thought to contain information about how to manipulate familiar tools in a conventional way, but not on how to use unfamiliar tools or familiar tools in a non-conventional way. In sum, the manipulation-based approach fails to explain the pattern of results obtained for these conditions.

For the reasoning-based approach, mechanical knowledge located within the left IPL (PF; Orban and Caruana, 2014) is useful for using tools whatever they are familiar or unfamiliar. Nevertheless, unfamiliar tool use might require a stronger activation of mechanical knowledge (Osiurak, 2014c). This prediction is confirmed by our results,

showing a specific involvement of the left IPL (PF, PFm, PFt/aSMG) for UNFAMILIAR (see also UNFAMILIAR > FAMILIAR). In addition, the specific activation of the left PMTG for FAMILIAR (see FAMILIAR > UNFAMILIAR) is consistent with the idea that function knowledge is involved only when tools are familiar. In broad terms, these findings provide support for this approach.

### ***4.1.3. Planning and execution***

Results concerning EXECUTION are relatively consistent with the literature in that we observed activation of most of the brain areas involved in the production system (phAIP, DIPSA, SPL, vPMC, dPMC, SPL). Reliable activation of the left IPS (phAIP, DIPSA) was found in PLANNING and PLANNING/EXECUTION. This result is consistent with both approaches, confirming that production system (i.e., primate prehension system) is systematically recruited to plan the appropriate handgrip in tool-use actions. We also found that the left IPL (PFt/aSMG) was activated in PLANNING/EXECUTION but not PLANNING. One possibility to account for this discrepancy is that, in most of the studies in PLANNING, participants had to produce pantomimes or to imagine tool-use actions without subsequent execution. This could have led participants to pay a greater attention as to how to grasp the tool (i.e., egocentric relationship) than how to use the tool with the object (i.e., allocentric relationship), notably when no object was present as in the case of pantomime production. The corollary is that the production system (i.e., prehension primate system) could have been preferentially recruited in order to plan the correct handgrip. By contrast, in most of the studies included in PLANNING/EXECUTION, participants had to plan not only how to grasp the tool but also how to use the tool with the object. So, in this condition, participants could have been more likely to plan both the correct handgrip (i.e., egocentric relationship) and the

mechanical interaction between the tool and the object (i.e., allocentric relationship). This possibility is consistent with the reasoning-based approach and our results, because we found activation of the left aSMG, a brain region that could be in charge of integrating egocentric and allocentric relationships (Orban and Caruana, 2014). According to this approach, we should also expect activation of the area PF since this area is supposed to support the mental creation of the appropriate mechanical interaction between a tool and an object (i.e., mechanical knowledge). However, our analysis did not confirm this prediction.

### *4.2. THE TOOL-USE NETWORK*

From the discussion so far, the reasoning-based approach appears to be more successful than the manipulation-based approach to account for the neurocognitive basis of human tool use. In the following lines, we will come back on the main cerebral areas identified by our meta-analysis and discuss their potential functional role in the light of the reasoning-based approach (see **Fig. 5**).

< Insert Fig. 5 about here >

#### ***4.2.1. Parietal cortex***

Concerning the left IPL, we identified two regions of interest, namely, PF and PFt/aSMG. The left PF was preferentially activated in ACTION and UNFAMILIAR, namely conditions where participants have to focus on how a tool has to be used appropriately with an object (i.e., allocentric relationship). These results provide support for the idea that mechanical knowledge might be located within the left IPL/SMG (Osiurak, 2014c), and particularly within the area PF (Orban and Caruana, 2014).

The left PFT/aSMG was not activated in ACTION and GESTURE, namely, situations where participants have to focus on either the mechanical interaction between the tool and the object (i.e., allocentric relationship) or the handgrip to be performed (i.e., egocentric relationship). However, activation of this area was clearly found in PLANNING/EXECUTION, where participants have to plan both the handgrip and the mechanical interaction. Taken together, these findings confirm the idea that the left PFT/aSMG might be an integration area between information coming from IPS (i.e., production system) and information coming from PF (i.e., mechanical knowledge; see Orban and Caruana, 2014; see **Fig. 5**).

Concerning the left IPS, we found an activation of this area (phAIP, DIPSA) in GESTURE, PLANNING and PLANNING/EXECUTION. As explained above, phAIP and DIPSA together represent the equivalent of monkey AIP and, as a result, are heavily involved in the grasping component of the primate prehension system (see Orban et al., 2006; Vanduffel et al., 2014). So, it is not surprising that these areas are preferentially recruited in PLANNING and PLANNING/EXECUTION. Moreover, they might also play a key role in terms of motor simulation, by allowing people to anticipate egocentric, tool-hand interactions (see Jeannerod, 1994). This rationale is based on the finding that both phAIP and DIPSA were activated for GESTURE, when no actual hand movement is planned or executed.

### ***4.2.2. Temporal cortex***

We found, in several conditions, activation of the left posterior temporal cortex (pMTG, pITC). The most likely hypothesis is that this region plays a critical role for the storage of function knowledge. This hypothesis would have been fully supported if we had observed that these areas are also recruited in CONTEXT conditions. Unfortunately,

we did not find this pattern. But, as discussed above, this lack of results can be explained by the tasks used to explore this aspect in neuroimaging experiments (see also Boronat et al., 2005; Kellenbach et al., 2003). Again this contrasts with evidence from neuropsychological literature that has shown a link between left temporal lobe lesions and impaired function knowledge (e.g., Goldenberg and Spatt, 2009; Hodges et al., 2000).

As suggested by the reasoning-based approach, the key role of function knowledge might be to enable people to organize their search in memory in order to get tools or objects that are not here now (see Osiurak, 2014c; Osiurak et al., 2008, 2010). In other words, function knowledge might be useful to store the usual function associated with a tool or an object in order to save them for future uses (Vaesen, 2012). This hypothesis can explain why the left pMTG and pSTG were more likely to be activated in FAMILIAR conditions.

A tricky point concerns the activation of pITC in GESTURE. One possible interpretation is that it is involved in the storage of manipulation knowledge, as suggested by Buxbaum et al. (2014). However, as explained above, this interpretation is highly debatable. Osiurak and Le Gall (2014) provided an alternative explanation to Buxbaum et al.'s (2014) results. In their study, Buxbaum et al. (2014) asked left brain-damaged patients to pantomime the use of tools presented in isolation. Given the evidence indicating a strong link in patients with left temporal lobe lesions between single tool use and function knowledge (e.g., see Hodges et al., 2000), it can be hypothesized that the presentation of a tool in isolation creates an additional demand on function knowledge to determine the potential usage. This can explain why they found an association between pantomime production and left posterior temporal lobe lesions.

### **4.2.3. Frontal cortex**

Three regions of the left frontal cortex were identified, namely, the middle frontal cortex (BA46), the vPMC and the dPMC. The left middle frontal cortex (BA46) was robustly activated in ACTION. Interestingly, the left vPMC was also involved in ACTION. One possibility to account for this activation is that the left middle frontal cortex (BA46) and the vPMC participate in the storage of mechanical knowledge. This possibility is however delicate because both real tool use and mechanical problem solving are generally not impaired following left frontal lobe lesions (e.g., De Renzi and Lucchelli, 1988; Goldenberg and Hagmann, 1998). Recently, Goldenberg and Spatt (2009) reported a link between damage to the left frontal cortex and real tool use/mechanical problem solving. Nevertheless, only patients with exclusively parietal lesions or fronto-parietal lesions scored below the normal range on both tasks. In sum, frontal lobe lesions alone were not sufficient to cause major impairment, ruling out the idea that mechanical knowledge might be located within the left frontal cortex<sup>7</sup>. Another possibility is that this activation reflects the planning of manual movements associated with tool use (e.g., Canessa et al., 2008; Grèzes and Decety, 2002; Kellenbach et al., 2003). Our results do not support this possibility given that the activation was found for ACTION conditions wherein no hand movement was required.

Evidence has indicated that the left vPMC subserves more abstract aspects of action control than selection and planning of hand movements (e.g., Petrides, 2005). The left inferior frontal cortex is also known to be involved in high-level executive function (Koechlin and Summerfield, 2007). In addition, one of the specificities of executive functions is the ability to organize a series of actions into a coherent sequence (Shallice, 1982). Therefore, in this frame, it can be hypothesized that these frontal areas might be



useful for maintaining over the time and organizing the different mental simulations of the tool-use actions generated by the left IPL (see Goldenberg and Spatt, 2009 for a somewhat similar interpretation).

Finally, dPMC was observed to be activated when participants have to plan and execute real tool-use actions (PLANNING, PLANNING/EXECUTION and EXECUTION), but not when no real tool-use action is required (ACTION, GESTURE, and CONTEXT). So, one possibility is that dPMC is mainly involved when people have to plan/execute real motor movements (i.e., egocentric relationship), but not when they have to conceive the corresponding tool-use actions (i.e., allocentric relationship). Consistent with this, it has been suggested that dPMC is involved in motor timing and motor sequencing (Bortoletto and Cunnington, 2010) as well as with the motor simulation of action (Stadler et al., 2011; see also Vingerhoets et al., 2011). Future research is needed to explore this possibility.

### **5. CONCLUSION AND PERSPECTIVES**

The reasoning-based approach appears to be the most appropriate framework to account for neuroimaging data on tool use. Yet, it is remarkable to observe that this approach has received only modest success from psychologists and neuroscientists alike as compared to the manipulation-based approach. One potential explanation for this lack of interest lies in the way scholars have framed the issue, perhaps putting an excessive emphasis on manipulation. To conclude, we would like to come back to this aspect and, particularly, to the epistemological beliefs that might have limited the interest of the reasoning-based approach for the understanding of the neurocognitive basis of human tool use.

### *5.1. EXPLANATION IS NOT UNDERSTANDING*

The present review clearly questions the manipulation knowledge hypothesis. An intriguing issue, however, is why scientists and scholars have tended, and still tend, to support this hypothesis. The recent enthusiasm for the embodied cognition approach is a good example of this. According to this approach, tool knowledge is based on the simulation of previous sensorimotor experiences with tools (e.g., Borghi et al., 2013; Thill et al., 2013; Van Elk et al., 2014; but see also Binkofski and Buxbaum, 2013; Buxbaum and Kalénine, 2010). In this frame, people do not reason when using tools, they simply manipulate them. This belief is also firmly ingrained in folk psychology, as illustrated by the implicit hierarchy of intellectual work over manual work, as if using a tool did not involve any kind of intelligence or reasoning, but only the hands. One potential explanation for this belief is that people – and scientists alike – might confound “explanation” with “understanding” (Bullock et al., 1982). Said differently, the idea would be that, if people are not able to explain what they do, then they do not understand what they do. Such a bias can also be reported in Piaget’s works, leading developmental psychologists to think that it is not until after the first year of life that infants begin to distinguish between adequate and inadequate support (Piaget, 1954; see Baillargeon and Hanko-Summers, 1990). Yet, a significant amount of evidence indicates that infants as young as 4.5 months of age understand that objects cannot remain stable without support (Baillargeon and Hanko-Summers, 1990; Baillargeon et al., 1992; Needham and Baillargeon, 1993). Technically, an object resting on a support is stable if a perpendicular line drawn through the object’s center of gravity falls within the support’s boundaries. Even though adults are generally unaware of this principle, they commonly adhere to it in their predictions, suggesting that it is not necessary to be able

to explain scientifically the principle of support/gravity to understand it (Baillargeon et al., 1992; Bullock et al., 1982). After all, humans did not have to wait for Newton's discovery of the law of gravity to apply it in everyday life! In sum, it is not because some kinds of knowledge are not declarative that they are not the basis for reasoning. Perhaps if we move toward the idea that non-declarative, mechanical knowledge is central to human tool use, fewer studies will be conducted with the assumption that human tool use is first and foremost a matter of gesture.

### *5.2. A FINAL WORD*

As mentioned, infants as young as 4.5 months of age are able to understand gravity. This contrasts markedly with studies showing that animal users have serious limitations to solve "gravity-based" problems (e.g., Povinelli, 2000; Visalberghi and Limongelli, 1994). Taken together, these findings and those reported here provide support for discontinuity theories of the evolution of human cognition, suggesting that humans alone possess mechanical knowledge, allowing them to reason about physical events (see Johnson-Frey, 2007; Orban and Caruana, 2014; Osiurak, 2014c; Osiurak et al., 2010; Penn et al., 2008; Povinelli, 2000; Wolpert, 2003). Several issues remain to be clarified in future research. First, studies on left brain-damaged patients with tool use disorders commonly focus on how these patients are able to produce tool-use gestures, such as pantomimes. Second, we found a robust activation of the left middle frontal cortex (BA46) and vPMC in the understanding of tool-use actions. However, frontal lobe lesions alone are not sufficient to provoke tool-use disorders (e.g., Goldenberg and Spatt, 2009). So, an outstanding issue is to determine the specific role of these brain areas in tool use.

**FOOTNOTES**

- <sup>1</sup> 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.
- <sup>2</sup> This hypothesis has been extensively developed in recent years with the concepts of structural actions or manipulative affordances (Bub et al., 2008; Bub and Masson, 2010; Thill et al., 2013; see also Binkofski and Buxbaum, 2013; Buxbaum and Kalénine, 2010). These concepts refer to the idea that specific manipulative, motor schemas can be activated from the structural components of objects. These schemas are not supposed to contain information about how to use objects skillfully, but only about how to grasp them such as, for instance, to move them from one location to another.
- <sup>3</sup> As mentioned below, there is evidence that nonhuman primates meet severe difficulties to establish analogical relationships in tool use tasks, namely, to transfer what they learn in one situation to other ones. Consistent with this, it has been suggested that in nonhuman primates, tool use might be only based on a kind of associational, domain-specific learning (Johnson-Frey, 2004; Frey, 2008; Peeters et al., 2009; Penn et al., 2008; Povinelli, 2000; Santos et al., 2006).
- <sup>4</sup> Apraxia can be defined as a disorder of skilled movement and tool use (De Renzi, 1989). The focus will be put here on apraxia of tool use, that is, difficulties to show how to use a tool without touching it (pantomime of tool use) or only with it in hand (single tool use), or to actually use the tool with its corresponding object (real tool use).

- <sup>5</sup> These tasks can require participants to select among several novel tools the one appropriate for bringing a target out from a box (Jarry et al., 2013, 2015; Osiurak et al., 2013) or for lifting a cylinder (Goldenberg and Hagmann, 1998).
- <sup>6</sup> Mental simulation of tool-use action refers here to the outcome of the reasoning based on mechanical knowledge. For instance, when someone has to pound a nail with a hammer, the mental simulation corresponds to the nail being pounded by the hammer (i.e., allocentric, tool-object relationship). Then, this mental simulation constrains the production system in the selection of the appropriate motor action to be performed (i.e., egocentric, tool-hand relationship: oscillatory movements of the elbow joint; see Osiurak and Badets, in press).
- <sup>7</sup> The involvement of frontal lobe lesions in the study of Goldenberg and Spatt (2009) could also be explained by a phenomenon of diaschisis given that patients were assessed at a relatively acute stage.

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**REFERENCES**

- Abdollahi, R.O., Kolster, H., Glasser, M.F., Robinson, E.C., Coalson, T.S., Dierkaer, D., Jenkison, N., Van Essen, D.C., Orban, G.A., 2014. Correspondences between retinotopic areas and myelin maps in human visual cortex. *NeuroImage* 99, 509–524.
- Ambrose, S., 2001. Paleolithic technology and human evolution. *Science* 291, 1748–1753.
- Arbib, M.A., 1985. Schemas for the temporal organisation of behaviour. *Hum. Neurobiol.* 4, 63–72.
- Baber, C., 2003. *Cognition and tool use*. Taylor & Francis, London.
- Bach, P., Peelen, M.V., Tipper, S.P., 2010. On the role of object information in action observation: An fMRI study. *Cereb. Cortex* 20, 2798–2809.
- Baillargeon, R., Hanko-Summers, S., 1990. Is the top object adequately supported by the bottom object? Young infants' understanding of support relations. *Cogn. Dev.* 5, 29–53.
- Baillargeon, R., Needham, A., DeVos, J., 1992. The development of young infants' intuitions about support. *Early Dev. Parent.* 1, 69–78.
- Barsalou, L.W., 2008. Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645.
- Bartolo, A., Daumüller, M., Della Sala, S., Goldenberg, G., 2007. Relationship between object-related gestures and the fractionated object knowledge system. *Behav. Neurol.* 18, 143–147.
- Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2003. fMRI responses to video and point-light displays of moving humans and manipulable objects. *J. Cogn. Neurosci.* 15, 991–1001.
- Beck, B.B., 1980. *Animal tool use behavior: The use and manufacture of tools by animals*. Garland STPM Press, New York.

- Beck, S.R., Apperly, I.A., Chappel, J., Guthrie, C., Cutting, N., 2011. Making tools isn't child's play. *Cognition* 119, 301–306
- Bellebaum, C., Tettamanti, M., Marchetta, E., Della Rosa, P., Rizzo, G., Cappa, S.F., 2013. Neural representations of unfamiliar objects are modulated by sensorimotor experience. *Cortex* 49, 1110–1125.
- Binder, J.R., Desai, R.H., Graves, W.W., Conant, L.I., 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796.
- Binkofski, F., Buxbaum, L.J., 2013. Two action systems in the human brain. *Brain Lang.* 127, 222–229.
- Boesch, C., 2005. Joint cooperative hunting among wild chimpanzees: Taking natural observations seriously. *Behav. Brain Sci.* 28, 692–693.
- Boesch, C. Tomasello, M., 1998. Chimpanzee and human cultures. *Curr. Anthropol.* 39, 591–604.
- Bohlhalter, S., Hattori, N., Wheaton, L., Fridman, E., Shamin, E.A., Garraux, G., Hallett, M., 2009. Gesture subtype-dependent left lateralization of praxis planning: An event-related fMRI study. *Cereb. Cortex* 19, 1256–1262.
- Borghi, A.M., 2004. Object concepts and action: Extracting affordances from objects parts. *Acta Psychol.* 115, 69–96.
- Borghi, A.M., Scorolli, C., Caligiore, D., Baldassarre, G., Tummolini, L., 2013. The embodied mind extended: Using words as social tools. *Front. Psychol.* 4, 214.
- Boronat, C.B., Buxbaum, L.J., Coslett, H.B., Tang, K., Saffran, E.M., Kimberg, D.Y., Detre, J.A., 2005. Distinctions between manipulation and function knowledge of objects: Evidence from functional magnetic resonance imaging. *Cogn. Brain Res.* 23, 361–373.

- Bortoletto, M., Cunnington, R., 2010. Motor timing and motor sequencing contribute differently to the preparation for voluntary movement. *NeuroImage*. 49, 3338–3348.
- Bozeat, S., Lambon Ralph, M.A., Patterson, K., Hodges, J.R., 2002. When objects lose their meaning: What happens to their use? *Cogn. Affect. Behav. Neurosci.* 2, 236–251.
- Bub, D.N., Masson, M.E.J., 2010. Grasping beer mugs: On the dynamics of alignment effects induced by handled objects. *J. Exp. Psychol. Hum. Percept. Perform.* 36, 341–358.
- Bub, D.N., Masson, M.E.J., Cree, G.S., 2008. Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition* 106, 27–58.
- Bullock, M., Gelman, R., Baillargeon, R., 1982. The development of causal reasoning, in: Friedman, W.J. (Ed.), *The developmental psychology of time*. Academic Press, New York, pp. 209–254.
- Buxbaum, L.J., 2001. Ideomotor Apraxia: A call to action. *Neurocase* 7, 445–448.
- Buxbaum, L.J., Giovannetti, T., Libon, D., 2000. The role of the dynamic body schema in praxis: Evidence from primary progressive apraxia. *Brain Cogn.* 44, 166–191.
- Buxbaum, L.J., Kalénine, S., 2010. Action knowledge, visuomotor activation, and embodiment in the two action systems. *Ann. New York Acad. Sci.* 1191, 201–218.
- Buxbaum, L.J., Kyle, K.M., Menon, R., 2005. On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Cogn. Brain Res.* 25, 226–239.
- Buxbaum, L.J., Kyle, K.M., Tang, K., Detree, J.A., 2006. Neural substrates of knowledge of hand postures for object grasping and functional object use: Evidence from fMRI. *Brain Res.* 1117, 175–185.
- Buxbaum, L.J., Saffran, E.M., 2002. Knowledge of object manipulation and object function: Dissociations in apraxic and nonapraxic subjects. *Brain Lang.* 82, 179–199.



- Buxbaum, L.J., Schwartz, M.F., Carew, T.G., 1997. The role of memory in object use. *Cogn. Neuropsychol.* 14, 219–254.
- Buxbaum, L.J., Shapiro, A.D., Coslett, H.B., 2014. Critical brain regions for tool-related and imitative actions: A componential analysis. *Brain*. Doi:10.1093/brain/awu111.
- Buxbaum, L.J., Sirigu, A., Schwartz, M.F., Klatzky, R., 2003. Cognitive representations of hand posture in ideomotor apraxia. *Neuropsychologia* 41, 1091–1113.
- Byrne, R.W. (2004) The manual skills and cognition that lie behind hominid tool use, in: Russon, A.E., Begun, D.R. (Eds.), *The evolution of thought*. Cambridge University Press, New York, pp. 31–44.
- Canessa, N., Borgo, F., Cappa, S.F., Perani, D., Falini, A., Buccino, G., Tettamanti, M., Shallice, T., 2008. The different neural correlates of action and functional knowledge in semantic memory: An fMRI study. *Cereb. Cortex* 18, 740–751.
- Caspers, S., Eickhoff, S.B., Geyer, S., Scheperjans, F., Molhberg, H., Zilles, K., Amunts, K., 2008. The human inferior parietal lobule in stereotaxic space. *Brain Struct. Funct.* 212, 481–495.
- Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., Zilles, K., 2006. The human inferior parietal cortex: Cytoarchitectonic parcellation and interindividual variability. *NeuroImage* 33,430–448.
- Chappell, J., Kacelnik, A., 2002. Tool selectivity in a non-primate species, the New Caledonian crow (*Corvus moneduloides*). *Anim. Cogn.* 5, 71–78.
- Chein, J.M., Fissell, K., Jacobs, S., Fiez, J.A., 2002. Functional heterogeneity within Broca's area during verbal working memory. *Physiol Behav* 77: 635–639.
- Choi, S.H., Na, D.L., Kang, E., Lee, K.M., Lee, S.W., Na, D.G., 2001. Functional magnetic resonance imaging during pantomiming tool-use gestures. *Exp. Brain Res.* 139, 311–317.

- Creem-Regehr, S.H., Dilda, V., Vicchirilli, A.E., Federer, F., Lee, J.N., 2007. The influence of complex action knowledge on representations of novel graspable objects: Evidence from functional magnetic resonance imaging. *J. Int. Neuropsychol. Soc.* 13, 1009–1020.
- Cubelli, R., Marchetti, C., Boscolo, G., Della Sala, S., 2000. Cognition in action: Testing a model of limb apraxia. *Brain Cogn.* 44, 144–165.
- Daprati, E., Sirigu, A., 2006. How we interact with objects: Learning from brain lesions. *Trends Cogn. Sci.* 10, 265–270.
- Darwin, C., 1981. *The descent of man and selection in relation to sex*. Princeton University Press, New Jersey. (Original work published 1871)
- De Beaune, S.A., 2008. *L’homme et l’outil*. CNRS Editions, Paris.
- De Renzi, E. (1989). Apraxia, in: Boller, F. Grafman, J. (Eds.), *Handbook of neuropsychology* (pp. 245–263). Elsevier Science Publishers, Amsterdam, pp. 245–263.
- De Renzi, E., Lucchelli, F., 1988. Ideational apraxia. *Brain* 111, 1173–1185.
- Dinstein, I., Hasson, U., Rubin, N., Heeger, D.J., 2007. Brain areas selective for both observed and executed movements. *J. Neurophysiol.* 98, 1415–1427.
- Ebisch, S.J.H., Babiloni, C., Del Gratta, C., Ferretti, A., Perrucci, M.G., Caulo, M., Sitskoorn, M.M., Romani, G.L., 2007. Human neural systems for conceptual knowledge of proper object use: A functional magnetic resonance imaging study. *Cereb. Cortex* 17, 2744–2751.
- Ehrsson, H.H., Fagergren, A., Forssberg, H., 2001. Differential fronto-parietal activation depending on force used in a precision grip task: An fMRI study. *J. Neurophysiol.* 85, 2613–2623.

- Ehrsson, H.H., Fagergren, A., Jonsson, T., Westling, G., Johansson, R.S., Forssberg, H., 2000. Cortical activity in precision- versus power-grip tasks: An fMRI study. *J. Neurophysiol.* 83, 528–536.
- Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation revisited. *Neuroimage* 59, 2349–2361.
- Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Hum. Brain Mapp.* 30, 2907–2926.
- Emmorey, K., McCullough, S., Mehta, S., Ponto, L.L.B., Grabowski, T.J., 2011. Sign language and pantomime production differentially engage frontal and parietal cortices. *Lang. Cogn. Process.* 26, 878–901.
- Forde, E.M.E., Humphreys, G.W., 2000. The role of semantic knowledge and working memory in everyday tasks. *Brain Cogn.* 44, 214–252.
- Frey, S.H., 2008. Tool use, communicative gesture and cerebral asymmetries in the modern human brain. *Phil. Trans. Roy. Soc. London* 363, 1951–1957.
- Fridman, E.A., Immisch, I., Hanakawa, T., Bohlhalter, S., Waldvogel, D., Kansaku, K., Wheaton, L., Hallett, M., 2006. The role of the dorsal stream for gesture production. *NeuroImage* 29, 417–428.
- Gainotti, G., 2013. Controversies over the mechanisms underlying the crucial role of the left fronto-parietal areas in the representation of tools. *Front. Psychol.* 4, 727.
- Georgieva, S., Peeters, R., Kolster, H., Todd, J.T., Orban, G.A., 2009. The processing of three-dimensional shape from disparity of the human brain. *J. Neurosci.* 29, 727–742.
- Geschwind, N., 1965. Disconnection syndrome in animal and man. *Brain* 88, 585–644.

- Gibson, K.R., 1993. Generative interplay between technical capacities, social relations, imitation and cognition, in: Gibson, K.R., Ingold, T. (Eds.), *Tools, language and cognition in human evolution*. Cambridge University Press, New York, pp. 251–269.
- Goldenberg, G., 2009. Apraxia and the parietal lobes. *Neuropsychologia* 47, 1449–1559.
- Goldenberg, G., 2013. *Apraxia: The cognitive side of motor control*. Oxford University Press, Oxford.
- Goldenberg, G., 2014. Apraxia in left-handers. *Brain*. Doi:10.1093/brain/awt181.
- Goldenberg, G., Hagmann, S., 1998. Tool use and mechanical problem solving in apraxia. *Neuropsychologia* 36, 581–589.
- Goldenberg, G., Hartmann-Schmid, K., Sürer, F., Daumüller, M., Hermsdörfer, J., 2007. The impact of dysexecutive syndrome on use of tools and technical devices. *Cortex* 43, 424–435.
- Goldenberg, G., Spatt, J., 2009. The neural basis of tool use. *Brain* 132, 1645–1655.
- Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25.
- Grèzes, J., Decety, J., 2002. Does visual perception of object afford action? Evidence from neuroimaging study. *Neuropsychologia* 40, 212–222.
- Hartmann, K., Goldenberg, G., Daumüller, M., Hermsdörfer, J., 2005. It takes the whole brain to make a cup of coffee: The neuropsychology of naturalistic actions involving technical devices. *Neuropsychologia* 43, 625–627.
- Heilman, K.M., Rothi, L.J.G., Mack, L., Feinberg, T., Watson, R.T., 1986. Apraxia after superior parietal lesions. *Cortex* 32, 141–150.
- Heilman, K.M., Rothi, L.J., Valenstein, E., 1982. Two forms of ideomotor apraxia. *Neurology* 32, 342–346.
- Heilman, K.M. Watson, R.T., 2008. The disconnection apraxias. *Cortex* 44, 975–982.

- Hermesdörfer, J., Terlinden, G., Mühlau, M., Goldenberg, G., Wohlschläger, A.M., 2007. Neural representations of pantomimed and actual tool use: Evidence from an event-related fMRI study. *NeuroImage* 36, 109–118.
- Higuchi, S., Imamizu, H., Kawato, M., 2007. Cerebellar activity evoked by common tool-use execution and imagery tasks: An fMRI study. *Cortex* 43, 350–358.
- Hodges, J.R., Bozeat, S., Lambon Ralph, M.A., Patterson, K., Spatt, J., 2000. The role of knowledge in object use: Evidence from semantic dementia. *Brain* 123, 1913–1925.
- Hodges, J.R., Spatt, J., Patterson, K., 1999. “What” and “how”: Evidence for the dissociation of object knowledge and mechanical problem-solving skills in the human brain. *Proc. Natl. Acad. Sci. USA* 96, 9444–9448.
- Imazu, S., Sugio, T., Tanaka, S., Inui, T., 2007. Differences between actual and imagined usage of chopsticks: An fMRI study. *Cortex* 43, 301–307.
- Inoue, K., Kawashima, R., Sugiura, M., Ogawa, A., Schormann, T., Zilles, K., Fukuda, H., 2001. Activation in the ipsilateral posterior parietal cortex during tool use: A PET study. *NeuroImage* 14, 1469–1475.
- Jarry, C., Osiurak, F., Baumard, J., Lesourd, M., Etcharry-Bouyx, F., Chauviré, V., Le Gall, D., 2015. Mechanical problem-solving and imitation of meaningless postures in left brain damaged patients: Two sides of the same coin? *Cortex* 63, 214–216.
- Jarry, C., Osiurak, F., Delafuys, D., Chauviré, V., Etcharry-Bouyx, F., Le Gall, D., 2013. Apraxia of tool use: More évidence for the technical reasoning hypothesis. *Cortex* 49, 2322–2333.
- Jastorff, J., Begliomini, C., Fabbri-Destro, M., Rizzolatti, G., Orban, G.A., 2010. Coding observed motor acts: Different organizational principles in the parietal and premotor cortex of humans. *J. Neurophysiol.* 104, 128–140.

- Jeannerod, M., 1994. The representing brain: Neural correlates of motor intention and imagery. *Behav. Brain Sci.* 17, 187–245.
- Jeannerod, M., Arbib, M.A., Rizzolatti, G., Sakata, H., 1995. Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends Neurosci.* 18, 314–320.
- Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. *Trends Cogn. Sci.* 8, 71–78.
- Johnson-Frey, S.H., 2007. What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex* 43, 368–375.
- Johnson-Frey, S.H., Grafton, S.T., 2003. From “acting on” to “acting with”: The functional anatomy of action representation, in: Prablanc, C., Pélisson, D., Rossetti, Y. (Eds.), *Progress in brain research*. Elsevier, New York, pp. 127–139.
- Johnson-Frey, S.H., Newman-Norlund, R., Grafton, S.T., 2005. A distributed left hemisphere network active during planning of everyday tool use skills. *Cereb. Cortex* 15, 681–695.
- Kellenbach, M.L., Brett, M., Patterson, K., 2003. Actions speak louder than functions: The importance of manipulability and action in tool representations. *J. Cogn. Neurosci.* 15, 30–46.
- Koechlin, E., Summerfield, C., 2007. An information theoretical approach to prefrontal executive function. *Trends Cogn. Sci.* 11, 229–235.
- Kroliczak, G., Frey, S.H., 2009. A common network in the left cerebral hemisphere represents planning of tool use pantomimes and familiar intransitive gestures at the hand-independent level. *Cereb. Cortex* 19, 2396–2410.
- Laird, A.R., Fox, M., Price, C.J., Glahn, D.C., Uecker, A.M., Lancaster, J.L., Turkeltaub, P.E., Kochunov, P., Fox, P.T., 2005. ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Hum. Brain Mapp.* 25, 155–164.

- Lancaster, J.L., Tordesillas-Gutierrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J.C., Fox, P.T., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. *Hum. Brain Mapp.* 28, 1194–1205.
- Lauro-Grotto, R. Piccini, C., Shallice, T., 1997. Modality-specific operations in semantic dementia. *Cortex*, 33 593–622.
- Leroi-Gourhan, A., 1971. *L'Homme et la matière*. Albin Michel, Paris.
- Lesourd, M., Baumard, J., Jarry, C., Etcharry-Bouyx, F., Belliard, S., Moreaud, O., Croisile, B., Chauviré, V., Granjon, M., Le Gall, D., & Osiurak, F., in press. Mechanical problem-solving strategies in Alzheimer's disease and semantic dementia. *Neuropsychology*. <http://psycnet.apa.org/doi/10.1037/neu0000241.search>
- Lewis, J.W., 2006. Cortical networks related to human use of tools. *Neuroscientist* 12, 211–231.
- Martin-Ordas, G., Call, J., Colmenares, F., 2008. Tubes, tables and traps: Great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Anim. Cogn.* 11, 423–430.
- Marzke, M.W., Wullstein, K.L., Viegas, S.F., 1992. Evolution of the power (squeeze) grip and its morphological correlates in hominids. *Am. J. Phys. Anthropol.* 89, 283–298.
- McGrew, W.C., 1992. *Chimpanzee material culture: Implications for human evolution*. Cambridge University Press, New York.
- McGrew, W.C., 1993. The intelligent use of tools: Twenty propositions, in: Gibson, K.R., Ingold, T. (Eds.), *Tools, language and cognition in human evolution*. Cambridge University Press, New York, pp. 151–171.
- McGrew, W.C., 2005. *The cultural chimpanzee: Reflections on cultural primatology*. Cambridge University Press, New York.

- Milner, A.D., Goodale, M.A., 2006. *The visual brain in action*. Oxford University Press, Oxford.
- Mizelle, J.C., Wheaton, L.A., 2010. The neuroscience of storing and molding tool action concepts: How “plastic” is grounded cognition? *Front. Psychol.* 1, 196.
- Mounoud, P., 1996. A recursive transformation of central cognitive mechanisms: The shift from partial to whole representation, in: Sameroff, A.J., Haith, M.M. (Eds.), *The five to seven year shift: the age of reason and responsibility*. Chicago University Press, Chicago, pp. 85–110.
- Napier, J.R., 1956. The prehensile movements of the human hand. *J. Bone Joint Surg.* 38, 902–913.
- Napier, J.R., 1960. Studies of the hands of living primates. *Proc. Zool. Soc. London* 134, 647–657.
- Needham, A., Baillargeon, R., 1993. Intuitions about support in 4.5-month-old infants. *Cognition* 47, 121–148.
- Negri, G.A., Lunardelli, A., Reverberi, C., Gigli, G.L., Rumiati, R.I., 2007. Degraded semantic knowledge and accurate object use. *Cortex* 43, 376–388.
- Nelissen, K., Borra, E., Gerbella, M., Rozzi, S., Luppino, G., Vanduffel, W., Rizzolatti, G., Orban, G.A., 2011. Action observation circuits in the macaque monkey cortex. *J. Neurosci.* 31, 3743–3756.
- Oakley, K.P., 1949. *Man the toolmaker*. British Museum, London.
- Ohgami, Y., Matsuo, K., Uchida, N., Nakai, T., 2004. An fMRI study of tool-use gestures: Body part as object and pantomime. *NeuroReport* 15, 1903–1906.
- Orban, G.A., Caruana, F., 2014. The neural basis of human tool use. *Front. Psychol.* 5, 310.



- Orban, G.A., Claeys, K., Nelissen, K., Smans, R., Sunaert, S., Todd, J.T., Wardak, C., Durand, J.B., Vanduffel, W., 2006. Mapping the parietal cortex of human and non-human primates. *Neuropsychologia* 44, 2647–2667.
- Orban, G.A., Sunaert, S., Todd, J.T., Van Hecke, P., Marchal, G., 1999. Human cortical regions involved in extracting depth from motion. *Neuron* 24, 929–940.
- Osiurak, F., 2013. Apraxia of tool use is not a matter of affordances. *Front. Hum. Neurosci.* 7, 890.
- Osiurak, F., 2014a. Mechanical knowledge, but not manipulation knowledge, might support action prediction. *Front. Hum. Neurosci.* 8, 737.
- Osiurak, F., 2014b. Tool use and manual actions: The human body as a means versus an end. *Cortex* 57, 281–282.
- Osiurak, F., 2014c. What neuropsychology tells us about human tool use? The four constraints theory (4CT): Mechanics, space, time, and effort. *Neuropsychol. Rev.* 24, 88-115.
- Osiurak, F., Aubin, G., Allain, P., Jarry, C., Richard, I., Le Gall, D., 2008b. Object usage and object utilization. A single-case study. *Neurocase* 14, 169–183.
- Osiurak, F., Badets, A., in press. Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychol. Rev.* <http://dx.doi.org/10.1037/rev0000027>
- Osiurak, F., Jarry, C., Allain, P., Aubin, G., Etcharry-Bouyx, F., Richard, I., Bernard, I., Le Gall, D., 2009. Unusual use of objects after unilateral brain damage. The technical reasoning model. *Cortex* 45, 769–783.
- Osiurak, F., Jarry, C., Le Gall, D., 2010. Grasping the affordances, understanding the reasoning. Toward a dialectical theory of human tool use. *Psychol. Rev.* 117, 517–540.
- Osiurak, F., Jarry, C., Le Gall, D., 2011. Re-examining the gesture engram hypothesis. New perspectives on apraxia of tool use. *Neuropsychologia* 49, 299–312.

- Osiurak, F., Jarry, C., Lesourd, M., Baumard, J., Le Gall, D., 2013. Mechanical problem-solving in left brain-damaged patients. *Neuropsychologia* 51, 1964–1972.
- Osiurak, F., Le Gall, D., 2014. Apraxia: A gestural or a cognitive disorder? *Brain*.  
Doi:10.1093/brain/awu238.
- Osiurak, F., Lesourd, M., 2014. What about mechanical knowledge? Comment on “Action semantics: A unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge” by Michiel Van Elk, Hein Van Schie and Harold Bekkering. *Phys. Life Rev.* 11, 269–270.
- Peeters, R.R., Rizzolatti, G., Orban, G.A., 2013. Functional properties of the left parietal tool use region. *NeuroImage* 78, 83–93.
- Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., Orban, G.A., 2009. The representation of tool use in humans and monkeys: Common and uniquely human features. *J. Neurosci.* 29, 11523–11539.
- Penn, D.C., Holyoak, K.J., Povinelli, D.J., 2008. Darwin’s mistake: Explaining the discontinuity between human and nonhuman minds. *Behav. Brain Sci.* 31, 109–130.
- Penn, D.C., Povinelli, D.J., 2007. Causal cognition in human and nonhuman animals: A comparative, critical review. *Ann. Rev. Psychol.* 58, 97–118.
- Petrides, M., 2005. Lateral and prefrontal cortex: Architectonic and functional organization. *Phil. Trans. Roy. Soc. London* 360, 781–795.
- Pezzulo, G., Barsalou, L.W., Cangelosi, A., Fischer, M.H., McRae, K., Spivey, M.J., 2013a. Computational grounded cognition: A new alliance between grounded cognition and computational modeling. *Front. Psychol.* 3, 612.
- Pezzulo, G., Candidi, M., Dindo, H., Barca, L., 2013b. Action simulation in the human brain: Twelve questions. *New Ideas Psychol.* 31, 270–290.
- Piaget, J., 1954. *The construction of reality in the child*. Basic Books, New York.

- Povinelli, D.J., 2000. *Folk physics for apes*. Oxford University Press, New York.
- Povinelli, D.J., Bering, J.M., Giambrone, S., 2000. Toward a science of other minds: Escaping the argument by analogy. *Cogn. Sci.* 24, 509–541.
- Rizzolatti, G. Matelli, M., 2003. Two different streams form the dorsal visual system: Anatomy and functions. *Exp. Brain Res.* 153, 146–157.
- Romanes, G.J., 1883. *Mental evolution in animals*. Appleton, New York.
- Rothi, L.J., Heilman, K.M., Watson, R.T., 1985. Pantomime comprehension and ideomotor apraxia. *J. Neurol. Neurosurg. Psychiatry* 48, 207–210.
- Rothi, L.J., Mack, L., Heilman, K.M., 1986. Pantomime agnosia. *J. Neurol. Neurosurg. Psychiatry* 49, 451–454.
- Rothi, L.J.G., Ochipa, C., Heilman, K.M., 1991. A cognitive neuropsychological model of limb praxis. *Cogn. Neuropsychol.* 8, 443–458.
- Roy, E.A., Square, P.A., 1985. Common considerations in the study of limb, verbal and oral apraxia, in: Roy, E.A. (Ed.), *Neuropsychological studies of apraxia and related disorders*. Elsevier, Amsterdam, pp. 111–161.
- Rumiati, R.I., Weiss, P.H., Shallice, T., Ottoboni, G., Noth, J., Zilles, K., Fink, G.R., 2004. Neural basis of pantomiming the use of visually presented objects. *Neuroimage* 21, 1224–1231.
- Santos, L.R., Pearson, H.M., Spaepen, G.M., Tsao, F., Hauser, M., 2006. Probing the limits of tool competence: Experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Anim. Cogn.* 9, 94–109.
- Sawamura, H., Orban, G.A., Vogels, R., 2006. Selectivity of neuronal adaptation does not match response selectivity: A single-cell study of the fMRI adaptation paradigm. *Neuron* 49, 307–318.

- Schubotz, R.I., von Cramon, Y., 2009. The case of pretense: Observing actions and inferring goals. *J. Cogn. Neurosci.* 21, 642–653.
- Shallice, T., 1982. Specific impairments of planning. *Phil. Trans. Roy. Soc. London* 298, 199–209.
- Silveri, M.C., Ciccarelli, N., 2009. Semantic memory in object use. *Neuropsychologia* 47, 2634–2641.
- Sirigu, A., Duhamel, J.R., Poncet, M., 1991. The role of sensorimotor experience in object recognition. *Brain* 114, 2555–2573.
- Spatt, J., Bak, T., Bozeat, S., Patterson, K., Hodges, J.R., 2002. Apraxia, mechanical problem solving and semantic knowledge: Contributions to object usage in corticobasal degeneration. *J. Neurol.* 249, 601–608.
- Stadler, W., Schubotz, R.I., von Cramon, D.Y., Springer, A., Graf, M., Prinz, W., 2011. Predicting and memorizing observed action: Differential premotor cortex involvement. *Hum. Brain Mapp.* 32, 677–687.
- Stout, D., Chaminade, T., 2007. The evolutionary neuroscience of tool making. *Neuropsychologia* 45, 1091–1100.
- Suddendorf, T., Whiten, A., 2001. Mental evolution and development: Evidence for secondary representation in children, great apes and other animals. *Psychol. Bull.* 127, 629–650.
- Sunaert, S., Van Hecke, P., Marchal, G., Orban, G.A., 1999. Motion-responsive regions of the human brain. *Exp. Brain Res.* 127, 355–370.
- Talairach, J., Tournoux, P., 1988. Co-planar stereotaxic atlas of the human brain. Thieme, New York.

- Thill, S., Caligiore, D., Borghi, A.M., Ziemke, T., Baldassarre, G., 2013. Theories and computational models of affordance and mirror system: An integrative review. *Neurosci. BioBehav. Rev.* 37, 491–521.
- Tomasello, M., Carpenter, M., Call, J., Behne, T. Moll, H., 2005. Understanding and sharing intentions: The origins of cultural cognition. *Behav. Brain Sci.* 28, 675–735.
- Tomassini, V., Jbabdi, S., Klein, J.C., Behrens, T.E., Pozzilli, C., Mathews, P.M., Rushworth, M.F.S., Johansen-Berg, H., 2007. Diffusion-weighted imaging tractography-based parcellation of the human lateral premotor cortex identifies dorsal and ventral subregions with anatomical and functional specializations. *J. Neurosci.* 27, 10259–10269.
- Toth, N., Schick, K.D., 1993. Early stone industries and inferences regarding language and cognition, in: Gibson, K.R., Ingold, T. (Eds.), *Tools, language and cognition in human evolution*. Cambridge University Press, New York, pp. 346–362.
- Tsuda, H., Aoki, T., Oku, N., Kimura, Y., Hatazawa, J., Kinoshita, H., 2009. Functional brain areas associated with manipulation of a prehensile tool: A PET study. *Hum. Brain Mapp.* 30, 2879–2889.
- Turkeltaub, P.E., Eden, G.F., Jones, K.M., Zeffiro, T.A., 2002. Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage* 16, 765–780.
- Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Hum. Brain Mapp.* 33, 1–13
- Vaesen, K., 2012. The cognitive bases of human tool use. *Behav. Brain Sci.* 35, 203–218.

- Van Elk, M., 2014. The left inferior parietal lobe represents stored hand-postures for object use and action prediction. *Front. Psychol.* 5, 333.
- Van Essen, D.C., 2005. A population-average, landmark- and surface-based (PALS) atlas of human cerebral cortex. *NeuroImage* 28, 635–662.
- Van Essen, D.C., Drury, H.A., Dickson, J., Harwell, J., Hanlon, D., Anderson, C.H., 2001. An integrated software suite for surface-based analyses of cerebral cortex. *J. Am. Med. Inform. Assoc.* 8, 443–459.
- Van Lawick-Goodall, J., 1970. Tool-using in primates and other vertebrates, In: Lehrman, D., Hinde, R., Shaw, E., (Eds.), *Advances in the study of behavior*. Academic Press, New York, pp. 195–249.
- Van Schaik, C.P., Deaner, R.O., Merrill, M.Y., 1999. The conditions for tool use in primates: Implications for the evolution of material culture. *J. Hum. Evol.* 36, 19–41.
- Vanduffel, W., Zhu, Q., Orban, G.A., 2014. Monkey cortex through fMRI glasses. *Neuron* 83, 533–550.
- Villarreal, M., Fridman, E.A., Amengual, A., Falasco, G., Gerscovitch, E.R., Ulloa, E.R., Leiguarda, R.C., 2008. The neural substrate of gesture recognition. *Neuropsychologia* 46, 2371–2382.
- Vingerhoets, G., 2008. Knowing about tools: Neural correlates of tool familiarity and experience. *NeuroImage* 40, 1380–1391.
- Vingerhoets, G., 2014. Contribution of the posterior parietal cortex in reaching, grasping, and using objects as tools. *Front. Psychol.* 5, 151.
- Vingerhoets, G., Acke, F., Alderweireldt, A.S., Nys, J., Vandemaele, P., Achten, E. (2012). Cerebral lateralization of praxis in right- and left-handedness: Same pattern, different strength. *Hum. Brain Mapp.* 33, 763–777.

- Vingerhoets, G., Alderweireldt, A.S., Vandemaele, P., Cai, Q., Van der Haegen, L., Brysbaert, M., Achten, E., 2013. Praxis and language are linked: Evidence from co-lateralization in individuals with atypical language dominance. *Cortex* 49, 172–183.
- Vingerhoets, G., Honoré, P., Vandekerckhove, E., Nys, J., Vandemaele, P., Achten, E., 2010. Multifocal intraparietal activation during discrimination of action intention in observed tool grasping. *Neuroscience* 169, 1158–1167.
- Vingerhoets, G., Nys, J., Honoré, P., Vandekerckhove, E., Vandemaele, P., 2013. Human left ventral premotor cortex mediates matching of hand posture to object use. *PLoS One* 8, e70480.
- Vingerhoets, G., Vandamme, K., Vercammen, A., 2009. Conceptual and physical object qualities contribute differently to motor affordances. *Brain Cogn.* 69, 481–489.
- Vingerhoets, G., Vandekerckhove, E., Honoré, P., Vandemaele, P., Achten, E., 2011. Neural correlates of pantomiming familiar and unfamiliar tools: Action semantics versus mechanical problem solving? *Hum. Brain Mapp.* 32, 905–918.
- Visalberghi, E., Limongelli, L., 1994. Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 108, 15–22.
- Wakusawa, K., Sugiura, M., Sassa, Y., Jeong, H., Yomogida, Y., Horie, K., Sato, S., Yokoyama, H., Kure, S., Takei, N. Mori, N., Kawashima, R., 2015. Adaptive ability to cope with atypical or novel situations involving tool use: An fMRI approach. *Neurosci. Res.* 90, 72–82.
- Weiss, P.H., Rahbari, N.N., Lux, S., Pietrzyk, U., Noth, J., Fink, G.R., 2006. Processing the spatial configuration of complex actions involves right posterior parietal cortex: An fMRI study with clinical implications. *Hum. Brain Mapp.* 27, 1004–1014.
- Whitehead, C., Marchant, J.L., Craik, D., Frith, C.D., 2009. Neural correlates of observing pretend play in which one object is represented as another. *SCAN* 4, 369–378.

Wolpert, L., 2003. Causal belief and the origins of technology. *Phil. Trans. Roy. Soc. London* 361, 1709–1719.

Wynn, T., 1993. Layers of thinking in tool behavior. In: Gibson, K.R., Ingold, T. (Eds.), *Tools, language and cognition in human evolution*. Cambridge University Press, New York, pp. 389–406.

Zilles, K., Schleicher, A., Palomero-Gallagher, N., Amunts, K., 2002. Quantitative analysis of cyto- and receptor architecture of the human brain. In: Mazziotta, J., Toga, A. (Eds.), *Brain mapping, the methods*. Elsevier, pp. 573–602.



**FIGURE CAPTIONS**

**Fig. 1.** The “common tool-use circuit”. ALE map derived from all studies included, viewed on two PALS-B12 left and right hemispheres atlas surface configurations (Van Essen, 2005): Lateral fiducial surfaces (Top) and flat maps (Bottom). White outlines: IPL (Peeters et al., 2013; see also Caspers et al., 2006). Green outlines: Other regions of interest (see Abdollahi et al., 2014; Georgieva et al., 2009; Jastorff et al., 2010; Orban et al., 1999; Sunaert et al., 1999; see also Orban and Caruana, 2014; Peeters et al., 2013). Horizontal white lines: Separation between dPMC and vPMC (Orban and Caruana, 2014; see also Tomassini et al., 2007). Note that (1) pMTG represents the union of MTGt and pMTG as defined by Orban and Caruana (2014) and (2) MT corresponds to the MT cluster as defined by Abdollahi et al. (2014). Explanations are given in the text.

**Fig. 2.** Action, gesture, and context. Panels A, B, and C, show the ALE maps resulting from all the studies included in ACTION, GESTURE and CONTEXT conditions, respectively, and mapped on two PALS-B12 left hemisphere atlas surface configurations (Van Essen, 2005): Lateral fiducial surfaces (Top) and flat maps (Bottom). Green outlines: Other regions of interest (see Abdollahi et al., 2014; Georgieva et al., 2009; Jastorff et al., 2010; Orban et al., 1999; Sunaert et al., 1999; see also Orban and Caruana, 2014; Peeters et al., 2013). Horizontal white lines: Separation between dPMC and vPMC (Orban and Caruana, 2014; see also Tomassini et al., 2007). Note that (1) pMTG represents the union of MTGt and pMTG as defined by Orban and Caruana (2014) and (2) MT corresponds to the MT cluster as defined by Abdollahi et al. (2014). Explanations are given in the text.

**Fig. 3.** Familiar and unfamiliar. Panels A and B show the ALE maps resulting from all the studies included in FAMILIAR and UNFAMILIAR conditions, respectively, and viewed on the PALS-B12 left hemisphere flat surface. Brain regions more robustly activated by one condition compared to the other are displayed in Panels C (FAMILIAR > UNFAMILIAR) and D (UNFAMILIAR > FAMILIAR), and viewed on the PALS-B12 left hemisphere flat surface (Van Essen, 2005). Green outlines: Other regions of interest (see Abdollahi et al., 2014; Georgieva et al., 2009; Jastorff et al., 2010; Orban et al., 1999; Sunaert et al., 1999; see also Orban and Caruana, 2014; Peeters et al., 2013). Horizontal white lines: Separation between dPMC and vPMC

(Orban and Caruana, 2014; see also Tomassini et al., 2007). Note that (1) pMTG represents the union of MTGt and pMTG as defined by Orban and Caruana (2014) and (2) MT corresponds to the MT cluster as defined by Abdollahi et al. (2014). Explanations are given in the text.

**Fig. 4.** Planning and execution. Panels A, B and C show the ALE maps resulting from all the studies included in PLANNING, PLANNING/EXECUTION and EXECUTION conditions, respectively, and viewed on the PALS left hemisphere flat surface (Van Essen, 2005). Green outlines: Other regions of interest (see Abdollahi et al., 2014; Georgieva et al., 2009; Jastorff et al., 2010; Orban et al., 1999; Sunaert et al., 1999; see also Orban and Caruana, 2014; Peeters et al., 2013). Horizontal white lines: Separation between dPMC and vPMC (Orban and Caruana, 2014; see also Tomassini et al., 2007). Note that (1) pMTG represents the union of MTGt and pMTG as defined by Orban and Caruana (2014) and (2) MT corresponds to the MT cluster as defined by Abdollahi et al. (2014). Explanations are given in the text.

**Fig. 5.** The functional roles of the different brain regions involved in tool use according to the reasoning-based approach. Explanations are given in the text. Abbreviations: vPMC, ventral premotor cortex; IPS, intraparietal sulcus; phAIP, putative human homologue of the anterior intraparietal area; DIPSA anterior dorsal IPS; PFt/aSMG, anterior portion of suparmarginal gyrus (SMG), which largely overlaps with the cytoarchitectonic area PFt of SMG; PF, cytoarchitectonic area PF of SMG; pMTG, posterior middle temporal gyrus; pITC, posterior inferior temporal cortex; pSTG, posterior superior temporal gyrus.









