



HAL
open science

On the Neurocognitive Co-Evolution of Tool Behavior and Language: Insights from the Massive Redeployment Framework

François Osiurak, Caroline Crétel, Natalie Uomini, Chloé Bryche, Mathieu Lesourd, Emanuelle Reynaud

► To cite this version:

François Osiurak, Caroline Crétel, Natalie Uomini, Chloé Bryche, Mathieu Lesourd, et al.. On the Neurocognitive Co-Evolution of Tool Behavior and Language: Insights from the Massive Redeployment Framework. *Topics in cognitive science*, 2021, 13 (4), pp.684-707. <10.1111/tops.12577>. <hal-04002167>

HAL Id: hal-04002167

<https://hal.science/hal-04002167v1>

Submitted on 23 Feb 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

On the Neurocognitive Co-Evolution of Tool Behavior and Language: Insights from the Massive Redeployment Framework

François Osiurak^{1,2}, Caroline Créteil¹, Natalie Uomini³,
Chloé Bryche¹, Mathieu Lesourd⁴, & Emanuelle Reynaud¹

¹Laboratoire d'Etude des Mécanismes Cognitifs, Université de Lyon, Lyon, France

²Institut Universitaire de France, Paris, France

³Department of Linguistic and Cultural Evolution, Max Planck Institute for Evolutionary Anthropology,
Leipzig, Germany

⁴Laboratoire de Psychologie, Université de Bourgogne Franche-Comté, Besançon, France

Correspondence

François Osiurak, Laboratoire d'Etude des Mécanismes Cognitifs (EA 3082), Institut de Psychologie, 5, avenue Pierre Mendès-France, 69676 Bron Cedex, France.

Email: Francois.Osiurak@univ-lyon2.fr

Running head: Co-Evolution of Tool Behavior and Language

Keywords: Tool Use; Tool Making; Language; Technical Reasoning; Cognitive Evolution; Parietal Cortex.

Abstract

Understanding the link between brain evolution and the evolution of distinctive features of modern human cognition is a fundamental challenge. A still unresolved question concerns the co-evolution of tool behavior (i.e., tool use or tool making) and language. The shared neurocognitive processes hypothesis suggests that the emergence of the combinatorial component of language skills within the frontal lobe/Broca's area made possible the complexification of tool-making skills. The importance of frontal lobe/Broca's area in tool behavior is somewhat surprising with regard to the literature on neuropsychology and cognitive neuroscience, which has instead stressed the critical role of the left inferior parietal lobe. Therefore, to be complete, any version of the shared neurocognitive processes hypothesis needs to integrate the potential interactions between the frontal lobe/Broca's area and the left inferior parietal lobe as well as their co-evolution at a phylogenetic level. Here we sought to provide first elements of answer through the use of the massive deployment framework, which posits that evolutionarily older brain areas are deployed in more cognitive functions (i.e., they are less specific). We focused on the left parietal cortex, and particularly the left areas PF, PGI, and AIP, which are known to be involved in tool use, language, and motor control, respectively. The deployment of each brain area in different cognitive functions was measured by conducting a meta-analysis of neuroimaging studies. Our results confirmed the pattern of specificity for each brain area and also showed that the left area PGI was far less specific than the left areas PF and AIP. From these findings, we discuss the different evolutionary scenarios depicting the potential co-evolution of the combinatorial and generative components of language and tool behavior in our lineage.

Keywords: Tool Use; Tool Making; Language; Technical Reasoning; Cognitive Evolution; Parietal Cortex.

1. Introduction

Tool-use and tool-making skills¹ are considered as a hallmark of the human lineage, which has evolved an extreme reliance on tool use and has taken tool making to an extreme level of diversity and cumulation. Until recent years, the oldest direct evidence of stone tool making, i.e., Oldowan tools, dated to 2.6 million years ago (Mya) and these tools were probably produced by several hominin taxa: *Australopithecus*, *Paranthropus*, *Homo*, and *Kenyanthropus* (Braun et al., 2019; Toth & Schick, 2018; Semaw et al., 1997). Oldowan tools are characterized by simple core tools, retouched or unretouched flakes, flake fragments and battered stones (Braun et al., 2019; Toth, 1985; Toth & Schick, 2018). Subsequent discoveries pushed back the date for the earliest known artefacts. The now oldest evidence of stone tool making, i.e., Lomekwian tools, dates to 3.3 Mya (Harmand et al., 2015). These tools were manufactured using movements similar to the hammer-on-anvil technique employed by nonhuman primates to crack nuts with tools, in contrast to the direct freehand percussion that can be seen in Oldowan tools. This difference suggests that Oldowan tools required greater bimanual coordination than Lomekwian tools. Acheulean tools emerged later, approximately 1.8 Mya (Gowlett, 2020; Wynn & Gowlett, 2018) and were associated to several technical innovations in terms of action organization, which differs from bifacial and unifacial patterns of Oldowan tools. The transitional Late Oldowan and Early Acheulean tools are characterized by longer and more planned manufacturing sequences of tool production than the previous tool industries (Muller et al., 2017). They also marked the beginning of

¹ Tool use can be defined as the external employment of a manipulable object to alter efficiently the form, position or condition of another object, and tool making as the structural modification of an object by the user so that the object serves more efficiently as a tool (Shumaker et al., 2011). We will use the term tool behavior as a more generic term encompassing both tool use and tool making. In this paper, we discuss both tool use and tool making. While they are not necessarily equivalent in our modern lifestyle, for prehistoric people, tool making is always a form of tool use, because one has to use a tool to make a stone tool) and, conversely, stone tools can be used for purposes beyond just to make a tool.

intentionally shaped tools to make hand axes, spears or picks characteristic of the Late Acheulean (Gowlett, 2020).

The question of the origins of the complexification of tool-making skills in our lineage has generated a multitude of different hypotheses. Among them, some have drawn a potential link with language skills, through the potential existence of a co-evolution between complex tool-making skills and language (Greenfield, 1991; Holloway, 1969; Parker & Gibson, 1979; Stout et al., 2008; Uomini, 2009; Uomini & Meyer, 2013). Estimates for the origins of language differ widely, from about 2 Mya to tens of thousands of years (Belfer-Cohen & Goren-Inbar, 1994; Coolidge & Wynn, 2005). The co-evolution of language and tool-making skills can be hypothesized in two ways, which are not exclusive. We refer to them as the shared neurocognitive processes hypothesis and the scaffolding hypothesis. Briefly, the shared neurocognitive processes hypothesis assumes that language and tool-making skills have co-evolved by sharing common neurocognitive processes, whereas the scaffolding hypothesis posits that language could have facilitated the social transmission of tool-related content and, as a result, the development of tool-making skills. Although the meta-analysis reported here was designed to explore in more details the shared neurocognitive processes hypothesis, we will begin by presenting the scaffolding hypothesis, which will be useful for discussing later in the paper some of our results.

1.1. The scaffolding hypothesis

The scaffolding hypothesis suggests that the complexification of tool-making skills results from an increase in the efficacy of social transmission through the use of language (Dean et al., 2012, 2014; Morgan et al., 2015; Tomasello et al., 2005; Uomini & Lawson, 2017; for discussion, see Caldwell et al., 2018; for a detailed review, see

Lombao et al., 2017). Indeed, there is no sign that communication was used to maintain the clear traditions (i.e., teaching with language) within Lomekwian/Oldowan tools prior to 2 Mya (Gärdenfors & Högberg, 2017; Stout et al., 2010). This suggests that less interactive forms of social learning (i.e., observation) along with preexisting cognitive skills could have been sufficient to maintain the technology over time (Morgan et al., 2015; Shipton & Nielsen, 2015; Toth, 1985; Stout et al., 2010, 2019). By contrast, the complexity of Acheulean tools and the homogeneity of their production (Sharon et al., 2011; Wynn & Gowlett, 2018) imply that the transmission of this technology was reliant on more interactive forms of social learning based on teaching with gestural or verbal (proto-)language (Gärdenfors & Högberg, 2017; Morgan et al., 2015; Stout et al., 2019). In broad terms, these more interactive forms of language-based transmission could have evolved during the Oldowan, progressively increasing the efficacy of transmission and the complexification of sequences of hierarchically organized actions, which characterize Acheulean tools (Mahaney, 2014; Uomini & Ruck, 2018).

Support for the scaffolding hypothesis comes, for instance, from the study of Morgan et al. (2015), who investigated the efficacy of transmission of Oldowan tool-making skills within a micro-society paradigm. Their micro-society paradigm consisted in a transmission chain of five or ten participants, with each participant learning from the previous participant and acting as a model to the next participant. There were five conditions: Reverse engineering (i.e., scrutinizing the product of the model), observation (i.e., observing the actions performed by the model; no interaction), basic teaching (i.e., observation *plus* learner-oriented demonstration e.g., the model could slow down the production), gestural teaching (i.e., observation *plus* interaction using gestures) and verbal teaching (i.e., observation *plus* verbal interaction). Results indicated that teaching conditions (particularly the verbal teaching condition) improved the quality of

transmission in that participants produced a higher number of usable sharp-edged flakes than in the other conditions. This suggests that less interactive forms of social learning such as observation could have been sufficient for the transmission of Oldowan tool-making skills, as suggested by Stout et al. (2019) in a replication experiment with Oldowan tools, but insufficient for the faithful transmission of potential innovations. Other studies using micro-society paradigms have confirmed that the efficacy of transmission of technical information is higher in verbal teaching conditions than in non-teaching conditions such as observation or reverse engineering (Caldwell & Millen, 2009; De Oliveira et al., 2019; Osiurak et al., 2016; Zwirner & Thornton, 2015; see also Caldwell et al., 2018). Although not all authors consider language to be essential in their models of prehistoric social learning (Gärdenfors & Högberg, 2017; Stout et al., 2019), the scaffolding hypothesis opens interesting avenues for understanding the co-evolution of language and tool-making skills. We will discuss further this hypothesis in the discussion section. Hereafter, we will focus our attention on the shared neurocognitive processes hypothesis, which is more specifically within the scope of the present article.

1.2. The shared neurocognitive processes hypothesis

The shared neurocognitive processes hypothesis posits that the complexification of tool-making skills results from the shared evolution of language and tool behavior at a neurocognitive level (Greenfield, 1991; Holloway, 1969). Contrary to Oldowan tools, the making of Acheulean tools requires high cognitive demands in terms of structured and hierarchical action plans. A parallel is drawn here by some authors with language and particularly the grammatical/combinatorial component of language, which consists in the arrangement of meaningful elements (Gibson, 1993; Ruck & Uomini, in press; Uomini & Meyer, 2013; see Uomini & Ruck, 2018 for a review). In tool making, the

“grammatical”/combinatorial component refers to the concatenation of unit operations that produces the tool (Gowlett, 1979; Holloway, 1969; Isaac, 1976; Muller et al., 2017; Steele & Uomini, 2009; Wynn, 1991). Given the key role of Broca’s area in the combinatorial component of language, it has been suggested that this brain area could be in charge of the production of hierarchically organized sequences in both the language domain and the tool behavior domain (e.g., Faisal et al., 2010; Greenfield, 1991; Holloway, 1969). In other words, the evolution of this brain structure could explain the co-emergence of complex forms of language and tool making (Faisal et al., 2010; Uomini & Meyer, 2013). Note that this hypothesis is also consistent with the theory of the recursive mind, which suggests that recursive skills could be unique to the genus *Homo* and, thus, explain the specific co-evolution of language, theory of mind, mental time travel, and tool use in this genus (e.g., Corballis, 2003, 2007a, 2007b, 2011).

Support for the shared neurocognitive processes hypothesis has come from the literature on patients with Broca’s aphasia, which has indicated that these patients can show difficulties in generating hierarchical structure not only in the language domain, but also when asked to combine objects together (see Greenfield, 1991). More recently, neuroscientific evidence has shown that Broca’s area is specialized in hierarchical structure building, with some regions being language-specific and others domain-general (Fedorenko et al., 2012; Friederici et al., 2006; Koechlin & Jubault, 2006; Mahaney, 2015). Neuroimaging findings also revealed that the right analogue of Broca’s area is involved in the making of Acheulean but not Oldowan tools, notably when participants are trained verbally to the tool-making technique (Putt et al., 2017). In another study using functional transcranial Doppler ultrasonography, a high correlation in terms of hemodynamics was found in the initial 10 seconds of an Acheulean tool-

making task (mainly concerned by the planning component and not the executive component) with a cued word generation task (Uomini & Meyer, 2013).

1.3. *Motor versus technical units*

The shared neurocognitive processes hypothesis as described above has been developed to account for the complexification of hierarchical structured sequences in tool-making skills. This approach is justified given the marked transition from the Oldowan to the Acheulean, which corresponds to the emergence of more hierarchical and structured sequences of actions (Goren-Inbar, 2011; Matsuzawa, 2008; Muller et al., 2017; Stout et al., 2010). Thus, the core assumption is that the evolution of language-related brain areas, and notably Broca's area, could have progressively recycled the preexisting tool-making skills, allowing our predecessors to generate hierarchical sequences of both language-related units and tool-related units. The idea that the frontal lobe/Broca's area is critical for the combinatorial capacities for both language and tool-making skills is certainly right. We will not discuss this aspect in more detail here. Instead, our attention will be focused on two aspects, which are generally overlooked, namely the nature of the tool-related units that are targeted by the combinatorial capacities of the frontal lobe/Broca's area and the role played by posterior brain regions – particularly the inferior parietal cortex – in the evolution of tool-use and tool-making skills. In the following lines, we will tackle these two aspects conjointly in light of the literature on neuropsychology and cognitive neuroscience.

Proponents of the shared neurocognitive processes hypothesis have provided different conceptions of the so-called tool-related units. For example, for Holloway (1969), these units seem to refer to “mechanical actions”, such as striking a flake, detaching a flake by pressure or rotating the stone. By contrast, Higuchi et al. (2009)

emphasized the motor nature of these units, which can be viewed as manipulative functions or manual sequences.

In broad terms, two divergent conceptions have been proposed, which can be summed up as follows (for discussion on this aspect in the field of psychology and cognitive neuroscience, see Osiurak & Badets, 2016, 2017). The first is that tool-related units are motor units, as suggested by Higuchi et al. (2009). Thus, according to this “manipulation-based” approach, a motor unit can be defined as the representation of a motor action, which characterizes an action performed by an effector (generally the hand) with a tool. The second is that tool-related units are technical units, as suggested by Holloway (1969). Thus, according to this “reasoning-based” approach, a technical unit refers to the representation of a mechanical action, which characterizes the interaction between a tool and an object.

1.4. Manipulation-based versus reasoning-based approaches

The manipulation-based approach to the tool-related units is widely shared, as illustrated by more recent evolutionary neuroscientific accounts of tool-making skills (e.g., Uomini & Meyer, 2013). In this respect, these accounts have perpetuated the long-standing idea initially developed by neuropsychologists that tool behavior is first and foremost a matter of manipulation (i.e., motor units). Indeed, major advances in understanding the neurocognitive bases of human tool-use skills have come from the study of brain-damaged patients with tool-use disorders, also called apraxia of tool use (De Renzi et al., 1968; Liepmann, 1908; Geschwind, 1975). The classical and still prevailing interpretation of these disorders is that they result from impaired manipulation knowledge, which corresponds to specific tool-use motor programs specifying the hand and arm movement parameters associated with the use of familiar

tools (e.g., for a hammer, a broad oscillation from the elbow joint and a power grip; Buxbaum, 2001; Heilman et al., 1982; Rothi et al., 1991; van Elk et al., 2014). Manipulation knowledge concerns only familiar tools because this knowledge is supposed to be progressively built from the experience people have with tools, hence familiar tools. A large body of evidence has indicated that tool-use disorders generally arise after damage to the left inferior parietal lobe, leading to the hypothesis that this brain region is critical for the storage of manipulation knowledge (Buxbaum, 2001; Buxbaum & Saffran, 2002; van Elk, 2014; van Elk et al., 2014). The term manipulation-knowledge hypothesis will be hereafter also employed to characterize the manipulation-based approach.

A viable alternative interpretation of tool-use disorders has been recently developed, namely the reasoning-based approach or technical-reasoning hypothesis, which is closer to the Holloway's (1969) technical-unit conception (Osiurak et al., 2010, 2020c; Osiurak & Badets, 2016; see also Gagnepain, 1990; Goldenberg, 2013; Le Gall, 1998). The core assumption is that tool-use disorders could reflect difficulties that belong more to the ideational/technical realm than to the motor realm. Thus, patients with tool-use disorders could perform incorrect motor actions because these motor actions are not guided by the correct representation of the mechanical action to perform with the tool and the object. Said differently, it remains likely that patients with tool-use disorders execute the motor actions that are *appropriate* to produce the *inappropriate* mechanical action they intend to perform. The shift presented here from the motor dimension to the technical dimension has allowed us to overcome some of the limitations of the manipulation-knowledge hypothesis concerning the nature of the difficulties reported in brain-damaged patients. For instance, these patients meet difficulties not only when using tools but also when selecting among several tools the

appropriate one to perform a given task (e.g., Jarry et al., 2013). This selection is necessarily guided by tool-object relationships and not by hand-tool relationships. As a result, the presence of impaired manipulation knowledge cannot account for such difficulties because this knowledge only provides information about how to manipulate a tool with the hand (i.e., hand-tool relationships). It has also been reported that these patients experience difficulties both when using familiar tools and solving mechanical problems through the selection, use and sometimes making of novel tools (e.g., Goldenberg & Hagmann, 1998; Goldenberg & Spatt, 2009; Heilman et al., 1997; Osiurak et al., 2009; for a review see Osiurak et al., 2020c). Likewise, the manipulation-knowledge hypothesis cannot explain how impaired manipulation knowledge, which is supposed to impact the manipulative component (i.e., hand-tool relationships) involved in the use of familiar tools, can produce deficits in terms of selection or tool making (i.e., tool-object relationships), particularly in mechanical problem-solving contexts.

The technical-reasoning hypothesis offers a comprehensive account for interpreting these findings in assuming that humans possess a key cognitive structure, i.e., technical reasoning, allowing them not only to use physical tools, but also to make them or even to build constructions (Osiurak et al., 2020c). Technical reasoning is a non-verbal reasoning², which is both causal (i.e., predicting the physical effects on the environment) and analogical (i.e., transfer of what is learnt from one situation to another). Technical reasoning is based on mechanical knowledge, which contains information about physical principles such as cutting, leverage or percussion. Evidence

² The literature on reasoning has suggested a dissociation between intuitive (i.e., low-effort and fast) and reflective (i.e., high-effort and slow) processes (e.g., Evans, 2010; see also Johnson-Laird, 2006). The technical-reasoning hypothesis posits that, in some cases, the process can be performed quickly (e.g., in some familiar tool-use activities) and, in others, more slowly (e.g., in some novel tool-use activities). The outstanding question is whether this reflects the existence of distinct intuitive *versus* reflective technical-related processes, as suggested by the aforementioned distinction. Future research is needed to explore this aspect.

indicates that the area PF within the left inferior parietal lobe is critical for technical-reasoning skills. For instance, it has been shown that damage to this brain area produces deficits in the selection and use of familiar tools as well as in the selection/use/making of novel tools to solve mechanical problems (for a review, see Osiurak et al., 2020c). Neuroimaging studies also reveal that the area PF is activated when participants perform tool-use tasks in which they have to focus on the mechanical action between a tool and an object and not on the motor action between a hand and a tool (Reynaud et al., 2016). In the latter case, the activations concern the intraparietal sulcus and notably the area AIP (anterior intraparietal area; Reynaud et al., 2016). Thus, the ability to determine the appropriate motor action to use a tool (i.e., hand-tool relationships) would not be supported by the left inferior parietal lobe contrary to what the manipulation-knowledge hypothesis predicts (see Lesourd et al., 2020). Instead, the technical-reasoning hypothesis posits that people first reason at a technical level to create a representation of the mechanical action appropriate to solve a physical problem (left area PF). Then, this representation biases the selection of the appropriate motor actions (intraparietal sulcus) to produce the mechanical action generated through technical reasoning. In this framework, manipulation knowledge is not needed to use tools (Goldenberg, 2013).

1.5. From the frontal lobe to the inferior parietal lobe

The literature on tool-use disorders and the technical-reasoning hypothesis developed from it offers an interesting framework to discuss the viability of the shared neurocognitive processes hypothesis described above. A first point of discussion concerns the nature of the tool-related units. If a parallel has to be drawn in the co-evolution of language and tool-making skills, it appears that it has to be done through an

interpretation in terms of technical units rather than motor units, as suggested by Holloway (1969).

A second point of discussion concerns the key role given to the evolution of the frontal lobe/Broca's area in the progressive complexification of tool-making action sequences. The shared neurocognitive processes hypothesis focuses on the differences between the Oldowan and the Acheulean. In this framework, the combinatorial capacities of the frontal lobe/Broca's area are viewed as critical for this shift. A potential prediction derived from this hypothesis is that damage to the frontal lobe/Broca's area should produce deficits in tool behavior. Some studies have reported a few cases of patients with frontal lobe lesions, who have tool-use disorders (e.g., De Renzi & Lucchelli, 1988). However, as discussed above, tool-use disorders occur generally after damage to the left inferior parietal lobe and not after frontal lobe lesions. It has been shown that the severity of the disorders can increase because of frontal lobe lesions. For instance, Goldenberg and Spatt (2009) found that patients with damage to both the left inferior parietal lobe and the left frontal lobe were more impaired at selecting/using familiar tools and novel tools to solve mechanical problems than patients with selective damage to the left inferior parietal lobe. However, patients with frontal lobe lesions do not show difficulties, contrary to most patients with damage to the inferior parietal lobe (see also Goldenberg & Hagmann, 1998). In broad terms, the importance of the frontal lobe/Broca's area in the co-evolution of language and tool behavior is somewhat surprising if we consider the importance of the left inferior parietal lobe in tool-use skills (see also Stout & Hecht, 2017). This is also true for the language domain given that language skills are clearly not associated only with the activity of the frontal lobe but also concern left posterior brain regions (i.e., temporal and parietal cortex).

Taken together, these findings stress that, to be complete, any version of the shared neurocognitive processes hypothesis must integrate the role of posterior and particularly parietal regions in the conception of how language and tool-use skills could have co-evolved to potentially lead to the complexification of tool-making skills. This integration requires a considerable effort in terms of empirical work from comparative neurophysiology, archaeology and evolutionary biology. In this context, the present study does not claim to provide the reader with any definite answer about how this integration can work. Our more modest goal is to highlight the value of this research. Thus, here we investigate the phylogenetic evolution of three left parietal areas supposedly known to be involved in tool use (left area PF), language (left area PGI), and motor control (left area AIP). We will use the massive redeployment framework developed by Anderson (2007, 2010) to initiate this investigation.

1.6. The massive redeployment framework

The massive redeployment framework is based on the core assumption that cognitive functions that originally evolved to serve a specific behavior or skill are reused for new behaviors or skills without disrupting their participation in existing functions (Anderson, 2007, 2010). The corollary is that there is a correlation between the phylogenetic age of a brain area and the frequency with which it is deployed in a variety of cognitive functions. The older a brain area is, the more cognitive functions it supports. To test this prediction, Anderson (2007) performed statistical analyses on 135 brain-imaging experiments and focused on four categories (attention, perception, imagery and language). Anderson found that the left Brodmann area 18 (occipital cortex) had a greater category diversity than, for instance, the left Brodmann area 38 (temporal cortex), which was mainly involved in language tasks. This result is plausible at an

evolutionary level in suggesting that language-related brain areas could be more recent than brain areas engaged initially in visual perception. This framework and the methods associated present clear limitations. For instance, the result depends on the number of publications concerned with each cognitive function. It is also only an indirect way of assessing the phylogenetic age of human brain areas. Nevertheless, as stressed above, it has great potential to initiate neuroscientific investigation of the co-evolution of language and tool-making skills.

In the present study, we chose to use this framework to explore the phylogenetic evolution of three left parietal areas, namely, the left areas PF, PGI and AIP. The choice to investigate the left areas PF and AIP was motivated by the neuropsychological and neuroscientific literature on tool use, which has indicated that the left area PF could be involved in technical reasoning and the area AIP in motor control (Reynaud et al., 2016; see above). Note that the technical-reasoning hypothesis considers that the motor-control system is supported by both the left and right areas AIP. Here, we decided to focus only on the left one because we restricted our analysis to the left parietal cortex. We also decided to investigate the left area PGI within the angular gyrus because of its known involvement in language skills (Geschwind, 1972; Price, 2000; Seghier, 2013). As explained in Methods, we identified six categories (Tool use, language, memory, attention/executive functions, motor system, sensory system). According to the massive redeployment framework, we predicted that the left area AIP, because of its initial “older” function linked to motor control, would show a greater functional diversity than the left areas PF and PGI. We also predicted that the left area PF is particularly specific to the tool-use category and the left area PGI to the language category. We did not make any prediction concerning the degree of functional diversity of the left areas PF and PGI.

2. Methods

Our analysis aimed at calculating the functional diversity across cognitive function categories for each of the brain areas of interest: PF, PGI and AIP (all three in the left cerebral hemisphere). The precise delineation of these three areas was based upon the parcellation of human cerebral cortex performed by Glasser et al. (2017), which characterizes 180 areas including PF, PGI and AIP. Then, we used the Caret software (van Essen et al., 2001) to obtain, from a flat representation of the left cerebral hemisphere, a set of coordinates that covered uniformly the surface of each brain area (see **Supplementary Materials**). The coordinates obtained were entered into the Neurosynth platform (neurosynth.org) with a radius of 3 mm. This search returned 3884 studies at the date of 17 February 2019. For each brain area, only the studies that reported at least two coordinates were included in the further analyses, i.e., a total of 660 studies. We restricted our selection to the studies that met the three following selection criteria:

- (1) Use of functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) as imaging modality;
- (2) Only neurologically and psychiatrically healthy adults;
- (3) Presence of a coordinate table in the publication (or in supplementary materials), which confirmed that activations concerned the same coordinates entered into Neurosynth.

This led us to identify 125 relevant studies (PF, $n = 41$; PGI, $n = 27$; AIP, $n = 57$). We divided these studies into six cognitive function categories: Tool use (i.e., use of a tool on another object, and not grasping or naming a tool), language (i.e., semantic, syntactic and phonological components), memory (i.e., associative learning or episodic memory), attention/executive functions (i.e., inhibition, working memory or selective attention),

motor system (i.e., imaging, planning or executing a motor action, such as finger movements or grasping an object without using it as a tool), and sensory system (i.e., sensory stimulation). The description of the studies is provided in **Supplementary Materials**. As detailed in Anderson et al. (2013; see also Uddin et al., 2014), the functional diversity of each brain area of interest was defined as a 6-dimensional vector, with each dimension corresponding to a cognitive function category. Each of these 6 values represented the proportion of local observations in the corresponding cognitive function category (i.e., local number of observations by the number of observations over the entire database, i.e., Neurosynth), normalized (i.e., all 6 values summed to 1). Thus, to carry out this normalization, we looked at the number of observations for each cognitive function category in the Neurosynth platform (i.e., 861 observations with the keyword “tool/object”, 1101 with the keyword “language”, 2744 with the keyword “memory”, 1831 with the keyword “attention”, 2565 with the keyword “motor”, and 1145 with the keyword “sensory”). Finally, to calculate the functional diversity across cognitive function categories for each brain area, we used the Shannon’s diversity index H (Shannon, 1948), as proposed by Anderson et al. (2013):

$$H = - \sum_{i=1}^S p_i \ln p_i$$

where $S = 6$ was the number of cognition function categories and p_i corresponded to the i th category proportion. We determined the range of possible estimates of functional diversity via a bootstrapping procedure (10,000 resamples; 80% confidence interval, as in Anderson et al., 2013). We conducted a between-subjects ANOVA with these resamples to compare the functional diversity between our three brain areas of interest (PF, PGI and AIP). Post-hoc t -tests (Bonferroni-Holm adjusted) were also used for pairwise comparisons.

3. Results

Results are given in **Table 1** and **Figures 1-2**. As shown, most of the activations reported for the left area PF concerned tool use (53%) and to a lesser extent language (16%), sensory system (15%), and memory (6%). For the left area PGI, about half of the studies concerned language (53%), and to a lesser extent tool use (23%), attention/executive functions (13%) and memory (9%). No study with activation in left PGI concerned the sensory system and only one the motor system. Most of the activations reported for the left area AIP concerned attention/executive functions (26%), motor system (26%) and sensory system (17%). Regarding functional diversity, the left area AIP was the area with the greatest diversity ($H = 1.66$). The left area PF ($H = 1.37$) had a greater diversity than the left area PGI ($H = 1.23$). The ANOVA revealed that the functional diversity differed significantly between the three brain areas, $F(2, 29997) = 7829.47, p < .001, \eta^2 = .34$. Post-hoc t -tests confirmed that PGI had a significantly greater functional diversity than PF, $t = 41.60, p < .001, d = 0.55$, and AIP, $t = 123.01, p < .001, d = 1.60$, and that PF had a significantly greater functional diversity than AIP, $t = 81.41, p < .001, d = 1.41$.

< Insert **Table 1** and **Figures 1-2** about here >

4. Discussion

The shared neurocognitive processes hypothesis suggests that the emergence of the language-related combinatorial capacities of the frontal lobe/Broca's area over evolution could have played a key role in the complexification of tool-making action sequences. This hypothesis offers a potential interpretation of the difference between the Oldowan and the Acheulean stone tool industries. However, this hypothesis generally overlooks the role played by left posterior, and notably parietal, areas in

language and tool-making skills. The goal of the present study was to propose a first investigation of the phylogenetic evolution of these parietal areas in order to initiate the development of a more comprehensive framework. Our analysis based on the massive redeployment framework provides interesting insights into this aspect. As mentioned in the introduction, the methodology employed remains indirect and no firm conclusions can be drawn from it. In this respect, the discussion of our findings presented below is necessarily speculative. In addition, all the studies included in the tool-use category concerned tool use and not tool making. This also contributes to temper our discussion given that the ultimate goal is to explain the complexification of tool-making skills more broadly and not only tool-use skills³. Regardless, our findings can lay the foundation for an integrative research program aiming to explore in more details the co-evolution of language and tool-making skills in our lineage.

4.1. Functional diversity of the left area AIP

Our first key finding is that the functional diversity of the left area AIP is higher than those of the left areas PF and PGI. This suggests that this brain area is phylogenetically older than the left areas PF and PGI, probably with an original function oriented toward the sensorimotor systems and attentional resources. AIP is the putative human homologue of AIP, which is known to support the grasping component of the prehension system in nonhuman primates (Orban et al., 2006; Vanduffel et al., 2014),

³ The present meta-analysis was based on neuroimaging studies in which participants had to perform tool-related tasks in a scanner. These tasks are obviously far from being comparable to tool-making activities in an ecological context (e.g., stone tool making). As mentioned, we acknowledge this difference, which clearly tempers our discussion. Nevertheless, it is important to remind that neuroimaging evidence has stressed the activation of the left area PF is preferentially when participants focused on the *mechanical actions* involving a tool and an object (Reynaud et al., 2016). Damage to this brain area is also known to generate difficulties in the use of familiar tools as well as the use, selection, and *making* of novel tools (for a review, see Osiurak et al., 2020c). In other words, even if much more evidence is obviously needed to reinforce the link drawn here between tool use in a scanner and tool making in an ecological context, these findings provide indirect evidence in favor of this link.

including in nonhuman primate species that do not possess “elaborated” forms of tool-use skills (e.g., macaques). This finding is consistent with the low involvement of AIP reported here in tool-use tasks, which corroborates the idea that this brain area is not dedicated to the understanding of mechanical actions as suggested by the technical-reasoning hypothesis (Osiurak et al., 2020c; Reynaud et al., 2016). In other words, even if the left area AIP can contribute to tool-use actions by selecting the appropriate motor actions in a tool-use context, this contribution is not specific to tool-use actions and can be generalized to any action directed toward the physical environment (e.g., non-tool-use actions such as object transport). The shared neurocognitive processes hypothesis as developed by Higuchi et al. (2009) suggests that the language-related combinatorial capacities of Broca’s area could have recycled over evolution the preexisting motor skills for object manipulation, thereby leading to a complexification of tool behavior. The important corollary is that tool behavior does not originate, strictly speaking, in Broca’s area (which nevertheless allows its complexification), but in the brain areas involved in motor skills, such as the intraparietal sulcus and notably the left AIP. As a consequence, one would predict that the left AIP is involved not only in the motor system category but also in the tool-use category. However, our findings rule out this possibility, as they indicate that the tool-use category is primarily associated with the left area PF. In broad terms, if Broca’s area is involved in the rearrangement of tool-related units, it is far more plausible that this rearrangement concerns technical units rather than motor units, and, as a result, connections with the left area PF.

4.2. Functional diversity of the left area PF

Our second key finding is that the tool-use category is primarily associated with the left area PF. The studies included in the tool-use category did not concern the motor

actions to perform when using a tool (i.e., hand-tool relationships) but rather the mechanical actions involving a tool and an object (i.e., tool-object relationships). This supports the idea that this brain area is critical for reasoning at a technical level to generate representations of potential mechanical actions (Osiurak et al., 2020c; Reynaud et al., 2016). This finding offers new perspectives for reinterpreting the shared neurocognitive processes hypothesis. As mentioned in the previous section, a left fronto-parietal network could support tool-making skills, with the frontal lobe/Broca's area being involved in the combinatorial rearrangement of technical units and the left area PF in the generation of these technical units. This proposal may appear at odds with the findings discussed in our introduction, which indicate that tool-use disorders generally occur after damage to the left inferior parietal lobe and not after frontal lobe lesions. However, a potential limitation of the tasks employed in neuropsychology and neuroimaging is that the combinatorial component is not really assessed (Le Gall, 2018). Thus, important insights could be gained by investigating in more detail the "generative" (i.e., generation of a cutting action as technical solution) and "combinatorial" (i.e., combination of a cutting action and a leverage action) components of tool-making skills in neuropsychology and cognitive neuroscience.

Another perspective concerns the evolution of the frontal lobe/Broca's area and the left area PF at a phylogenetic level. According to the shared neurocognitive processes hypothesis, the complexification of tool-making action sequences results from the emergence of the language-related combinatorial capacities of the frontal lobe/Broca's area. However, this hypothesis has been formulated by emphasizing the importance of the combinatorial component without considering the potential role of the left parietal cortex in the evolution of tool-making skills. Thus, our findings lead to formulate two plausible evolutionary scenarios for the shared neurocognitive processes

hypothesis. The first scenario is that the evolution of the left area PF/technical-reasoning skills enhanced tool-making skills, in allowing the manufacture of Oldowan tools but not Acheulean tools because of the absence of the combinatorial capacities of the frontal lobe/Broca's area (**Figure 3a**). In other words, the emergence of a combinatorial component marked a step in the complexification of tool-making skills (i.e., the Late Oldowan and Early Acheulean), even if preexisting technical-reasoning skills allowed our predecessors to make less complex forms of tools (i.e., the Lomekwian and Oldowan). The second scenario is that the emergence of the left area PF/technical-reasoning skills was sufficient to support the complexification of tool-making skills (i.e., the Acheulean) even in the absence of the combinatorial component (**Figure 3b**). One corollary is that the making of Oldowan tools did not necessarily require such reasoning skills (Faisal et al., 2010). Another corollary is that the lack of a combinatorial component made our predecessors less effective in their way of combining technical units and, as a result, they had to rely much more on a linear sequence of actions each arising in reaction to the previous action, rather than planned hierarchically organized actions (Harmand et al., 2015; Gowlett, 2011; Wynn, 2002). In this scenario, the emergence of the combinatorial component increased their efficacy on this aspect, either through the emergence of language skills or through a kind of Baldwin effect, allowing them to progressively evolve the capacity to mentally internalize the combinatorial component. Future research is needed to generate predictions to test these two scenarios more specifically.

< Insert **Figure 3** about here >

4.3. Functional diversity of the left area PGI

The third key finding of our study is that the left area PGI is highly specific to language tasks and is associated with the lowest functional diversity. This corroborates the results obtained by Anderson (2007) with a similar methodology. This finding is far from surprising given the many accounts that have stressed the evolutionary precedence of tool making over language (e.g., Morgan et al., 2015). Although this finding is relatively trivial, it nevertheless questions the validity of the shared neurocognitive processes hypothesis. Indeed, this hypothesis posits that the emergence of the combinatorial component of language skills supported the complexification of tool-making skills. However, it remains silent about how the language components located within Broca's area and left posterior brain areas co-evolved. The finding reported here, that the left area PGI is greatly less diverse in terms of cognitive function categories than the left areas PF and AIP, raises the question of this co-evolution. Instead, it suggests a third evolutionary scenario, according to which the combinatorial component of the frontal lobe/Broca's area appeared before the emergence of tool-making skills and language (**Figure 3c**). In other words, this combinatorial component could not be language-specific (e.g., Fedorenko et al., 2012; Higuchi et al., 2009). Instead, this component could have been initially involved in motor control and potentially later exapted for both tool-making skills and language, which is consistent with the theory of the recursive mind⁴ (Corballis, 2003, 2007a, 2007b, 2011). This speculative scenario, if confirmed, would considerably challenge the shared neurocognitive processes

⁴ This theory also posits that combinatorial/recursive skills are not language-specific and could have evolved primarily to permit motor control (see also Arbib, 2005). Thus, these skills could have been also reused for the emergence of, first, gestural language and, then, verbal language. This scenario implies a strong interconnection between gestural communication and sensorimotor regions. Empirical evidence has supported this interconnection (e.g., Iani et al., 2018; Ping et al., 2014; see also Barsalou, 2008; Iani, 2019).

hypothesis in suggesting that tool-making skills and language did not really co-evolve, but have simply been the targets of the same recycling mechanism (i.e., the preexisting combinatorial capacities; Steele & Uomini, 2009; Uomini, 2009).

This third scenario questions the validity of the shared neurocognitive processes hypothesis, but not of the scaffolding hypothesis. As mentioned in the introduction, our study did not aim to evaluate the predictions derived from this hypothesis. Nevertheless, some of our results can be interpreted within this framework. Indeed, several studies included in the tool-use category were interested in the observation of actions including tool-use actions (e.g., Spunt & Lieberman, 2012; Spunt et al., 2010). Therefore, a potential alternative interpretation is that the PF specificity reported here for the tool-use category did not concern the understanding of mechanical actions but rather the observation of tool-use actions – or more generally of physical actions including non-tool-use actions. A large body of evidence has identified a fronto-temporo-parietal network involved in the observation of others' actions made by others with a great number of homologies between human and nonhuman primates (Buccino et al., 2001; Caspers et al., 2010). Recently, we conducted a meta-analysis of neuroimaging studies to explore in more detail whether the action-observation network varies according to whether participants observe non-tool-use (e.g., object grasping or transport) *versus* tool-use actions performed by others (Reynaud et al., 2019). Note that the main difference between these two conditions is that tool-use actions require both mechanical actions (i.e., tool-object relationships) and motor actions (i.e., hand-tool relationships) whereas non-tool-use actions require only motor actions (i.e., hand-tool relationships). We found that both conditions share the aforementioned action-observation network. However, the observation of tool-use actions activates notably the left area PF, confirming its involvement in the understanding of mechanical actions. As a

consequence, it is unlikely that our tool-use category was an “action observation” category. In addition, the presence of studies interested in tool-use action observation and associated with the left area PF in the present study corroborates the results of our previous meta-analysis.

This result also offers an interesting way to discuss the scaffolding hypothesis. The involvement of the left area PF in the observation of tool-use actions implies that people reason at a technical level not only when they use tools but also when they observe others using tools (for discussion, see Stout & Hecht, 2017). This finding is in line with the recent extension of the technical-reasoning hypothesis to cumulative technological culture, which assumes that technical-reasoning skills allow humans to be unique social learners in the technical domain (Osiurak & Reynaud, 2020; Osiurak et al., 2020a, 2020b). In other words, it posits that the transmission of technical content is based on the learner’s ability to understand the physical principles at stake irrespective of the social-learning condition (i.e., reverse engineering, observation, teaching). It is also consistent with the scaffolding hypothesis in assuming that language-based forms of social learning (e.g., teaching) enable a better transmission of technical content. The technical-reasoning hypothesis provides nevertheless an alternative to the scaffolding hypothesis in emphasizing the role of the technical dimension of human cognition in the evolution of tool-making skills (for a discussion about the lack of technical cognition models in archaeology, see Wynn et al., 2014, 2017).

4.4. Apraxia and aphasia

Before concluding, we would like to stress the interest of our findings for neuropsychology. The question of the cognitive independence between apraxia and aphasia has been repeatedly addressed in neuropsychology (Bidula & Króliczak, 2015;

Duffy & Duffy, 1981; Finkelnburg, 1870; Frey, 2008; Goldenberg et al., 2003; Goldenberg & Randerath, 2015; Goodglass & Kaplan, 1963; Króliczak et al., 2011; Liepmann, 1908; Vingerhoets et al., 2013). The main reason for this focus is that apraxia is frequently accompanied by aphasic disturbances, particularly after damage to posterior brain regions. This co-occurrence can be interpreted as evidence for common cognitive processes involved in both language and tool use. Another way of interpreting this co-occurrence is that both language and tool-use skills rely on brain regions that are very close at a neuroanatomical level and, as a result, that can be more frequently damaged conjointly. The present findings speak in favor of the neuroanatomical proximity interpretation in indicating that the left area PF is specific to the tool-use category whereas the left area PGI is specific to the language category. There is also a marked difference in terms of functional diversity between the two brain areas, which implies that the left area PF is phylogenetically older than the left area PGI. In other words, our findings do not support the idea that language and tool-use skills share common cognitive processes within the left inferior parietal lobe. Importantly, this is not to say that some frontal lobe regions can be involved in both domains, such as Broca's area as discussed above. This is also not to say that language and tool-use skills do not interact together. In this respect, it is noteworthy that the studies included in the tool-use category for the left area PF and the left area PGI differed. Whereas the former was more concerned with action-observation tasks, the latter was more concerned with pantomime tasks (see **Supplementary Materials**). This difference is interesting if we consider the accounts that have stressed that gestural language precedes verbal language at both a phylogenetic level and an ontogenetic level (e.g., Arbib, 2005; Corballis, 1999; Gentilucci & Corballis, 2006; Goldin-Meadow & Singer, 2003; Iverson & Goldin-Meadow, 2005). This primacy of gesture is also consistent with recent findings

that tool-use pantomime could be at the crossroads between tool-use skills and communicative/language skills (Finkel et al., 2018; see also Goldenberg, 2013). In a way, our findings can contribute to better understand better how language and tool behavior interact together.

5. Conclusion

To conclude, the present study highlights the importance of the left inferior parietal lobe in the emergence and development of tool-making skills, confirming the predictions of the technical-reasoning hypothesis. Our findings also provide a potential way of completing the shared neurocognitive processes hypothesis, which has focused so far mainly on the role played by the frontal lobe/Broca's area. We have proposed a series of scenarios, which are obviously speculative. Further work is needed to collect empirical data to test these different scenarios more specifically and, thus, to increase our understanding of the co-evolution of language and tool-making skills in the human lineage.

6. Acknowledgments

This work was performed within the framework of the LABEX CORTEX (ANR-11-LABX-0042) of Université de Lyon, within the program "Investissements d'Avenir" (ANR-11-IDEX-0007) operated by the French National Research Agency (ANR). NU was supported by the Max Planck Society and a grant from the Templeton World Charity Foundation (<https://www.templetonworldcharity.org/>) #0271. The opinions expressed in this publication are those of the authors and do not necessarily reflect the views of Templeton World Charity Foundation, Inc.

7. References

Anderson, M. L. (2007). Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist*, 13, 1-9.

- Anderson, M. L. (2010). Neural reuse: A fundamental organizational principle of the brain. *Behavioral and Brain Sciences*, *33*, 245–313.
- Anderson, M. L., Kinnison, J., & Pessoa, L. (2013). Describing functional diversity of brain regions and brain networks. *NeuroImage*, *73*, 50–58.
- Arbib, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences*, *28*, 105–167.
- Barsalou, L. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617–645.
- Belfer-Cohen, A., & Goren-Inbar, N. (1994). Cognition and communication in the Levantine Lower Paleolithic. *World Archaeology*, *26*, 144–157.
- Bidula, S. P., & Króliczak, G. (2015). Structural asymmetry of the insula is linked to the lateralization of gesture and language. *European Journal of Neuroscience*, *41*, 1438–1447.
- Braun, D. R., Aldeias, V., Archer, W., Arrowsmith, J. R., Baraki, N., Campisano, C. J., et al. (2019). Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proceedings of the National Academy of Sciences*, *116*, 11712–11717.
- Bruner, E. (2018). Human paleoneurology and the evolution of the parietal cortex. *Brain, Behaviour, and Evolution*, *91*, 136–147.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buxbaum, L. J. (2001). Ideomotor apraxia: A call to action. *Neurocase*, *7*, 445–458.
- Buxbaum, L. J., & Saffran, E. M. (2002). Knowledge of object manipulation and object function: Dissociations in apraxic and nonapraxic subjects. *Brain and Language*, *82*, 179–199.
- Caldwell, C. A., & Millen, A. E. (2009). Social learning mechanism and cumulative cultural evolution. Is imitation necessary? *Psychological Science*, *20*, 1478–1487.
- Caldwell, C. A., Renner, E., & Atkinson, M. (2018). Human teaching and cumulative cultural evolution. *Review of Philosophy and Psychology*, *9*, 751–770.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*, 1148–1167.
- Coolidge, F. L., & Wynn, T. (2005). Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal*, *15*, 5–26.
- Corballis, M. C. (1999). The gestural origins of language. *American Scientist*, *87*, 138–145.
- Corballis, M. C. (2003). Recursion as the key to the human mind. In K. Sterelny & J. Fitness (Eds.), *From mating to mentality: Evaluating evolutionary psychology* (pp. 155–171). New York: Psychology Press.
- Corballis, M. C. (2007a). Recursion, language, and starlings. *Cognitive Science*, *31*, 697–704.
- Corballis, M. C. (2007b). The uniqueness of human recursive thinking. *American Scientist*, *95*, 240–248.
- Corballis, M. C. (2011). *The recursive mind: The origins of human language, thought, and civilization*. Princeton: Princeton University Press.
- De Oliveira, E., Reynaud, E., & Osieurak, F. (2019). Roles of technical reasoning, theory of mind, creativity, and fluid cognition in cumulative technological culture. *Human Nature*, *30*, 326–340.
- De Renzi, E., & Lucchelli, F. (1988). Ideational apraxia. *Brain*, *111*, 1173–1185.
- De Renzi, E., Pieczuro, A., & Vignolo, L.A. (1968). Ideational apraxia: A quantitative study. *Neuropsychologia*, *6*, 41–52.
- Dean, L. G., Kendal, R. L., Schapiro, B., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*, 1114–1118.
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews*, *89*, 284–301.

- Duffy, R. J., & Duffy, J. R. (1981). Three studies of deficits in pantomimic expression and pantomimic recognition in aphasia. *Journal of Speech and Hearing Research, 14*, 70–84.
- Evans, J. St. B. T. (2010). Intuition and reasoning: A dual-process perspective. *Psychological Inquiry, 21*, 313–326.
- Faisal, A., Stout, D., Apel, J., & Bradley, B. (2010). The manipulative complexity of Lower Paleolithic stone toolmaking. *PLoS ONE, 5*, e13718.
- Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Current Biology, 22*, 2059–2062.
- Finkel, L., Hogrefe, K., Frey, S. H., Goldenberg, G., & Randerath, J. (2018). It takes two to pantomime: Communication meets motor cognition. *Neuroimage: Clinical, 19*, 1008–1017.
- Frey, S. H. (2008). Tool use, communicative gesture and cerebral asymmetries in the modern human brain. *Philosophical Transactions of the Royal Society of London B, 363*, 1951–1957.
- Finkelnburg, F. C. (1870). Sitzung der Niederrheinischen Gesellschaft in Bonn. Medizinische Section. *Berliner Klinische Wochenschrift, 7*, 449–450, 460–462.
- Friederici, A.D., Bahlmann, J., Heim, S., Schubotz, R.I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proceedings of the National Academy of Sciences, 103*, 2458–2463.
- Gagnepain, J. (1990). *Du vouloir dire. Du signe, de l'outil*. Bruxelles: De Boeck Université.
- Gärdenfors, P., & Högberg, A. (2017). The Archaeology of Teaching and the Evolution of *Homo docens*. *Current Anthropology, 58*, 188–208.
- Gentilucci, M., & Corballis, M. C. (2006). From manual gesture to speech: A gradual transition. *Neuroscience and Biobehavioral Reviews, 30*, 949–960.
- Geschwind, N. (1972). Language and the brain. *Scientific American, 226*, 76–83.
- Geschwind, N. (1975). The apraxias: Neural mechanisms of disorders of learned movement. *American Scientist, 63*, 188–195.
- Gibson, K. R. (1993). Tool use, language and social behavior in relationship to information processing capacities. In K. R. Gibson & T. Ingold (Eds.), *Tools, language and cognition in human evolution* (pp. 251–269). Oxford: Oxford University Press.
- Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., et al. (2017). A multi-modal parcellation of human cerebral cortex. *Nature, 536*, 171–178.
- Goldenberg, G. (2013). *Apraxia: The cognitive side of motor control*. Oxford: Oxford University Press.
- Goldenberg, G., & Hagmann, S. (1998). Tool use and mechanical problem solving in apraxia. *Neuropsychologia, 36*, 581–589.
- Goldenberg, G., Hartmann, K., & Schlott, I. (2003). Defective pantomime of object use in left brain damage: Apraxia of asymbolia? *Neuropsychologia, 41*, 1565–1573.
- Goldenberg, G., & Randerath, J. (2015). Shared neural substrates of apraxia and aphasia. *Neuropsychologia, 75*, 40–49.
- Goldenberg, G., & Spatt, J. (2009). The neural basis of tool use. *Brain, 132*, 1645–1655.
- Greenfield, P. M. (1991). Language, tools, and brain: The development and evolution of hierarchically organized sequential behavior. *Behavioral and Brain Sciences, 14*, 531–595.
- Goldin-Meadow, S., & Singer, M.A. (2003). From children's hands to adults' ears: Gesture's role in teaching and learning. *Developmental Psychology, 39*, 509–520.
- Goodglass, H., & Kaplan, E. (1963). Disturbance of gesture and pantomime in aphasia. *Brain, 86*, 703–720.
- Goren-Inbar, N. (2011). Culture and cognition in the Acheulian industry: A case study from Gesher Benot Ya'aqov. *Philosophical Transactions of the Royal Society B, 366*, 1038–1049.
- Gowlett, J. A. J. (1979). Complexities of cultural evidence in the Lower and Middle Pleistocene. *Nature, 278*, 14–17.

- Gowlett, J. A. J. (2011). The Empire of the Acheulean strikes back. In J. Sept & D. Pilbeam (Eds.), *Casting the net wide: Papers in honor of Glynn Isaac and his approach to human origins research* (pp. 93–114). Oxford: Oxbow Books.
- Gowlett, J. A. J. (2020). Deep structure in the Acheulean adaptation: technology, sociality and aesthetic emergence. *Adaptive Behavior*, 1059712320965713.
- Harmand, S. Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., et al. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, 521, 310–315.
- Heilman, K. M., Maher, L. M., Greenwald, M. L., & Rothi, L. J. G. (1997). Conceptual apraxia from lateralized lesions. *Neurology*, 49, 457–464.
- Heilman, K. M., Rothi, L. J., & Valenstein, E. (1982). Two forms of ideomotor apraxia. *Neurology*, 32, 342–346.
- Higuchi, S., Chaminade, T., Imamizu, H., & Kawato, M. (2009). Shared neural correlates for language and tool use in Broca's area. *NeuroReport*, 20, 1376–1381.
- Holloway, R. L. (1969). Culture: A human domain. *Current Anthropology*, 10, 47–64.
- Iani, F. (2019). Embodied memories: Reviewing the role of the body in memory processes. *Psychonomic Bulletin & Review*, 26, 17471–766.
- Iani, F., Burin, D., Salatino, A., Pia, L., Ricci, R., & Bucciarelli, M. (2018). The beneficial effect of a speaker's gestures on the listener's memory for action phrases: The pivotal role of the listener's premotor cortex. *Brain and Language*, 180–182, 8–13.
- Isaac, G. (1976). Stages of cultural elaboration in the Pleistocene: Possible archaeological indicators of the development of language capabilities. *Annals of the New York Academy of Sciences*, 280, 275–288.
- Iverson, J. M., & Goldin-Meadow, S. (2005). Gesture paves the way for language development. *Psychological Science*, 16, 367–371.
- Jarry, C., Osiurak, F., Delafuys, D., Chauviré, V., Etcharry-Bouyx, F., & Le Gall, D. (2013). Apraxia of tool use: More evidence for the technical reasoning hypothesis. *Cortex*, 49, 2322–2333.
- Johnson-Laird, P.N. (2006). *How we reason*. Oxford: Oxford University Press.
- Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron*, 50, 963–974.
- Króliczak, G., Piper, B. J., & Frey, S. H. (2011). Atypical lateralization of language predicts cerebral asymmetries in parietal gesture representations. *Neuropsychologia*, 49, 1698–1702.
- Lombao, D., Guardiola, M., & Mosquera, M. (2017). Teaching to make stone tools: new experimental evidence supporting a technological hypothesis for the origins of language. *Scientific Reports*, 7, 1–14.
- Le Gall, D. (1998). *Des apraxies aux atechnies. Propositions pour une ergologie clinique*. Bruxelles: De Boeck Université.
- Leakey, M. D. (1971). *Olduvai Gorge, Volume 3: Excavations in beds I and II, 1960–1963*. Cambridge: Cambridge University Press.
- Lesourd, M., Naëgelé, B., Jaillard, A., Detante, O., & Osiurak, F. (2020). Using tools efficiently despite defective hand posture: A single-case study. *Cortex*, 129, 406–422.
- Liepmann, H. (1908). *Drei aufsatze aus dem apraxiegebiet*. Berlin: Karger.
- Mahaney, R. A. (2014). Exploring the complexity and structure of Acheulean stoneknapping in relation to natural language. *PaleoAnthropology*, 2014, 586–606.
- Mahaney, R. A. (2015). *Cognition and planning in Paleolithic technology: Studies in experimental archaeology*. Ph.D. thesis, Indiana University, Bloomington.
- Matsuzawa, T. (2008). Primate foundations of human intelligence. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 3–25). Tokyo: Springer.

- Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., et al. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, 6, 6029.
- Muller, A., Clarkson, C., & Shipton, C. (2017). Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. *Journal of Anthropological Archaeology*, 48, 166–180.
- Orban, G. A., Claeys, K., Nelissen, K., Smans, R., Sunaert, S., Todd, J. T., et al. (2006). Mapping the parietal cortex of human and non-human primates. *Neuropsychologia*, 44, 2647–2667.
- Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological Review*, 123, 534–568.
- Osiurak, F., & Badets, A. (2017). Use of tools and misuse of embodied cognition. *Psychological Review*, 124, 361–368.
- Osiurak, F., De Oliveira, E., Navarro, J., Lesourd, M., Claidière, N., & Reynaud, E. (2016). Physical intelligence does matter to cumulative technological culture. *Journal of Experimental Psychology: General*, 145, 941–948.
- Osiurak, F., De Oliveira, E., Navarro, J., & Reynaud, E. (2020a). The castaway island: Distinct roles of theory of mind and technical reasoning in cumulative technological culture. *Journal of Experimental Psychology: General*, 149, 58–66.
- Osiurak, F., Jarry, C., Allain, P., Aubin, G., Etcharry-Bouyx, F., Richard, I., et al. (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. *Psychological Review*, 117, 517–540.
- Osiurak, F., Lasserre, S., Arbanti, J., Brogniart, J., Bluet, A., Navarro, J., & Reynaud, E. (2020b). Technical reasoning is important for cumulative technological culture.
- Osiurak, F., Lesourd, M., Navarro, J., & Reynaud, E. (2020c). Technition: When tools come out of the closet. *Perspectives on Psychological Science*, 15, 880–897.
- Osiurak, F., & Reynaud, E. (2020). The elephant in the room: What matters cognitively in cumulative technological culture. *Behavioral and Brain Sciences*, 43, e156.
- Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences*, 2, 367–408.
- Ping, R. M., Goldin-Meadow, S., & Beilock, L. (2014). Understanding gesture: Is the listener's motor system involved? *Journal of Experimental Psychology: General*, 143, 195–204.
- Price, C.J. (2010). The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191, 62–88.
- Putt, S. S., Wijekumar, S., Franciscus, R. G., & Spencer, J. P. (2017). The functional brain networks that underlie early stone age tool manufacture. *Nature Human Behaviour*, 1, 102.
- Reynaud, E., Lesourd, M., Navarro, J., & Osiurak, F. (2016). On the neurocognitive origins of human tool use: A critical review of neuroimaging data. *Neuroscience & BioBehavioral Reviews*, 64, 421–437.
- Reynaud, E., Navarro, J., Lesourd, M., & Osiurak, F. (2019). To watch is to work: A critical review of neuroimaging data on Tool-use Observation Network (ToON). *Neuropsychology Review*, 29, 484–497.
- Rothi, L. J. G., Ochipa, C., & Heilman, K. M. (1991). A cognitive neuropsychological model of limb praxis. *Cognitive Neuropsychology*, 8, 443–458.
- Ruck, L., & Uomini, N. (in press). Artefact, praxis, tool and symbol. In A. Lock & N. Gontier (Eds.), *Oxford Handbook of Symbolic Evolution*. Oxford: Oxford University Press.
- Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *The Neuroscientist*, 19, 43–61.
- Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N., et al. (1997). 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature*, 385, 333–336.

- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27, 379–423, 623–656.
- Sharon, G., Alperson-Afil, N., & Goren-Inbar, N. (2011). Cultural conservatism and variability in the Acheulian sequence of Gesher Benot Ya'aqov. *Journal of Human Evolution*, 60, 387–397.
- Shipton, C., & Nielsen, M. (2015). Before cumulative culture: The evolutionary origins of overimitation and shared intentionality. *Human Nature*, 26, 331–345.
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior*. Baltimore: John Hopkins University Press.
- Spunt, R. P., & Lieberman, M. D. (2012). Dissociating modality-specific and supramodal neural systems for action understanding. *Journal of Neuroscience*, 32, 3575–3583.
- Spunt, R. P., Satpute, A. B., Lieberman, M. D. (2010). Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. *Journal of Cognitive Neuroscience*, 23, 63–74.
- Steele, J., & Uomini, N. (2009). Can the archaeology of manual specialization tell us anything about language evolution? A survey of the state of play. *Cambridge Archaeological Journal*, 19, 97–110.
- Stout, D., & Hecht, E. E. (2017). Evolutionary neuroscience of cumulative culture. *Proceedings of the National Academy of Sciences*, 114, 7861–7868.
- Stout, D., Rogers, M. J., Jaeggi, A. V., & Semaw, S. (2019). Archaeology and the origins of human cumulative culture: a case study from the earliest Oldowan at Gona, Ethiopia. *Current Anthropology*, 60, 309–340.
- Stout, D., Semaw, S., Rogers, M. J., & Cauche, D. (2010). Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution*, 58, 474–491.
- Stout, D., Toth, N., Schick, K., & Chaminade, T. (2008). Neural correlates of Early Stone Age toolmaking: Technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society of London B*, 363, 1939–1949.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28, 675–735.
- Toth, N. (1985). The Oldowan reassessed: a close look at early stone artifacts. *Journal of Archaeological Science*, 12, 101–120.
- Toth, N., & Schick, K. (2018). An overview of the cognitive implications of the Oldowan Industrial Complex. *Azania: Archaeological Research in Africa*, 53, 3–39.
- Uddin, L. Q., Kinnison, J., Pessoa, L., & Anderson, M. L. (2014). Beyond the tripartite cognition–emotion–interoception model of the human insular cortex. *Journal of Cognitive Neuroscience*, 26, 16–27.
- Uomini, N. (2009). Prehistoric left-handers and prehistoric language. In S. A. de Beaune & F. L. Coolidge (Eds.), *The emergence of cognitive abilities: The contribution of neuropsychology to archaeology* (pp. 37–55). Cambridge: Cambridge University Press.
- Uomini, N., & Lawson, R. (2017). Effects of handedness and viewpoint on the imitation of origami-making. *Symmetry*, 9, 182.
- Uomini, N., & Meyer, G. F. (2013). Shared brain lateralization patterns in language and acheulean stone tool production: A functional transcranial Doppler ultrasound study. *PLoS One*, 8, e72693.
- Uomini, N., & Ruck, L. (2018). Manual laterality and cognition through evolution: An archaeological perspective. *Progress in Brain Research*, 238, 295–323.
- Van Elk, M. (2014). The left inferior parietal lobe represents stored hand-postures for object use and action prediction. *Frontiers in Psychology*, 5, 333.
- van Elk, M., van Schie, H., & Bekkering, H. (2014). Action semantics: A unifying conceptual framework for the selective use of multimodal and modality-specific object knowledge. *Physics of Life Review*, 11, 220–250.

- 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. *Journal of the American Medical Informatics Association*, 8, 443–459.
- Vanduffel, W., Zhu, Q., & Orban, G. A. (2014). Monkey cortex through fMRI glasses. *Neuron*, 83, 533–550.
- 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.
- Wynn, T. (1991). Tools, grammar and the archaeology of cognition. *Cambridge Archaeological Journal*, 1, 191–206.
- Wynn, T. (2002). Archaeology and cognitive evolution. *Behavioral & Brain Sciences*, 25, 389–438.
- Wynn, T., & Coolidge, F. L. (2014). Technical cognition, working memory and creativity. *Pragmatics & Cognition*, 22, 45–63.
- Wynn, T., & Gowlett, J. (2018). The handaxe reconsidered. *Evolutionary Anthropology: Issues, News, and Reviews*, 27, 21–29.
- Wynn, T., Haidle, M. N., Lombard, M., & Coolidge, F. L. (2017). The expert cognition model in human evolutionary studies. In T. Wynn & F. L. Coolidge (Eds.), *Cognitive models in paleolithic archaeology* (pp. 21–44). Oxford: Oxford University Press.
- Zwirner, E., & Thornton, A. (2015). Cognitive requirements of cumulative culture: teaching is useful but not essential. *Scientific Reports*, 5, 16781.

Co-Evolution of Tool Behavior and Language

Table 1. Functional diversity across cognitive function categories by the brain area (PF, PGI, AIP)

Brain area	Studies reported	Cognitive function categories						Functional diversity <i>H</i>
		Tool use	Language	Memory	Attention/ Exe. funct.	Motor system	Sensory system	
PF	<i>N</i>	16	6	6	4	3	6	1.37 [0.39-2.36]
	<i>Proportion</i>	0.39	0.15	0.15	0.10	0.07	0.15	
	<i>Normalized proportion</i>	0.54	0.16	0.06	0.06	0.03	0.15	
PGI	<i>N</i>	4	12	5	5	1	0	1.23 [0.30-2.17]
	<i>Proportion</i>	0.15	0.44	0.19	0.19	0.04	0.00	
	<i>Normalized proportion</i>	0.23	0.53	0.09	0.13	0.02	0.00	
AIP	<i>N</i>	4	6	3	17	16	11	1.66 [0.57-2.74]
	<i>Proportion</i>	0.07	0.11	0.05	0.30	0.28	0.19	
	<i>Normalized proportion</i>	0.13	0.15	0.03	0.26	0.17	0.26	

Exe. funct., executive functions. Values in brackets are 80% confidence intervals.

Normalized % were obtained based on the entire database (i.e., 861 observations with the keyword “tool/object”, 1101 with the keyword “language”, 2744 with the keyword “memory”, 1831 with the keyword “attention”, 2565 with the keyword “motor”, and 1145 with the keyword “sensory”).

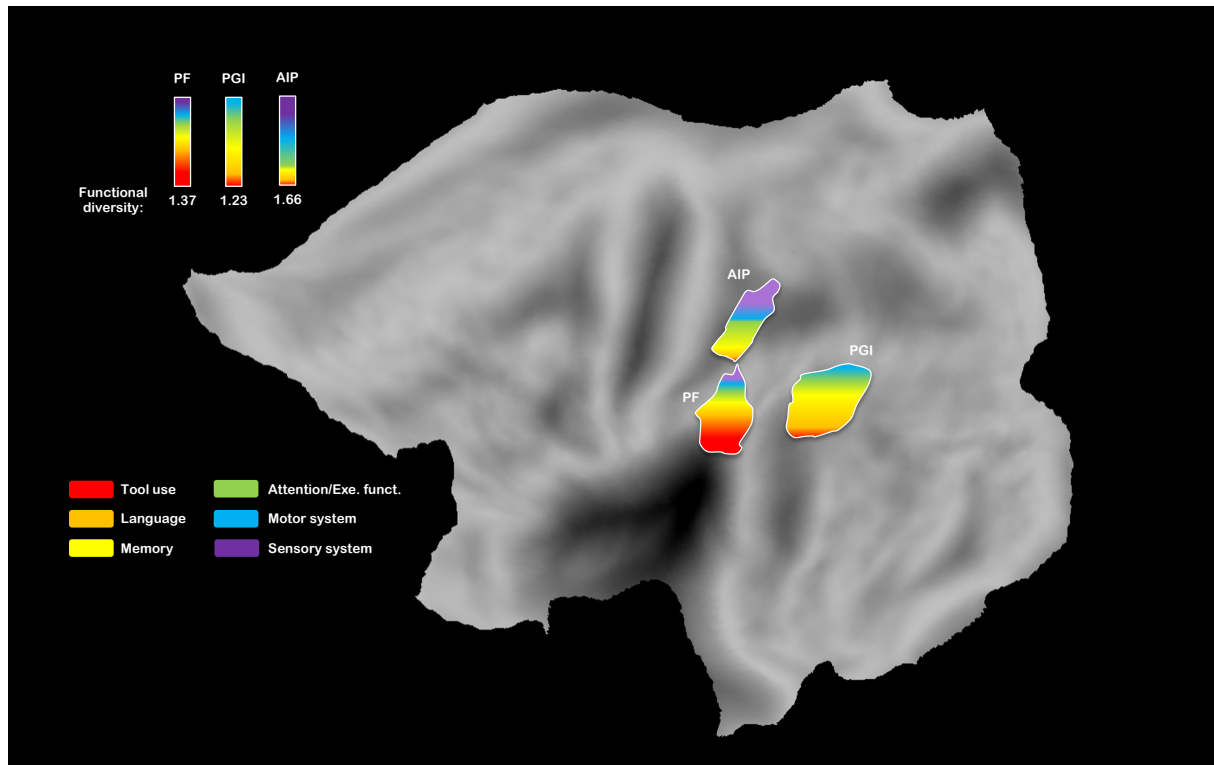


Figure 1. Functional diversity across cognitive function categories for each brain area (PF, PGI and AIP; left cerebral hemisphere). As shown, the diversity is greater for PGI than PF and AIP, and greater for PF than AIP. Colored surface represents the normalized proportion of studies for a category given. For instance, for PGI, most of the surface is covered with orange color because 53% of the studies concerned by the area PGI reported activations for language tasks. In contrast, most of the surface of the area PF is covered with red color (i.e., tool use). More details are given in Table 1.

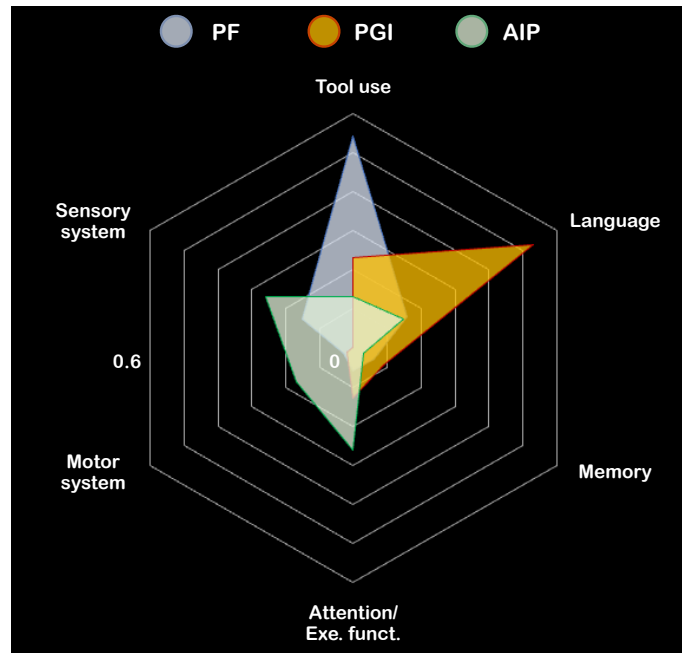


Figure 2. Functional diversity across cognitive function categories for each brain area (PF, PGI and AIP; left cerebral hemisphere). More details are given in Table 1.

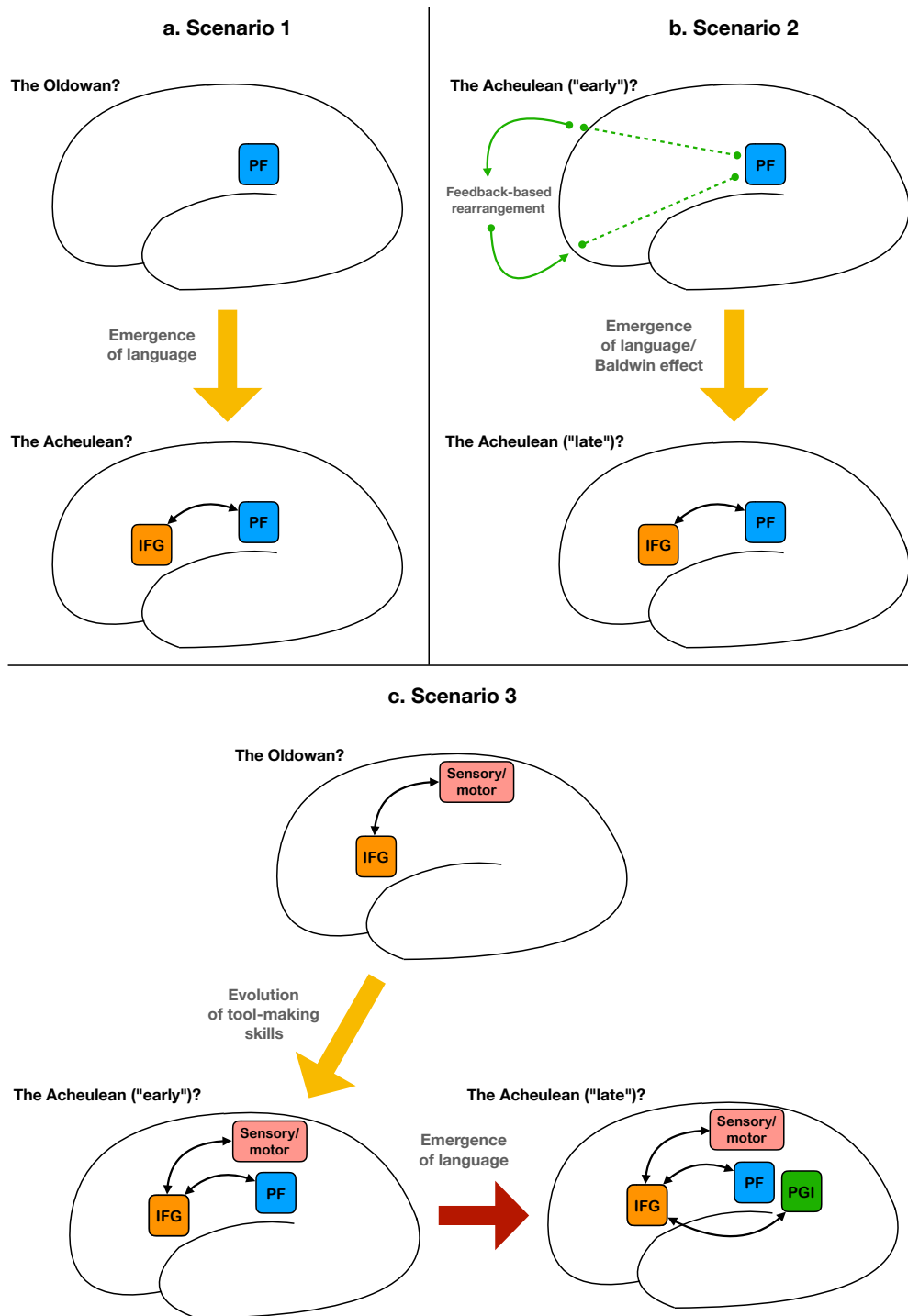


Figure 3. Three potential evolutionary scenarios that include the interaction between the combinatorial component of the frontal lobe/Broca's area (inferior frontal gyrus, IFG) and the generative component of the left area PF. In (a), the emergence of language produces the shift from the Oldowan to the Acheulean. In (b), technical-reasoning skills (left area PF) are sufficient for the Acheulean because the combinatorial capacities are compensated by feedbacks occurring through the progression of the task. Later, these combinatorial capacities are internalized either by the emergence of language or by a kind of Baldwin effect. In (c), the combinatorial capacities of the frontal lobe/Broca's area are initially not language-related but are used for other purposes (e.g., sensorimotor systems). These capacities are reused later in recycling first technical-reasoning skills and then language skills. The "?" stresses the speculative nature of the scenarios depicted here.