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REVIEW

To Watch is to Work: a Review of NeuroImaging Data on Tool Use Observation Network

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Abstract

Since the discovery of mirror neurons in the 1990s, many neuroimaging studies have tackled the issue of action observation with the aim of unravelling a putative homolog human system. However, these studies do not distinguish between non-tool-use versus tool-use actions, implying that a common brain network is systematically involved in the observation of any action. Here we provide evidence for a brain network dedicated to tool-use action observation, called the tool-use observation network, mostly situated in the left hemisphere, and distinct from the non-tool-use action observation network. Areas specific for tool-use action observation are the left cytoarchitectonic area PF within the left inferior parietal lobe and the left inferior frontal gyrus. The neural correlates associated with the observation of tool-use reported here offer new insights into the neurocognitive bases of action observation and tool use, as well as addressing more fundamental issues on the origins of specifically human phenomena such as cumulative technological evolution.

Keywords Tool use · Action observation · Left inferior parietal cortex · Meta-analysis

Introduction

Imagine a friend giving you a hand to fix shelves. Because it is nice of them, you promised yourself you would let them do as they think best. Yet, you cannot help intervening because you think of a better technical solution. You also remember that when your parent helped you to do so 5 years ago, you did not foresee what they intended to do, and learnt a lot by observing them. These two scenarios illustrate a phenomenon we all experience frequently, namely, watching someone work involves a critical observation of the tool-use actions performed. Surprisingly, this phenomenon has received little attention, because studies generally do not distinguish between non-tool-use versus tool-use actions (Peeters, Rizzolatti, & Orban, 2013; Peeters et al., 2009), implying as a consequence the hypothesis of a common brain network de facto involved in the observation of any action. Because humans are social animals that use many tools in everyday life for many purposes (e.g., communicating, eating, grooming), we spend a great amount of time watching others use tools. This behavior has been suggested to be critical for the social transmission of technological traits across and within generations (Boyd & Richerson, 1996; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Therefore, a fundamental issue is whether some neurocognitive mechanisms are more specifically involved in the observation of tool-use actions. Our goal is to tackle this issue based on a review of neuroimaging data on non-tool-use versus tool-use action observation.

One of the fundamental functions of the brain is to allow us to act and react in an appropriate manner to the world. Action is the means through which we interact with the environment. Because we are social animals, more than often we observe others interacting with the world through their own actions. The brain areas engaged when we observe others performing actions have been intensively studied, and have been labelled

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the action observation network (Buccino et al., 2001; Caspers, Zilles, Laird, & Eickhoff, 2010). The interest in the action observation network has grown dramatically in the last two decades, notably because it has been considered as the core network underlying critical social abilities such as action understanding, imitation and social learning (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Decety & Grezes, 1999; Iacoboni, 2009; Meltzoff & Moore, 1977). The brain areas composing the action observation network could contain neurons exhibiting functional properties similar to the ones discovered by the seminal work from Rizzolatti's team in the macaque, the so-called "mirror neurons" (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). These visuomotor neurons, situated in area F5 of the premotor cortex, fire when the macaque performs an action or observes another individual performing a similar action. In humans, it has been shown that observing an action leads to the activation of a brain network somehow similar to the one subserving its execution. This phenomenon of motor resonance (Uithol, van Rooij, Bekkering, & Haselager, 2011) has been well documented (Buccino et al., 2001; Chong, Williams, Cunnington, & Mattingley, 2008; Dinstein, Hasson, Rubin, & Heeger, 2007; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Johnson-Frey et al., 2003; Rizzolatti et al., 1996) and could occur in the premotor and parietal cortices. It has been suggested that we use this motor resonance to understand others' actions and intentions (Fadiga, Craighero, & Olivier, 2005; Iacoboni, 2009; Van Overwalle & Baetens, 2009). More specifically, mirror neurons could mediate the understanding of observed actions by the means of shared representations, when observing an action performed by another individual, a motor representation is activated in the observer's cortex. This representation matches the one that would be generated by the execution of the same action, whose intention and goal are known by the observer. This intention is then assigned to the observed action. In this respect, the "mirror neuron system" might allow us to infer the others' intentions by recreating their actions in our own mind and therefore to access their hidden intentions (Gallese & Goldman, 1998).

The idea that mirror neurons provide the basis of action understanding has nevertheless been challenged (Dinstein, Gardner, Jazayeri, & Heeger, 2008; Hickok, 2009, 2014; Lingnau, Gesierich, & Caramazza, 2009). One of the main arguments concerns the nature of what is meant by "action understanding" (see Hickok, 2009 for other compelling arguments; see also Brass & Heyes, 2005 for an alternative proposal). Action can be divided into two – and even three levels (see below). Let us illustrate with the Dr. Jekyll and Mr. Hyde example provided by Jacob and Jeannerod (2005). The lower level is the motor action (e.g., grasping a scalpel). The higher level is the intention, that is, the "ultimate" goal of this motor action (e.g., offering help versus obtaining pleasure by killing). The fact is that the same motor action can be initiated by different intentions. So, as suggested by Jacob and Jeannerod (2005), observing a motor action is not sufficient for understanding others' intentions. An intermediate level can even be considered, particularly in the tool-use context. This level is the mechanical action (e.g., cutting). Likewise, the observation of a motor action is not enough to infer a mechanical action given that the same motor action (e.g., back and forth movement) can be performed for distinct mechanical actions (e.g., cutting with a knife versus using a eraser) and vice versa.

In most of the studies of the action observation network, neither theoretical nor methodological distinctions are made between tool-use and non-tool-use actions (Peeters et al., 2009, 2013). In this context, an outstanding, critical issue is whether a common network is at work irrespective of the involvement of a tool in the action observed. To address this issue fully, it is necessary to specify the different forms of interaction underlying tool-use actions and particularly those that are specific to these actions compared to non-tool-use actions. A major methodological issue is that some tool-use actions can require the mere manipulation of a tool that does not interact mechanically with another object (e.g., smartphone). This kind of tool-use actions is difficult to distinguish from non-tool-use actions where a tool, which is also an object, is simply grasped. Therefore, a better framework to investigate the neurocognitive processes involved specifically in tool-use actions is to limit tool-use actions to actions where a tool interacts physically with an object. Based on this, our rationale is as follows. As shown in Fig. 1, we focus on tool-use action observation that engages a hand-tool interaction (i.e., a motor action) as well as a tool-object interaction (i.e., a mechanical action). The non-tool-use action observation situation involves a hand-object interaction only. A tool is also an object. When using a tool we also grasp this tool. Here a tool will be defined as a specific case of an object mediating the interaction between the hand and the final object (Osiurak, Rossetti, & Badets, 2017). In this framework, it is clear that both tool-use and non-tool-use actions require hand-tool to object interactions (i.e., motor actions). However, tool-use actions differ from non-tool-use actions by the presence of an additional tool-object interaction (i.e., mechanical actions). Therefore, contrasting these two situations will allow us to explore the cerebral correlates associated with the tool-object component, a critical point for understanding whether a specific network is at work when observing tool-use actions.

On a neuroanatomic level, humans are equipped with a fine-tuned prehension system located in the superior parietal lobe (SPL), the intraparietal sulcus (IPS) and dorsal premotor areas. This dorso-dorsal system is concerned with motor actions and is not specific to tool use. More relevant to our concerns, evidence from neuropsychology and neuroimaging has indicated that the supramarginal gyrus (SMG) in the left inferior parietal lobe (IPL) within the ventro-dorsal system might play a central

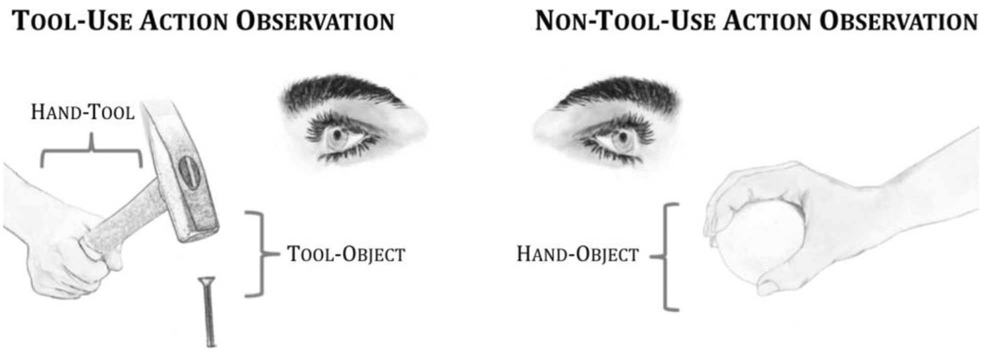

Fig. 1 Tool-use action observation and non-tool-use action observation

role in human tool use (Buxbaum, 2001; Heilman, Rothi, & Valenstein, 1982; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Vingerhoets, 2014). Therefore, the left IPL appears to be the most likely candidate for playing a key role in the observation of tool-use actions made by others. The issue is, what is this role?

Most of our understanding of the neurocognitive basis of tool use comes from neuropsychology, and notably from patients with left brain-damage and apraxia, a disorder of skilled movements (De Renzi, 1989; Osiurak & Rossetti, 2017). This disorder concerns not only transitive gestures (i.e., tool-related actions, such as real tool use or pantomime of tool use), but also intransitive gestures (i.e., non-tool-related actions, such as symbolic or meaningless gestures). A significant body of literature has indicated that imitation, recognition, and production of actions could dissociate for both transitive and intransitive gestures (Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Garcea, Dombovy, & Mahon, 2013; Halsband et al., 2001; Negri et al., 2007; Rumiati, Zanini, Vorano, & Shallice, 2001; Tessari, Canessa, Ukmar, & Rumiati, 2007; for reviews see Mahon & Caramazza, 2005, 2008). These findings challenge any theories assuming that motor production processes are necessary to recognize or imitate actions, including the mirror neuron theory of action understanding (for discussion, see Mahon & Caramazza, 2005, 2008; see also Hickok, 2009).

These findings have also led to the thereotical development of an influential model, hereafter called the manipulation-based approach, aiming to account for apraxia and notably tool-use disorders (Buxbaum, 2001; Cubelli et al., 2000; Gonzalez Rothi, Ochipa, & Heilman, 1991; Heilman et al., 1982; van Elk, van Schie, & Bekkering, 2014). Buxbaum (2017) recently synthetized this approach based on the distinction between the ventro-dorsal system and the dorso-dorsal system. The core idea is that the left IPL – and more generally the ventro-dorsal system also including posterior parts of the temporal cortex – "subserves storage of abstract, multimodal manipulation knowledge" (Buxbaum, 2017; p.348) that can be defined as specific motor programs containing information about the postural and kinematic components of hand movements during their use. Manipulation knowledge is specific to the use of familiar tools in a conventional way, thus providing "desired state" or "goal state" model template for inverse, internal models (i.e., a visuokinesthetic representation of the movement) that are critical to guide hand movements (Buxbaum, 2017; Daprati & Sirigu, 2006). The adjustement of these internal models to current environmental constraints is operated via the dorso-dorsal system (SPL, IPS, superior parts of the IPL and dorsal premotor areas), which predicts the consequence of one's own motor commands. These predictions are compared with actual sensory input as movement unfolds. Any discrepancy is used for online refinement and correction of the predictive model (Wolpert, Ghahramani, & Jordan, 1995). The dorso-dorsal system is not specific to tool use and could also be involved in non-tool-use actions such as meaningless gestures (for somewhat similar interpretations, see Buxbaum, Giovannetti, & Libon, 2000; Cubelli et al., 2000; Gonzalez Rothi et al., 1991). The manipulation-based approach offers a potential prediction for what is specific to tool-use action observation. The observation of someone else using tools could engage manipulation knowledge, which could be helpful for the observer to understand the tool-use action carried out by the model. Based on this inference, it can be predicted that the observation of tool-use actions compared to non-tool-use actions should preferentially activate the left IPL.

More recently, an alternative approach has been offered based on neuropsychological evidence indicating a strong link in patients between familiar tool use and mechanical problem solving, which is not predicted by the manipulation-based approach (Goldenberg & Hagmann, 1998; Goldenberg & Spatt, 2009; Hartmann, Goldenberg, Daumüller, & Hermsdörfer, 2005). This alternative approach, called the reasoning-based approach, posits that the left IPL within the ventro-dorsal system might be critical to reason about mechanical actions involving tools and objects (Osiurak et al., 2009; Osiurak, 2014a, b; Osiurak & Badets, 2016; Osiurak & Heinke, 2018; Osiurak, Jarry, & Le Gall, 2010). Goldenberg and colleagues, amongst others, have provided similar interpretations (Goldenberg & Hagmann, 1998; Goldenberg & Spatt, 2009; Goldenberg, 2013; Orban & Caruana, 2014).

These technical-reasoning skills would allow the user to generate a mental simulation of the tool-use action, particularly the mechanical action involving the tool and the object (i.e., tool-object interactions). Then, this mental simulation could trigger the appropriate motor action through the prehension system, dorso-dorsal system (IPS, SPL), in charge of ruling the hand-tool interaction needed to complete the motor action. For a detailed description of the reasoning-based approach of tool use see Osiurak and Badets (2016).

The reasoning-based approach has received additional support from a recent meta-analysis on neuroimaging data in healthy subjects (Reynaud, Lesourd, Navarro, & Osiurak, 2016). In this review, neuroimaging studies were divided into two conditions athough none of the studies concerned the observation of actions made by others, only judgements on tool-related situations. The first condition (i.e. comparison between a situation eliciting specific cognitive processes and a baseline situation) included tasks in which participants were asked to judge whether the hand posture shown was correct, or not, to use a given tool (hand-tool interaction condition). The second condition consisted of tasks in which participants had to focus on the appropriateness of the mechanical action performed between a tool and an object (tool-object interaction condition). Results revealed activation of the IPS in the hand-tool interaction condition. The left IPL, and particularly the area PF, was preferentially activated in the tool-object interaction condition. In broad terms, these findings are consistent with the idea that hand-tool interactions could be supported by a prehension, dorso-dorsal system involving the IPS or the SPL, and tool-object interactions by technical-reasoning skills involving the left IPL. These brain areas, associated with additional ventral and dorsal premotor areas, constitute the tool-use network, useful for planning how to interact with tools efficiently.

Our goal here is to disentangle the tool-use observation network[1] from the action observation network. More particularly, we aim to determine whether some brain areas (notably the left IPL or area PF) are engaged in the observation – and potentially the understanding – of mechanical actions made by others. To do so, we conducted a three-step analysis. The first step of this study aims at unravelling the consistent activations associated to the action observation network (i.e., both tool-use and non-tool-use actions), by re-analyzing available neuroimaging data on action observation. We then attempted to identify the neural substrate specific to the tool-use observation network by including studies focusing only on tool-use actions. The last step was to specify the brain areas of the tool-use observation network dedicated only to tool-use actions (i.e., tool-use actions minus non-tool-use actions). The rationale of this last step was as follows. The tool-use action observation condition and the non-tool-use action observation condition share the hand-tool to object component, but the tool-use action observation condition has an additional component of interest, namely, the tool-object interaction (see Fig. 1). Substracting the tool-use action observation condition from the non-tool-use action observation condition therefore will allow us to isolate the tool-object component of the situation, that is, what is specific to tool-use actions. Based on both the manipulation-based approach and the reasoning-based approach, we hypothesized that the left IPL should be preferentially involved in the observation of tool-use actions compared to non-tool-use actions. To fulfill this threefold objective, we synthesized recently published neuroimaging studies on the action observation network in a comprehensive coordinate-based meta-analysis (Turkeltaub, Eden, Jones, & Zeffiro, 2002) based on a quantitative approach and activation likelihood estimation (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012).

Methods

We aim to provide an overview of the functional brain activity related to tool-use action observation, by integrating functional neuroimaging results from available studies (for more details about the Methods, see Supplementary Information). Studies concerning the human action observation network have employed a wide range of tasks and task comparisons. Meta-analysis facilitates identification of consistent activations across studies and delimits activations that do not replicate and might be due to variations in the design, experimental material, preprocessing, analysis, scanner, or statistical errors (Salimi-Khorshidi, Smith, Keltner, Wager, & Nichols, 2009; Samartsidis, Montagna, Johnson, & Nichols, 2017; Tench, Tanasescu, Constantinescu, Auer, & Cottam, 2017; Wager, Lindquist, Nichols, Kober, & Van Snellenberg, 2009; Yarkoni, Poldrack, Van Essen, & Wager, 2010).

Selection of Studies

We focused on studies where participants could observe a human model performing non-tool-use or tool-use actions (i.e., videoclips). So, we did not consider many studies where participants had to produce responses from pictures (e.g., semantic matching; Boronat et al., 2005), had to watch a model pantomiming the use of a tool without holding it in the hand (Rumiati et al., 2004) or had to execute meaningless hand movements (Dinstein et al., 2008). As the terms non-tool-use and tool-use actions are not frequently employed in the research community, we considered that the terms "action" that could concern both non-tool-use and tool-use actions and "grasping" that could concern more specifically non-tool-use

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[1] The term *network* used here must be understood as a *collection of brain areas*, with no assessment of the structural or functional connectivity that could exist between these areas.

actions were of interest for our literature review. Candidate studies for inclusion were initially identified using a search through the databases PubMed and ScienceDirect. To narrow our search, we used the logical conjunction of keywords: (((observation or observed) and (grasping or action)) and ("functional magnetic resonance imaging" or "fMRI" or "PET" or "Positron Emission Tomography" or «neuroimaging »))). This search returned 1124 studies at the date of 12/18/2017.

We evaluated candidate papers for inclusion, according to a series of selection criteria:

(1) Theoretical papers and reviews were excluded.
(2) Papers used functional magnetic resonance imaging or positron emission tomography as imaging modality.
(3) Studies included neurologically healthy and adult participants.
(4) Studies were on the topic of action observation.

This first set of criteria led to more thorough consideration of 361 studies, screened with a second set of criteria, defined as follows:

(5) Studies reporting specific comparisons between two action observation conditions were excluded, as the results were related to the inserted cognitive component of interest, supposingly differing between the two contrasted conditions.
(6) Neuroimaging results were based on whole-brain scanning. Regions of Interest analyses were therefore excluded from our selection.
(7) The complete list of activation peaks (i.e., foci) with their coordinates must have been reported in a stereotactic space.
(8) Studies had a sample size of at least 5 participants.
(9) We selected only reported results corrected for multiple comparisons with a statistical significance threshold of $p < 0.05$, without any restriction on the method employed for correction. We did require that the same threshold be applied uniformly across the whole brain. Results derived from Regions of Interest or Small Volume Correction analyses were excluded. Because our meta-analytic statistical tests assumed that foci were spatially randomly distributed across the whole brain under the null hypothesis, it was important to avoid experimenter-induced bias in the locations at which effects could be identified.
(10) Analyses must have been conducted within the General Linear Modeling analysis framework, excluding Multi-Voxel Pattern Analyses or Independent Component Analyses.
(11) Because tool use almost always implies hand action, we selected studies on action observation with "hand-only" conditions, therefore excluding studies with stimuli depicting "whole-body" actions (e.g., dance), as contrasts between tool-use and non-tool-use actions need not to be influenced by other body parts perceived by participants.

Two authors independently searched the literature, 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 ($n = 2$ studies). This quality assessment resulted in 30 studies and 42 experiments providing data on 596 healthy participants (see Table S1 for a detailed description of the main characteristics of each selected study), and comprised 591 peaks of activation, reported in either Talairach or Montreal Neurological Institute space. Experiments were divided in two categories, namely, the *Tool-Use Action Observation* category, in which studies employed tool-use actions as experimental stimuli, and the *Non-Tool-Use Action Observation* category, in which only hands grasping objects were used. A potential confound for the distinction between the two categories of actions (i.e., non-tool-use versus tool-use actions) could be that participants systematically observed two hands in the *Tool-Use Action Observation* category and only one hand in the *Non-Tool-Use Action Observation* category. This possibility is nevertheless unlikely given the proportion of one hand versus two hands observed in the experments of either category (*Tool-Use Action Observation*: 3 experiments with two hands and 10 experiments with one hand; *Non-Tool-Use Action Observation*: 2 experiments with two hands and 27 experiments with one hand).

Data Analysis

Our meta-analysis was conducted using the revised version of the activation likelihood estimation method (ALE; Eickhoff et al., 2012), as implemented by the GingerALE 2.3.6 software (http://www.brainmap.org/ale/; Eickhoff, Laird, Fox, Lancaster, & Fox, 2017). Activation likelihood estimation is a coordinate-based method for pooling neuroimaging study results designed for revealing brain regions consistently activated across studies. Based on the stereotactic coordinates of activation peaks in each study included in the meta-analysis, the ALE method estimates the probability, at each voxel, 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 creation of 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 local maximum (i.e. activation peak) were collected for all the clusters surviving the multiple correction method employed under each included condition. The meta-analysis was performed in the Talairach reference space. Coordinates that were reported in the Montreal Neurological Institute space were first converted to Talairach space using the Lancaster transformation tool (icbm2tal) implemented in the GingerALE software (Lancaster et al., 2007). 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 are dependent on the sample size. Studies with a larger sample size therefore have a stronger impact on the results whereas small sample size studies can still be included but with less impact.

The probability distributions of all foci in the respective experiment are combined in a modelled activation map. The union of all modelled activation 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 of $p < .01$. This false discovery rate rate leads to a recommended minimal cluster size, ensuring that clusters above this size should not be made up entirely of false positives. Therefore, the volume threshold for reporting clusters is set to 400 mm^3, just above all thresholds for the individual condition maps and leads to a reasonable number of reported foci of activation.

For specific contrasts between two conditions (subtraction analysis), the ALE maps generated for each condition are compared by directly subtracting one image from the other. GingerALE creates simulated null data to correct for unequal sample sizes by pooling foci and randomly dividing the foci into two groupings that are equal in size to the original data sets. One simulation dataset is subtracted from the other and compared to the true data. This subtraction produces voxel-wise p value images that show where the true data sit in relation to the distribution of values within that voxel. The p value images are converted to z-scores. At the contrast level, ALE individual maps corresponding to each condition were thresholded at a level of $p < .05$ (false discovery rate 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 $p < .05$ (false discovery rate corrected) and minimum cluster size set to 300 mm^3, which was above the recommended threshold corresponding to the selected false discovery rate correction.

Significant clusters were overlaid onto a standard brain in Talairach space and the 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).

Results

The Action Observation Network

When pooling data from the 42 experiments and 591 foci of activation, the meta-analysis revealed a bilateral network dedicated to action observation (Fig. 2; see Table S2 for a detailed description of the foci). This temporo-parieto-frontal network extends over left and right dorsal and ventral premotor cortex (vPMC and dPMC), IPL, IPS, SPL, left posterior inferior temporal cortex (pITC) and bilateral middle temporal visual areas (MT/V5).

The Tool-Use Observation Network

We considered here only experiments implying the use of a tool. Thirteen *Tool-Use Action Observation* experiments were included in this first meta-analysis, representing 214 healthy participants and 226 peaks of activation. The analysis revealed a network of brain areas consistently recruited by experiments involving observation of actions performed with a tool. This tool-use observation network comprised a set of brain regions in the left hemisphere, the PMC, the IPS, the IPL and middle temporal (MT) cluster. Additionaly, the MT cluster was recruited in the right hemisphere (Fig. 3; see Table S3 for a detailed description of the foci).

A Network Specific to Tools?

We aim here to specify the functional role of the brain areas of the tool-use observation network, and to understand their potential involvement and specificity for tool-use action observation. Before doing so, we first report the network associated with the observation of non-tool-use actions as a mean of disantengling what is specific to tool use from what is common to the observation of any action.

Observation of Non-tool-use Actions

We considered here experiments implying non-tool-use actions. Twenty-nine *Non-Tool-Use Action Observation* experiments were included, representing 382 healthy participants and 365 peaks of activation. The analysis revealed preferential bilateral activations of vPMC, dPMC, IPS, MT cluster, and a left activation of ITC (see Fig. 4; see Table S4 for a detailed description of the foci).

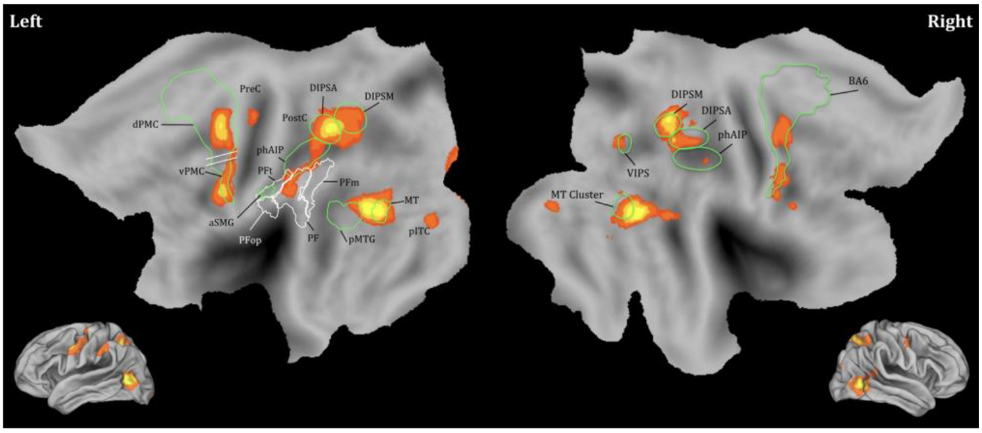

Fig. 2 **The Action Observation Network.** ALE map derived from all studies included, viewed on two PALS-B12 left and right hemispheres atlas surface configuration (Van Essen, 2005): Lateral fiducial surfaces (mini-figure) and flat maps (main figure). White outlines IPL (Caspers et al., 2006; Peeters et al., 2013). Green outlines others regions of interest (Abdollahi et al., 2014; Georgieva, Peeters, Kolster, Todd, & Orban, 2009; Jastorff, Begliomini, Fabbri-Destro, Rizzolatti, & Orban, 2010; Orban, Sunaert, Todd, Van Hecke, & Marchal, 1999; Orban & Caruana, 2014; Peeters et al., 2013; Sunaert, Van Hecke, Marchal, & Orban, 1999). Horizontal white lines outlines separation between dPMC and vPMC (Orban & Caruana, 2014; Tomassini et al., 2007). Note that (1) pMTG represents the union of MTGt and pMTG as defined by Orban and Caruana (Orban & Caruana, 2014) and (2) MT corresponds to the MT cluster as defined by Abdollahi et al. (Abdollahi et al., 2014). Abbreviations: vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex, including BA6; PreC, precentral cortex; PostC, postcentral cortex; phAIP, putative human homologue of the anterior intraparietal area; DIPSA, dorsal IPS anterior; DIPSM, dorsal IPS medial; vIPS, ventral IPS; PFt/aSMG, anterior portion of supramarginal gyrus, which largely overlaps with the cytoarchitectonic area PFt of SMG; PF, PFm, PFt, PFop and PFm, cytoarchitectonic areas of SMG; pMTG, posterior middle temporal gyrus; pITC, posterior inferior temporal cortex; MT, MT cluster.

Tool-Specific Areas

We compared the brain areas engaged in tool-use action observation, namely, the tool-use observationbrain network, with brain areas related to non-tool-use actions. The result of these contrasts is shown in Fig. 5 (see Table S5 for a detailed description of the foci**).**

Tool-Use Action Observation Greater than Non-tool-use Action Observation Two regions in the left hemisphere were consistently more active for the *Tool-Use Action Observation* condition compared to the *Non-Tool-Use Action Observation* condition, namely, the IPL and the inferior frontal gyrus (IFG). More specifically, this contrast engaged the left PF area in the IPL.

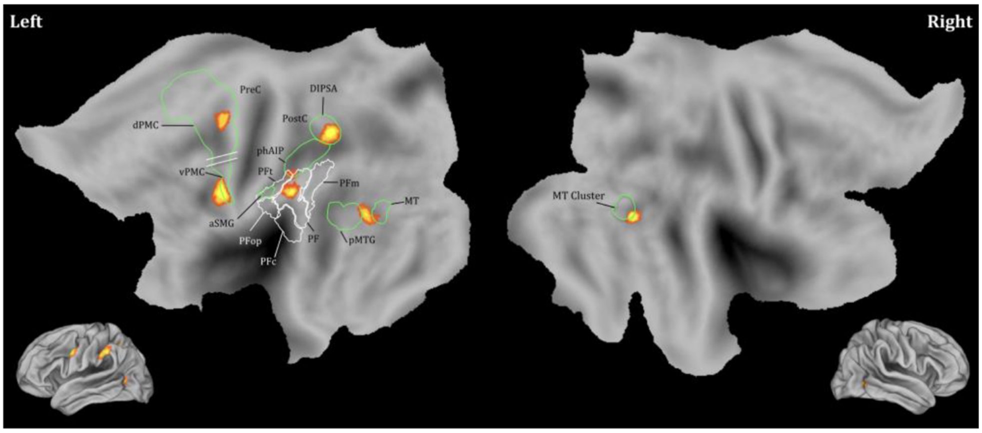

Fig. 3 **The Tool-use Observation Network.** ALE map derived from all studies included, viewed on two PALS-B12 left and right hemispheres atlas surface configuration (Van Essen, 2005), lateral fiducial surfaces (mini-figure) and flat maps (main figure). White outlines IPL (Caspers et al., 2006; Peeters et al., 2013). Green outlines others regions of interest (Abdollahi et al., 2014; Georgieva et al., 2009; Jastorff et al., 2010; Orban et al., 1999; Orban & Caruana, 2014; Peeters et al., 2013; Sunaert et al., 1999). Horizontal white lines indicate separation between dPMC and vPMC (Orban & Caruana, 2014; 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. (Abdollahi et al., 2014). Abbreviations: vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; PreC, precentral cortex; PostC, postcentral cortex; phAIP, putative human homologue of the anterior intraparietal area; DIPSA, dorsal IPS anterior; PFt/aSMG, anterior portion of supramarginal gyrus, which largely overlaps with the cytoarchitectonic area PFt of SMG; PF, PFm, PFt, PFop and PFm, cytoarchitectonic areas of SMG; pMTG, posterior middle temporal gyrus; MT, MT cluster.

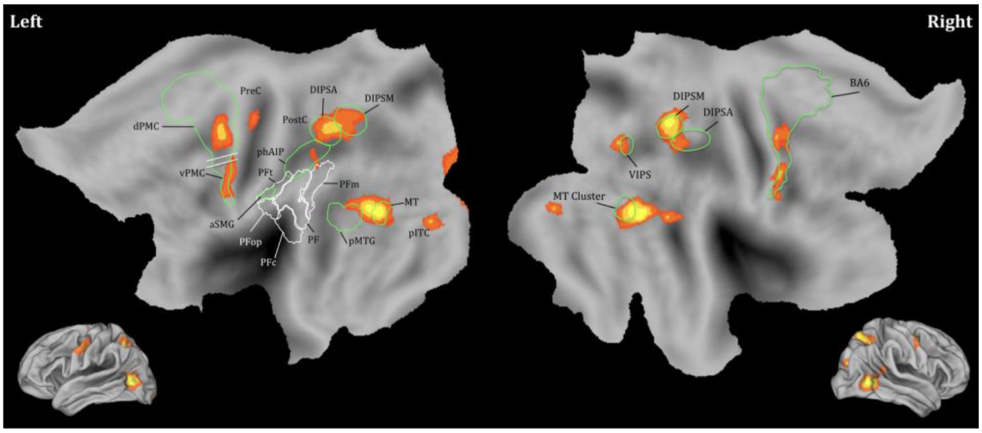

Fig. 4 Observation of non-tool-use actions. ALE map derived from all studies included, viewed on two PALS-B12 left and right hemispheres atlas surface configuration (Van Essen, 2005), lateral fiducial surfaces (mini-figure) and flat maps (main figure). White outlines IPL (Caspers et al., 2006; Peeters et al., 2013). Green outlines others regions of interest (Abdollahi et al., 2014; Georgieva et al., 2009; Jastorff et al., 2010; Orban et al., 1999; Orban & Caruana, 2014; Peeters et al., 2013; Sunaert et al., 1999). Horizontal white lines indicate separation between dPMC and vPMC (Orban & Caruana, 2014; 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. (Abdollahi et al., 2014). Abbreviations: vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex (including BA6); PreC, precentral cortex; PostC, postcentral cortex; phAIP, putative human homologue of the anterior intraparietal area; DIPSA, dorsal IPS anterior; DIPSM, dorsal IPS medial; vIPS, ventral IPS; PFt/aSMG, anterior portion of supramarginal gyrus, which largely overlaps with the cytoarchitectonic area PFt of SMG; PF, PFm, PFt, PFop and PFm, cytoarchitectonic areas of SMG; pMTG, posterior middle temporal gyrus; pITC, posterior inferior temporal cortex; MT, MT cluster.

Non-tool-use Action Observation Greater than Tool-Use Action Observation The analysis revealed no significant cluster.

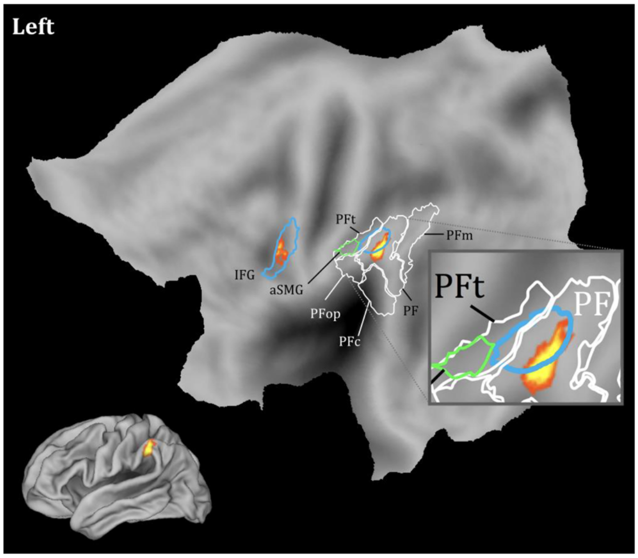

Fig. 5 Brain areas specific to tool-use actions. ALE map derived from all studies included, viewed on the PALS-B12 left hemisphere atlas surface configuration (Van Essen, 2005), lateral fiducial surfaces (mini-figure) and flat maps (main figure). White outlines IPL (Caspers et al., 2006; Peeters et al., 2013). Green outlines others regions of interest (Orban & Caruana, 2014; Peeters et al., 2013). Blue outlines activations reported in the tool-object interaction condition from Reynaud et al. (Reynaud et al., 2016). Abbreviations: PFt/aSMG,]anterior portion of supramarginal gyrus, which largely overlaps with the cytoarchitectonic area PFt of SMG; PF, PFm, PFt, PFop and PFm, cytoarchitectonic areas of SMG; IFG, inferior frontal gyrus.

Convergence with Previous Results on Tool-Use Understanding

In the previous section, we established that the tool-use observation network engaged two areas (left PF and left IFG) that seemed specific to the *Tool-Use Action Observation* condition. These areas were similar to the areas found in a recent work where we studied the neural bases of human tool use through a comprehensive meta-analysis of neuroimaging studies related to tool use (Reynaud et al., 2016). It has to be stressed that none of the experiments we used for this previous work were used for the present work. In this previous work, we examined a condition related to *Action* experiments, where participants had to understand the tool-object interaction, with no judgment on the appropriateness of the hand posture shown. The areas consistently activated by this *Action* condition (i.e., the left area PF and the left IFG) were similar to the areas found in the present *Tool-Use Action Observation* greater than *Non-Tool-Use Action Observation* contrast. Figure 5 depicts the overlap between the areas found in the present work and those found in this previous work (outlined in blue).

Discussion

The aim of our work was to investigate the brain areas supporting tool-use action observation. Then we sought to investigate in this network the areas related to tool use as well as the areas related to observation only, that is to say the areas related to observing someone else performing an action.

Based on both the manipulation-based approach and the reasoning-based approach, we hypothesized that the left IPL should be preferentially activated in the observation of tool-use actions compared to non-tool-use actions. Three key findings resulted from this work. First, we replicated previous findings on the action observation network. Second, we found that the tool-use observation network differs slightly from the general action observation network. Third, we examined more closely the differences that might exist between the tool-use observation network and the action observation network. We found that two areas were specifically activated for tool-use action observation, namely, the left IFG and the cytoarchitectonic area PF within the left IPL. These two areas might be involved in the observation and potentially the understanding of tool-object interaction as suggested by both aforementioned approaches to tool use. In the following sections, we will examine these findings in turn.

Our results first replicate previous evidence on brain areas involved in the action observation network (Buccino et al., 2001; Cross et al., 2009; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Kilner, 2009; Rizzolatti et al., 1996; Van Overwalle & Baetens, 2009) but also reveal that tool-use action observation engages specific brain areas, mostly in the left hemisphere (the left area PF and the left IFG). Before discussing further this point, we will focus here on the brain areas related to the observation of any actions including tool-use actions (i.e., areas found in the action observation network, tool-use observation network and non-tool-use action observation network: left IPS, left dPMC, left vPMC, and MT cluster).

The **left IPS**, and more precisely of the putative human homologue of the anterior intraparietal area (phAIP; see Figures) and anterior dorsal IPS (DIPSA) are known to support the grasping component of the primate prehension system (Orban et al., 2006; Vanduffel, Zhu, & Orban, 2014). This component of the left IPS could play a role in terms of motor simulation when no actual hand movement is planned nor executed, irrespectively of whether a tool is engaged in the action or not. In the case of tool-use action observation, this grasping component could help to prepare egocentric, hand-tool interactions through motor simulation (Jeannerod, 1994). This interpretation is also consistent with previous findings suggesting that the anterior IPS is activated both for action execution and action observation (Shmuelof & Zohary, 2006), confirming that this area could be a part of the putative human mirror system.

The **left dPMC** and **vPMC** are recruited when observing others performing actions with or without tools. It has been suggested that dPMC plays a role not only in motor timing and motor sequencing (Bortoletto & Cunnington, 2010) but also in motor simulation (Stadler et al., 2011). The vPMC could relate to the control of action needed for maintaining over time and integrating into a coherent sequence the different action steps (Petrides, 2005), which could be even more important when using tools. It is noteworthy that these two frontal areas were also found to be involved in tool manipulation tasks (Ishibashi, Pobric, Saito, & Lambon Ralph, 2016) and tool recognition through different sensory modalities (Binkofski, Buccino, Zilles, & Fink, 2004). This latter interpretation remains tentative because these premotor areas also support non-tool-use action observation.

A plausible explanation for **MT cluster** activation is that this area is involved in biological movement perception. Area MT/V5 is known to contribute to motion perception and tracking of visual information (Culham et al., 1998; Tootell et al., 1995; Watson et al., 1993; Zeki et al., 1991). Besides this motion perception component, the activation of MT cluster extends to a more anterior part of the extrastriate cortex that could be compatible with Extrastriate Body Area (EBA; Taylor, Wiggett, & Downing, 2007). These two regions are in close spatial proximity and could have been assimilated as a single cluster, probably because of the nature of the meta-analysis computational steps. EBA area has been shown to respond selectively to small body parts, but not to moving stimuli and is in very close spatial proximity to a hand-preferring region in the extrastriate cortex. The cluster emcompassing MT and EBA could therefore be linked to the perception of moving body parts (Peelen & Downing, 2005) implied in both non-tool-use and tool-use actions.

Because the previous components could be dedicated to generic aspects of action observation, but not specifically tool-use actions, our second aim was to isolate in this network the components that were related to tool use (i.e., the tool-object component; Fig. 1). For this, areas in the tool-use observation network have been compared to the brain network engaged in the non-tool-use action observation. The contrast between *Tool-Use Action Observation* and *Non-Tool-Use Action Observation* conditions revealed two brain areas more consistently activated for tool use, namely, left cytoarchitectonic **area PF** and **left IFG**. These results offer new insights into the neurocognitive bases of tool use.

First of all, the two tool-use-related areas found here (i.e., left area PF and left IFG) overlay the two areas activated in the tool-object interaction condition by Reynaud et al. (2016), observed with a completely different set of data. Importantly, in this earlier study, participants had not to observe real actions made by others, but only to judge whether the tool-object mechanical actions depicted by pictures were correct or not. In broad terms, participants had to focus on tool-object interactions. This tool-object interaction is also the only thing that remains when activation in the *Non-Tool-Use Action Observation* is subtracted from *Tool-Use Action Observation*. Interestingly, both the manipulation-based approach and the reasoning-based approach predict that the left IPL should be engaged in the observation of tool-use actions. In this way, our results confirm the converging predictions derived from both approaches. However, different interpretations can be offered according to the approach.

For the manipulation-based approach, the activation of the left IPL can be interpreted as the involvement of manipulation knowledge that could be useful to understand the tool-use action observed. This interpretation finds support from studies in patients with apraxia, generally due to damage to the left IPL, that have shown that these patients might have a specific deficit on tasks assessing tool-hand relationships (e.g., matching tools based on their manipulation) but not tool-object relationships (e.g., matching tools based on their function; Buxbaum & Saffran, 2002; Evans, Edwards, Taylor, & Ietswaart, 2016; see also Garcea et al., 2013). Additional support for this inference also comes from brain stimulation studies indicating that virtual lesions of the left IPL interfere with tasks assessing tool-hand relationships (Evans et al., 2016; Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; for discussion see Lesourd, Osiurak, Navarro, & Reynaud, 2017). Nevertheless, this interpretation is tentative because manipulation knowledge is thought to contain information about hand-tool interactions, but not about tool-object interactions. Here, the activation of the left IPL precisely concerns the tool-object component of the action. Therefore, even if our results do not rule out this approach, a theoretical effort is needed here to explain how manipulation knowledge could be the support of the tool-object component during the observation of tool-use actions.

The reasoning-based approach postulates that we reason on physical object properties to understand how tools and objects work together. For this approach, tool use is a matter of reasoning (Goldenberg, 2013; Osiurak, 2014a, b; Osiurak et al., 2010) involving the left area PF. The specific involvment of this area in the tool-use observation network implies that some kind of technical reasoning takes place when we see others using tools. When someone watches another person use a tool, two kinds of mechanisms are at work (1) mechanisms involved in the observation of others, and (2) mechanicams involved in the understanding of the tool-use action per se. In broad terms, watching someone work is to work. For example, when observing someone trying to hang shelves on a wall, the technical reasoning of the observer is at work, judging which appropriate tool, screws and wall plugs should be used, which actions should be performed first, etc. Observation renders the process of technical reasoning contagious, as one cannot help to reason too about the physical situation at stake. Interestingly, technical reasoning is thought to be specifically involved in tool-object interactions. Therefore, the preferential activation of the left area PF for the tool-object component provides substantial support for the reasoning-based approach to tool-use action observation. This finding contributes to question the mirror neuron theory of action understanding or any other motor theories of action recognition or imitation in the context of tool use, suggesting that the understanding of actions made by others might be based on neurocognitive processes (i.e., technical reasoning, left area PF) that are not motoric by nature (see Osiurak & Badets, 2016; for a somewhat similar viewpoint, see (Hickok, 2009; Mahon & Caramazza, 2005, 2008).

Besides, the activation of the left area PF contrasts with the earlier involvement of the left area aSMG, a rostral sector of IPL (see Fig. 5), found in a study on observation of tool-use action performed by Peeters et al. (Orban & Rizzolatti, 2012; Peeters et al., 2009, 2013). The area aSMG, unique to humans, is distinct from the biological hand-action observation circuit and, therefore, could support the understanding of tool-use actions based on the appreciation of the relationship between the intended use and the result obtained with it. The present results do not replicate these previous findings but are not in open conflict with them. An exciting issue for future research is to discover whether these two areas (PF and aSMG) could be connected in an extended network dedicated to tool-use observation.

The role of the **left IFG** in tool use is by far less straightforward to understand. A first possibility is that this area is observation-specific in the context of tool use. However, this does not seem plausible since this activation was also reported in the context of tool-use understanding (Reynaud et al., 2016), suggesting that it is not observation-specific but rather generic to tool use. A second possibility is that it is involved in technical-reasoning skills, as is PF. Neuropsychological evidence seems to rule out this possibility. For instance, Goldenberg and Spatt (2009) asked 38 patients with left brain-damaged to use both familiar and novel tools. Three key findings were obtained based on a voxel-based lesion symptom analysis. First, misuse of both familiar and novel tools generally occurs after damage to the left IPL. Second, deficits can increase after frontal lobe lesions. Third, patients with selective damage to the frontal lobe do not meet difficulties in selecting and using tools. Taken together, these findings suggest that the left frontal lobe is not critically involved in the use of tools per se. A more likely, third possibility is that the left IFG is involved in syntaxic processing that occurs not only in language but also in tool use in order to connect tools and objects together to form a meaningful action (Greenfield, 1991; Higuchi, Chaminade, Imamizu, & Kawato, 2009; Zhang, Sun, Humphreys, & Song, 2017). A fourth possibility is that this activation reveals the processing of high-level goals (i.e., the final outcome of the action sequence) that could emerge preferentially when we observe others using tools but not carrying out non-tool-use actions (Hamilton & Grafton, 2006). Consistent with this, a recent study in left brain-damaged patients indicated that the detection of action outcomes during action observation was impaired following damage to the left IFG (Kalénine, Shapiro, & Buxbaum, 2013). A last possibility is that the involvement of the left IFG is a function of incidental characteristics of the tasks used to assess tool-use action observation (e.g., difficult response selection; Goghari & MacDonald, 2009; Rajah, Ames, & D'Esposito, 2008; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; see Kalénine, Buxbaum, & Coslett, 2010).

A clear limit to the results reported here emerges from the difficulty to isolate the "tool-use action observation" component from the simple "tool observation" component, both potentially confounded in the tool-use observation network reported here. As viewing tools does elicit "action representations" (Chao & Martin, 2000; Creem-Regehr & Lee, 2005), it is hard to disambiguate, in the brain activity corresponding to tool-use action observation, the part related to the observation of the action from the part related to just observing a tool. Because studies on tool use do not consider tools as simple, useless objects and unrelated to any action, they often imply tools in their action-related form, either clearly stated, or by the instructions given to the participants. As an example, a recent paper by Chen, Garcea, Jacobs, and Mahon (2018) uses a "tool identification" task, but the instructions given to participants were to "think about the features of the objects, including its name, its associated actions, function, weight, context in which it is found, and material properties". In such a task, the tool-related action observation component is also, in our opinion, solicited. Indeed, when considering tools, it is quite hard and unnatural to isolate the object from the action.

The question of the neural correlates of the observation of tool-use actions has been largely overlooked in the literature except by two studies (Peeters et al., 2009, 2013). Here we offer a bigger picture of the brain network in charge of observing using tools. In this network, the left area PF might play a key role, perhaps by allowing people to reason about the mechanical actions made by others. The main limitation of our study is that we focus on the observation of tool-use actions involving interactions between a tool and an object. So an outstanding issue is whether the same tool-use observation network can be found for tool-use actions that only need the mere manipulation of a tool without any additional object (e.g., smartphone). Regardless, the results reported here raise interesting issues about understanding some particularities of human tool use, such as the ability to constantly improve tools by accumulating changes. Previous research on the neurocognitive abilities allowing human societies to exhibit cumulative technological evolution has shown that the ability to reason about physical properties of tools (i.e., technical-reasoning skills) is of primary importance for this cumulative evolution (Osiurak et al., 2016; Osiurak, De Oliveira, Navarro, & Reynaud, 2019), together with the ability to understand others' intentions (Tomasello et al., 2005). If technical reasoning is one of the bases for this phenomenon and if this capacity is subserved by area PF, and if, as shown here, area PF is also activated when we observe someone using tools, that could signify that we also reason about others using tools. This could provide a basis for learning by observation. When watching someone using a saw for cutting down a tree, we would reason on the correct angle to apply between the tree and the tool, the appropriate way to apply maximal strength in this operation, and so on. By observing, we would become better future users of this tool, as we reasoned while observing someone else using it. The peculiarly human talent to reason about tools could provide a possible cognitive basis of cumulative technological evolution, and by extension could also explain why human societies are the only ones to constantly improve their technological culture, making the great inventions that have filled our history.

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Author Contribution Statement E.R. and F.O. designed the study. E.R. and F.O. analyzed the data. All authors discussed the results and commented on the manuscript.

Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with Ethical Standards

Competing Interests The authors declare no competing interests.

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