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Semantic and action tool knowledge in the brain: identifying common and distinct networks

Running title: Semantic and action tool knowledge in the brain

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Abstract

Most cognitive models of apraxia assume that impaired tool use results from a deficit occurring at the conceptual level, which contains dedicated information about tool use, namely, semantic and action tool knowledge. Semantic tool knowledge contains information about the prototypical use of familiar tools, such as function (e.g., a hammer and a mallet share the same purpose) and associative relations (e.g., a hammer goes with a nail). Action tool knowledge contains information about how to manipulate tools, such as hand posture and kinematics. The present review aimed to better understand the neural correlates of action and semantic tool knowledge, by focusing on activation, stimulation and patients' studies (left brain-damaged patients). We found that action and semantic tool knowledge rely upon a large brain network including temporal and parietal regions. Yet, while action tool knowledge calls into play the intraparietal sulcus, function relations mostly involve the anterior and posterior temporal lobe. Associative relations engaged the angular and the posterior middle temporal gyrus. Moreover, we found that hand posture and kinematics both tapped into the inferior parietal lobe and the lateral occipital temporal cortex, but no region specificity was found for one or the other representation. Our results point out the major role of both posterior middle temporal gyrus and inferior parietal lobe for action and semantic tool knowledge. They highlight the common and distinct brain networks involved in action and semantic tool networks and spur future directions on this topic.

Keywords: action relations; function relations; associative relations; tool use; left-brain damaged patients

1. Introduction

Studying the neurocognitive basis of tool use has been the subject of extensive research over the past decades and has widely been inspired by the observation of left brain-damaged (LBD) patients. A lesion in the left hemisphere can lead to apraxia, a cognitive disorder of motor control, and therefore impacts object-related actions through a deterioration of the representations that support these actions (Goldenberg & Hagmann, 1998; Jarry et al., 2013; for a review see Baumard, Osiurak, Lesourd, & Le Gall, 2014). Most cognitive models of apraxia assume that, in order to use a tool, people have to form a representation of the action to be performed with it (i.e., conceptual stage) and to translate this representation into motor commands (i.e., executive stage; e.g., Buxbaum, 2001; Roy & Square, 1985). These two-stage models suggest that tool use can be affected in LBD patients as a consequence of a deficit at the conceptual level or/and at the executive stage (Heilman, Rothi, & Valenstein, 1982)¹. In this framework, two kinds of knowledge have been suggested at the conceptual level to represent dedicated information about tool use, namely, action tool knowledge and semantic tool knowledge. Whereas numerous studies exist on the neurocognitive bases of action tool and semantic tool knowledge, a comprehensive review on the topic is lacking. The goal of the present review is to fill this gap (1) by giving an overview of the functional brain organization of action and semantic tool representations according to activation (e.g., fMRI) and stimulation (e.g., TMS) studies in healthy subjects; and (2) to examine neuropsychological dissociations in LBD patients. To do that, we focused only on the conceptual level by considering semantic explicit tasks classically used in clinical and experimental settings (see section 1.2 for details). Consequently, production tasks (e.g., pantomime of tool use) classically used to assess apraxia do not fall into the scope of the present work².

¹ Whereas dissociations exist between tool representations and action production (Buxbaum et al., 1997; Negri, Lunardelli, Reverberi, Gigli, & Rumiati, 2007), there are also several pieces of evidence that suggest tool representations can significantly predict object-related actions (Baumard et al., 2016; Jarry et al., 2013; Lesourd et al., 2017, 2019; Lesourd, Baumard, Jarry, Le Gall, & Osiurak, 2017).

² Apraxia is classically assessed with production tasks, that is, imitation of intransitive gestures, actual use of tools and pantomime of tool use (Goldenberg, 2009). Recent reviews have dealt with each of these tasks (Baumard et al., 2014; Lesourd et al., 2018; Niessen et al., 2014; Reynaud et al., 2016).

1.1. Tool knowledge

1.1.1. Action tool knowledge

Action tool knowledge has received a variety of labels: knowledge of object manipulation (Buxbaum & Saffran, 2002), gesture engrams (Buxbaum et al., 2007), manipulation knowledge (Almeida, Fintzi, & Mahon, 2013; Garcea & Mahon, 2012), action semantics (van Elk, van Schie, & Bekkering, 2014). Action tool knowledge is tool-hand centered as it contains information about how to manipulate tools and is “thought to contain the features of gestures which are invariant and critical for distinguishing a given gesture from others.” (Buxbaum, 2001, p.452). Alterations in action tool knowledge particularly impact pantomime production (i.e., the mime of the use of a tool) and tool use (Buxbaum, 2001). Action tool knowledge, as “*to know how*” enables us to grasp tools in a correct fashion and to use them in a meaningful way (van Elk et al., 2014). For example, a *hammer* (i.e., the tool) is used to drive a *nail* (i.e., the object); action tool knowledge contains the information that a hammer is grasped at the handle and used with a back-and-forth swinging movement. Tool-related actions contain two main components, hand posture and kinematics, hypothesized to tap into distinct brain networks in the left hemisphere (Buxbaum, Shapiro, & Coslett, 2014; Martin et al., 2017; see section 1.4 for more details).

1.1.2 Semantic tool knowledge

Semantic tool knowledge has also received many terms in the field of tool use, namely, semantic knowledge about tool function (Gonzalez Rothi, Ochipa, & Heilman, 1991), semantic knowledge about tool use (Baumard et al., 2016; Lesourd, Naëgelé, Jaillard, Detante, & Osiurak, 2020), functional knowledge (Bozeat, Lambon Ralph, Patterson, & Hodges, 2002; Goldenberg, 2013), instruction of use (Goldenberg & Hagmann, 1998), conceptual knowledge (Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000), or semantic memory (Buxbaum et al., 1997). Semantic tool knowledge is tool-centered, as it contains information about the prototypical use of familiar tools. When there are several possible ways of using a tool, they are likely to be weighted as a function of their familiarity and frequency (Goldenberg, 2013). Semantic tool knowledge may inform individuals about where to find tools if not present in the visual field (Osiurak, 2014). Tool use depends on explicit semantic knowledge about tool-object usual relationships (i.e., associative relations; a hammer goes with a nail) and tool function (i.e., function relations; a hammer and a mallet share the same purpose). Function relations can be seen as taxonomic (Kalénine & Buxbaum,

2016; Mirman, Landrigan, & Britt, 2017), meaning relations based on shared features (e.g., saw – knife). Associative relationships can be seen as thematic, that is, contiguity relations between objects that often belong to distinct semantic categories but have complementary roles (e.g., saw – wood). Semantic tool knowledge (at least with function relations) differs from action tool knowledge as a double dissociation has been shown between these two forms of knowledge in apraxic patients compared to non-apraxic patients (i.e., preserved semantic tool knowledge and impaired action tool knowledge in apraxic patients and the opposite pattern in non-apraxic patients; Buxbaum & Saffran, 2002).

1.2. Clinical and experimental tasks

Tasks traditionally used in clinical or experimental settings can be summarized according to the type of relations (action or semantic) and the type of stimuli (tool-tool or hand-tool) (see **Figure 1**).

< Insert **Figure 1** about here >

1.2.1. Action tool tasks

Action tool knowledge can be assessed with two kinds of manipulation tasks: tool-tool compatibility tasks and tool-hand compatibility tasks.

Tool-tool compatibility tasks consist in asking participants to decide if two tools are grasped (i.e., hand posture component; Andres et al., 2013) or manipulated in the same way (i.e., kinematic component; Canessa et al., 2008). If participants are explicitly asked to focus either on hand posture or on kinematics, some studies do not distinguish between these two components of action, considering manipulation as a whole (e.g., Boronat et al., 2005). In tool-hand compatibility tasks, also called recognition of gesture tasks (e.g., Jarry et al., 2013; Osiurak et al., 2009), participants have to decide if a tool is correctly held in hand among several distractors (Baumard et al., 2016; Decroix & Kalénine, 2019; Jarry et al., 2013; Osiurak et al., 2009). In a variant of this task, participants have to choose among several hand postures the one that is suitable for grasping a target tool (Kleineberg et al., 2018; Pelgrims, Olivier, & Andres, 2011). Tool-hand tasks can also focus on the kinematics component of action by asking participants if the motion of the tool held in hand is correct or not (e.g., Martin et al., 2017). The main difference between tool-tool and tool-hand compatibility tasks, apart from the experimental variations (e.g., number of distractors), is the presence of a hand only for the latter tasks.

1.2.2. Function and associative tasks

A classical way to assess semantic tool knowledge is to propose tool-tool compatibility tasks, in which participants have to make a decision/choice based on the characteristics that are shared or not by the stimuli.

In function tasks, participants are instructed to choose among several tools, the two that share the same purpose or goal. For instance, in the presence of a knife, a saw and a screwdriver, participants have to choose the knife and the saw, as these two tools share the same function of ‘cutting’ (Buxbaum & Saffran, 2002; De Bellis et al., 2018; Kalénine & Buxbaum, 2016). In a variant of this task, participants are presented with two tools, and have to decide if they share the same purpose (e.g., knife-saw; Canessa et al., 2008).

Associative tasks consist in choosing among several objects (e.g., nail and screw) or contexts (e.g., kitchen or garage) the one that is usually associated with a target tool (e.g., hammer) in events. Two tools may also be presented and participants have to decide if they can be found in the same context (e.g., knife-saw; Perini, Caramazza, & Peelen, 2014). Finally, one tool and one object can be presented and participants have to decide if they are functionally related or not (e.g., hammer-nail).

1.3. Brain networks supporting tool knowledge

1.3.1. Neurocognitive account of semantic tool and action tool knowledge

During the past decades, several neurocognitive models have tempted to explain how tool knowledge is organized in the brain (see **Table 1**). Theories about semantic knowledge have stressed the central role of the anterior temporal lobe (ATL) (Jefferies, Thompson, Cornelissen, & Smallwood, 2020; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Schwartz et al., 2011), whereas theories centered on tool use have pointed out the major role of the left inferior parietal lobe (IPL), the intraparietal sulcus (IPS), and recently the posterior middle temporal gyrus (pMTG), which is located in the lateral occipitotemporal cortex (LOT) (Buxbaum et al., 2014; Goldenberg, 2009, 2013; Ishibashi, Pobric, Saito, & Ralph, 2016; Kalénine & Buxbaum, 2016; Kalénine, Buxbaum, & Coslett, 2010; Reynaud, Lesourd, Navarro, & Osiurak, 2016).

< Insert **Table 1** about here >

According to the Controlled Semantic Cognition (CSC) and Hub-and-spoke model, conceptual knowledge relies on two mechanisms: (1) multimodal experiences are encoded in modality-specific cortices, which are distributed across the brain; and (2) cross-modal interactions for all modality-specific cortices are mediated at least in part by a single transmodal hub situated bilaterally in the ATLs (Lambon Ralph et al., 2017). The CSC and Hub-and-spoke model also posits the existence of a control system, located in the inferior frontal gyrus (IFG), the angular gyrus (AG) and the pMTG, which manipulates activation within the representational system to generate appropriate behaviors for each task context. According to this framework, the ATL is engaged in all conceptual representations and the distributed modality-specific regions, which are relying upon the ATL, are specialized in different features of objects knowledge (e.g., IPL for praxis or ventral temporal lobe for object visual features). In the Dual Hub theory, the ATL is considered as a taxonomic hub, whereas AG/pMTG represent a thematic hub (Schwartz et al., 2011).

In theories of tool use, the left IPL plays a critical role in action production but also in knowledge supporting the ability to use tools (Buxbaum, 2001; Haaland, Harrington, & Knight, 2000; Ishibashi, Pobric, Saito, & Lambon Ralph, 2016). According to the two action systems plus (2AS+) model, the left IPL stores manipulation knowledge (Buxbaum, 2017), while the Reasoning-based approach (RBA) assumes that the left IPL is composed of several close and functionally distinct areas connected to an integrative area (aSMG/PFt; Lesourd, Osiurak, Navarro, & Reynaud, 2017; Orban & Caruana, 2014; Osiurak, Lesourd, Navarro, & Reynaud, 2020; Reynaud et al., 2016). These areas are also connected with (1) the IPS (i.e., production system) which is responsible for action planning and grasping; and (2) the posterior inferior temporal gyrus (pITG), a more distant brain region, involved in function knowledge (Reynaud, Lesourd, Navarro, & Osiurak, 2016). The pMTG is also involved in action tool knowledge, as it supports the recognition of hand-tool actions (Kalénine & Buxbaum, 2016; Reynaud et al., 2016; Tarhan, Watson, & Buxbaum, 2015). As a part of the LOTC, the pMTG is itself involved, as the surrounding brain areas, in the perception of tools, of bodies and hands, of action observation, and of visual motion (for a review see Lingnau & Downing, 2015). Finally, the RBA and the 2AS+ both stress the role of frontal regions in goal/motor control.

1.3.2. Action tool and semantic tool knowledge

Patient studies have reported that semantic tool knowledge relies upon temporal lobes and particularly the left one (Goldenberg & Spatt, 2009; Hodges et al., 2000), yet fMRI

studies have acknowledged the involvement of temporal and also parietal regions (for a review see Noppeney, 2008). For instance, a recent study found that semantic tool task was associated with changes of neural activity in AG (Kleineberg et al., 2018). Concerning function relations, fMRI studies have also reported that the contrast function about tools versus control condition was associated with changes of neural activity in the left parietal temporal occipital junction, in the left inferior parietal lobe (IPL), and in the bilateral superior parietal lobe (SPL) (Boronat et al., 2005; Ebisch et al., 2007; Kellenbach, Brett, & Patterson, 2003), suggesting that function relations depend not only on semantic temporal areas but also tap into brain networks dedicated to the representation of action and action planning. Thus, function tool relations may be different from taxonomic relations in that they are at the interface of semantic tool and action tool knowledge. A few studies have contrasted thematic and taxonomic relations: bilateral cuneus were engaged in taxonomic relations whereas bilateral IPL and bilateral pMTG were engaged in thematic relations, specifically for manipulable tools compared to non-manipulable tools (Kalénine et al., 2009). However, a recent TMS study did not find any effect of stimulations neither in pMTG nor in supramarginal gyrus (SMG) for thematic manipulable tools relations (De Bellis et al., 2018).

Action tool knowledge can be impacted following lesions occurring in the left IPL (Buxbaum, 2001; Buxbaum et al., 2007; Haaland et al., 2000; Martin et al., 2017). Lesion occurring in the left pMTG can also impair performance in action tool knowledge tasks (Kalénine & Buxbaum, 2016; Martin et al., 2017; Tarhan, Watson, & Buxbaum, 2015), suggesting that access or retrieval of action tool knowledge may require the coupling of networks in both ventral and dorsal pathways (Hutchison & Gallivan, 2018). Concerning specifically hand posture and kinematics, a recent study in LBD patients has shown that a lesion in the left IPL affected the ability to identify correct hand postures whereas a lesion in left pMTG was associated with an impaired ability to identify correct kinematic of gestures (Martin et al., 2017). However, Buxbaum et al. (2014) found the opposite pattern, that is, pMTG supports hand posture and IPL supports kinematics.

The empirical observation that apraxic patients are impaired in action tool tasks but not in function tasks suggests a dissociation between action and semantic tool knowledge (Buxbaum & Saffran, 2002; Garcea, Dombovy, & Mahon, 2013; for the opposite side of the dissociation see Sirigu, Duhamel, & Poncet, 1991; for a review see Garcea & Mahon, 2019). Moreover, some brain areas are more sensitive to action tool compared to function tasks (i.e., IPL; Boronat et al., 2005) whereas other brain areas are specifically engaged in function tasks compared to action tool tasks (ATL and FG; Chen, Garcea, & Mahon, 2016; Kleineberg et al.,

2018). However, action and semantic tool knowledge share some common neural networks as commonalities have been observed in posterior inferior temporal cortex for tasks assessing both forms of knowledge (Canessa et al., 2008). Moreover, in the tool domain, if function and associative relations are occurrences of taxonomic and thematic relations respectively, they are distinct in that they are tuned to action. Taken together, these data indicate that the nature and the precise contribution of brain networks involved in the processing of action and semantic tool knowledge remain partly unclear. If some of the discrepancies observed could be partly explained by the variability of experimental tasks (e.g., matching vs priming) and the nature of stimuli (e.g., manipulable vs non-manipulable objects, natural vs artifact objects), a systematic review on this topic is missing. This study aims to investigate the neural correlates of tasks classically used for assessing action and semantic tool knowledge, as well as the factors that modulate the involvement of these brain networks.

1.4. Scope and purpose of the present review

The present work aims to better understand the neural underpinnings of action and semantic tool knowledge by performing a systematic comparison of neural networks engaged in action tool tasks versus function and associative tasks.

Semantic tool knowledge appears to be mainly supported by temporal regions. For instance, the ATL and pMTG should support both function and associative relations. Additional parietal regions (AG) should be involved in associative relations. If function relations are at the interface of action and semantic tool knowledge, then they should recruit both semantic tool network including temporal: ATL and pMTG; and parietal regions that are classically involved in the representation of tool use actions: IPL and intraparietal sulcus (IPS). Moreover, the observation of neuropsychological dissociations and double dissociations in LBD patients' performance in function and action tasks should inform us as to whether or not the cognitive processes underlying these tasks are independent. Action tool tasks appear to engage fronto-parietal networks (particularly the left IPL and the left IPS) and additional temporal areas. Concerning hand posture and kinematic components, contradictory results have been reported in the literature: hand posture and kinematics have been found to rely upon the left IPL and the left pMTG respectively (Martin et al., 2017), but the opposite pattern has also been found (Buxbaum et al., 2014). We will try to better identify the relation between hand posture/kinematic components and IPL/pMTG.

We carried out a comprehensive review of activation studies (e.g., fMRI), stimulation studies (e.g., TMS), and patients' studies (i.e., behavioral performance of brain damaged patients). It is widely accepted that tool use and associated knowledge is supported by a left-lateralized brain network (for reviews see Ishibashi, Pobric, Saito, & Lambon Ralph, 2016; Lewis, 2006; Reynaud, Lesourd, Navarro, & Osiurak, 2016). Consequently, we focus our analyses on the left hemisphere³ only.

2. Methods

2.1. Selection of studies

We identified relevant studies for inclusion using two databases: PubMed and Web of Science. A manual screening of studies was also carried out. For the selection of studies, we first used the terms “action” AND “semantic” AND “tools”. This search returned 115 studies at the date of 01/05/2020. This review deals with explicit retrieving of action and semantic tool knowledge. To be considered in the present analysis, a study must include one of the following tasks: action tool-tool compatibility tasks (tools held and moved in the same manner), action hand-tool compatibility task (i.e., recognition of gesture tasks; e.g., choosing the correct hand posture associated with a tool), function (tools used for the same purpose) or associative (tools/objects found in the same context or typically used together). Moreover, for the sake of equivalence between each task, the presence of a tool was required, thus the recognition of pantomime was only considered if participants/patients were presented with a tool, whether it was before or after the demonstration of the pantomime (see for example Bartolo, Daumüller, Della Sala, & Goldenberg, 2007). More specific selection criteria are also given in the next section.

³ In the field of apraxia, several studies have shown that a perturbation of the right hemisphere could lead to a deficit in gesture imitation (for a review see Lesourd et al., 2018) or in the use of tools (Salazar-López et al., 2016). However, the few data available in the field prevent us from making a systematic examination of the role of the right hemisphere in action tool or semantic tool knowledge.

2.2. Data analysis

2.2.1. *fMRI studies*

We selected neuroimaging studies according to a series of selection criteria: (1) reviews were excluded; (2) studies had to use functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) as imaging modality; (3) studies had to include only neurologically intact participants; (4) relevance of the tasks used in relation to the scope of the present study (see above); (5) the complete list of activation peaks of main effects (e.g., action tool > control; Kellenbach, Brett, & Patterson, 2003), contrasts (e.g., action tool > function; Canessa et al., 2008), or region of interest (ROI) analyses with their coordinates had to be reported in a stereotaxic space; and (7) only the results corrected for multiple comparisons (e.g., FWE or FDR) with a statistical threshold of $p < .05$ were considered. The final selection resulted in 6 studies including 97 healthy subjects and 61 peaks of activation. These studies are described in **Table 2**. Based on these criteria, a quantitative meta-analysis of neuroimaging studies could not be performed (e.g., Activation Likelihood Estimation method) because too few studies have been conducted specifically in the field of action tool and semantics tool tasks. Thus, only cortical activation sites (i.e., peak maxima coordinates) were reported for the different conditions considered in the present work, that is, action tool, function and association (see Niessen, Fink, & Weiss, 2014 for a similar methodology). Activation sites are projected on flat-map representations of a left hemisphere (PALS-B12: Population Average, Surface- and Landmark-based human cortical atlas; Van Essen, 2005), using Caret, version 5.65 (<http://brainmap.wustl.edu/caret.html>; Van Essen et al., 2001). If activation peaks were reported in Talairach-coordinates, we first transformed them in MNI-space (Lacadie, Fulbright, Constable, & Papademetris, 2008).

< Insert **Table 2** about here >

2.2.2. *Stimulation studies*

We selected stimulation studies according to a series of selection criteria: (1) studies had to employ stimulation parameters known to interfere with brain activity; (2) studies had to include only neurologically intact participants; (3) relevance of the tasks used in relation to the scope of the present study (see above); (4) stimulation coordinates had to be reported in a stereotaxic plane (i.e., MNI or Talairach). The final selection resulted in 6 studies including 114 healthy subjects and 9 stimulation sites. These studies are described in **Table 3**. The virtual lesions were processed from the information available (i.e. stimulation coordinates) in

the studies involved in this review. First, if needed, stimulation coordinates were transformed in MNI space. Second, every stimulation coordinate was depicted on a flat-map representation of a left hemisphere (PALS-B12: Population Average, Surface- and Landmark-based human cortical atlas; Van Essen, 2005), using Caret, version 5.65 (<http://brainmap.wustl.edu/caret.html>; Van Essen et al., 2001). Third, the coordinate was depicted by a specific color according to a given study.

< Insert **Table 3** about here >

2.2.3. *Left Brain-Damaged (LBD) patients*

Regarding brain-damaged patients, we focused our analysis on behavioral performance. We selected brain-damaged studies according to a series of selection criteria: (1) single case studies were not included; (2) Only patients presenting exclusively LBD were considered; (3) presence of a control group⁴; (4) relevance of the tasks used in relation to the scope of the present study (see above); (5) Tasks using verbal material were not considered because of the potential presence of aphasia (Buxbaum, Kyle, & Menon, 2005; Buxbaum, Sirigu, Schwartz, & Klatzky, 2003). The final selection resulted in 7 studies including 138 LBD patients. These studies are described in **Table 4**. As for fMRI studies, the lack of data prevents us from conducting quantitative meta-analysis of behavioral performance. Thus, we resorted to a qualitative meta-analysis methodology developed by our group (Baumard et al., 2014; Lesourd et al., 2013), leading us to enable direct comparisons between distinct studies. First, for each study and condition, mean raw scores obtained by the patients' group were converted to percent by dividing each mean raw score by the maximum score on the task. The same procedure was applied for the matched control groups. Second, we calculated a mean difference score, corresponding to the difference between the percent score of the patient group and that of the matched control group (e.g., patients' mean difference score = 60%, controls' mean difference score = 90%, difference between patients and matched controls = 30%). The greater the difference is between patients and controls the more impaired the patients are. Third, we used a graphical illustration of the results in which each study was represented by a different colored disk, the size of which depended on the number of patients included in the study. When a study documented several conditions or distinct groups of

⁴ A control group can be another group of patients. For instance, a group of LBD patients without apraxia can be considered as a control group for LBD patients with apraxia (see for instance Buxbaum & Saffran, 2002).

patients (e.g., apraxic and non-apraxic patients; Buxbaum, Sirigu, Schwartz, & Klatzky, 2003), then several disks of the same color appear on the figure.

< Insert **Table 4** about here >

Finally, when patients' individual scores and controls' mean and standard deviation were reported, we calculated the percentage of patients showing a deficit in each experimental task using the Crawford-Garthwaite Bayesian test for single-case analysis (Crawford & Garthwaite, 2007). Additionally, if controls' individual scores were reported/available, we calculated for each patient, the presence of dissociations between tasks using the Revised Standardized Difference Test (RSDT; Crawford & Garthwaite, 2005). We then reported classical dissociation: for a patient P_A , one score is in the normal range for the task T_1 while the other is pathological in the task T_2 ; and strong dissociation: for a patient P_A , both scores are pathological in tasks T_1 and T_2 and the difference between both is significant. We also examined double dissociation (i.e., two patients showing an opposite pattern).

3. Results

3.1. General consideration about tasks

We found a total of 20 studies among which 16 studies included action tool tasks ($n = 18$ tasks) and 20 studies included semantic tool tasks ($n = 27$ tasks). When scanning the literature for studies on action and semantic tool tasks, we found that there were as many different task names as there were studies, which may lead to some confusions.

For semantic tool knowledge, about half of the tasks focused on associative relations (48%, $n = 13$) and the other half on function relations (48%, $n = 13$). One task was unspecified because of unclear description (i.e., context or function; 4%, $n = 1$). The terms "Function" (33%, $n = 9$) and "Functional" (22%, $n = 6$) were the most encountered but they referred to both function and associative relations, which may lead to some confusions as (1) the term function is not restricted to function relations; and (2) function and associative relations may depend on distinct cerebral networks. Another potential confusion comes from the term "taxonomic" and "thematic" which are used for "function" and "associative", respectively. Indeed, these terms are not specific to "tools" category (e.g., mixed of natural and artifact objects; Kalénine et al., 2009). Some studies blended manipulable and non-manipulable tools (Boronat et al., 2005), whereas others include only manipulable tools (De

Bellis et al., 2018). All the tasks used to assess semantic tool knowledge were matching or judgment tasks with some variations between them (e.g., number of distractors).

For action tool knowledge, the most frequently encountered task names were “Action” (17%, $n = 3$) and “Manipulation” (22%, $n = 4$). All studies on action tool knowledge focused on either the hand posture component (33%, $n = 6$) or the kinematic component (50%, $n = 9$) and some did not distinguish between the two (17%, $n = 3$). Tool-tool compatibility tasks (72%, $n = 13$) were the most used, where participants had to select two of several tools among several or decide if two tools were related according to a manipulation criterion. Hand-tool compatibility tasks (28%, $n = 5$), in which participants had to decide if a given hand posture was appropriated or not to use a target tool, were also found.

3.2. fMRI data

The cortical activation sites (i.e., peak maxima coordinates) corresponding to the different conditions and contrasts considered in the present work are represented in **Figure 2**.

< Insert **Figure 2** about here >

Only two studies have reported peak activations for action tool versus control contrasts and three studies have reported peak activations for semantic tool versus control contrasts. Moreover, concerning semantic tool tasks, studies have focused only on function relations but not on associative relations. Both kinds of tasks are associated with changes in neural activity in fronto-parietal regions, inferior frontal gyrus and inferior temporal cortex (FFC). However, whereas semantic tool tasks are associated with activations in AG (PGi and PGs) and superior LOTC, action tool tasks are rather associated with activations in AG (PFop), AG (PGs/PGp) and IPS (IP2).

Distinct patterns emerged when contrasting both conditions. semantic tool>action tool contrasts were associated with scattered activations in the left hemisphere, comprising lateral temporal cortex and ventral stream of the visual cortex (TE1a/TGd), AG (PGi and PGs), but also medial prefrontal cortex (mPFC; 10d/10v) and in posterior cingulate cortex (7m/31pd).

Action tool>semantic tool contrasts were associated with changes in neural activity in inferior premotor cortex (6r) and superior premotor cortex (i6-8/6a) gyrus, in visual association areas of the lateral occipital and posterior temporal cortex (PH), in temporo-parietal occipital junction (TPOJ2) and mostly in parietal regions, that is, in SMG (PFt), IPS (AIP, IP2, LIPd and IP1) and in AG (PGi). We found that a similar brain region in the AG (PGi) could be engaged in both action>semantic and semantic>action contrasts. This apparent

discrepancy can be explained easily by the nature of the tasks included in these contrasts. In Kleineberg et al. (2018), the semantic tool task focused on associative relations (e.g., hammer-nail), whereas in Boronat et al. (2005), the semantic tool task focused on function relations (e.g., lighter – match). Thus, function relations elicit less changes in neural activity than action relations in AG (PGi/PGs), whereas the opposite pattern of activation is observed for associative relations.

Concerning stimulus modality, we found that the presentation of either words or pictures or both pictures and words engaged similar brain regions. In both action tool and semantic tool conditions, pictures and words engaged an extensive network in the left hemisphere comprising dorsolateral and ventrolateral frontal cortex, SMA, IPL and pMTG (Boronat et al., 2005; Ebisch et al., 2007).

Finally, action tool studies focusing on either hand posture or kinematics components invoked the same posterior brain regions, that is, SMG (PFt), IPS (AIP and IP2) and LOTC (TPOJ2 and PH).

3.3. Stimulation data

The location of stimulation sites and their impact on behavioral performance in action, function and associative tasks are represented in **Figure 3**. Stimulation studies that focused on action tool and semantic tool tasks targeted several nodes of the semantic and tool use networks, that is, IPL (SMG), IPS, LOTC and ATL.

< Insert **Figure 3** about here >

We found that action tool tasks were systematically impaired following virtual lesions in IPS and IPL (Andres, Pelgrims, & Olivier, 2013; Pelgrims et al., 2011). However, Pelgrims et al. (2011) did not find any effect of a stimulation in left IPL (SMG/PF) in a hand-tool compatibility task, in which participants had to judge if a hand posture was compatible with a given tool (i.e., both hand and tool were presented on the screen). In the other conditions/studies where a negative impact of IPL (SMG/PF) stimulation was found (Andres et al., 2013; Pelgrims et al., 2011), the participants had to judge if two tools were manipulated in the same way, but no hand was present on the screen. These data may suggest that action tool tasks are not systematically impacted following lesions in IPL.

We found that function tasks could be affected following virtual lesions in IPL/SMG and pMTG (PHT/TE1p; De Bellis et al., 2018). Moreover, virtual lesions made in IPS (AIP/IP2) did not impact function tasks at all whereas lesions in ATL systematically did

(Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; Ishibashi, Mima, Fukuyama, & Pobric, 2018). Ishibashi et al. (2011, 2018) used words as stimuli instead of the other studies which only used pictures.

Concerning associative tasks, few data were available and stimulation sites were only found in IPL and LOTC. The most robust result was that no impact on associative tasks was found following stimulation in IPL. In the LOTC, associative tasks (e.g., judging if two tools can be found in the same context) were affected following stimulations in pMTG (Andres et al., 2013) but not in lateral occipital cortex (i.e., MT; visual motion area; Perini, Caramazza, & Peelen, 2014). Moreover, De Bellis et al. (2018) did not find any effects in an associative task following pMTG stimulation, but the stimulation was made during the presentation of a prime and not during the associative task itself. Thus, the role of LOTC/pMTG in associative tasks is not clear regarding stimulation data.

3.4. LBD patients' data

The control-patient differences are presented in **Figure 4**. In LBD patients, we first found a dissociation between action tool task variants: tool-tool compatibility tasks (difference control-patients = 15-48.1%, excluding non-apraxic patients' performance) were more impaired than hand-tool compatibility tasks (difference control-patients = 3.4-11.4%).

< Insert **Figure 4** about here >

Second, we found a gradient in the performance of tool-tool compatibility tasks between action, function and associative relations: the largest difference between controls and patients was observed for action relations (range = 2.4%-48.1%), followed by function relations (range = 2.4%-30.7%), and finally by associative relations (range = 2%-19.8%). Considering that non-apraxic LBD patients perform in sub-normal range in action tool-tool tasks (i.e., control-patient difference = 2.4%; Buxbaum et al., 2003), the difference between controls and patients for action (range = 15%-48.1%) is even more important than the two other tasks. This gradient was systematically observed for the studies that tested several conditions in the same group of patients (Bartolo et al., 2007; Buxbaum & Saffran, 2002; Buxbaum et al., 2003; Kalénine & Buxbaum, 2016; Lesourd, Budriesi, Osiurak, Nichelli, & Bartolo, 2019; Osiurak et al., 2009). When trying to control for the difficulty between function and associative conditions (Kalénine & Buxbaum, 2016), the control-patient difference was indeed reduced, but the authors found that both patients and controls identified significantly faster associative relationships compared to function relationships.

We examined the proportion of impaired patients and dissociations between tasks in LBD patients using single case statistics (Crawford & Garthwaite, 2005; Crawford & Garthwaite, 2007). These results are presented in **Table 4**. The proportion of patients showing significant impairments in action and semantic tool tasks confirmed the gradient observed in **Figure 4**. When individual data for both patients and controls were available, we also calculated dissociations between tasks (Crawford & Garthwaite, 2005). Dissociations were found among all the tasks investigated in the present review and particularly between function and associative tasks (range = 29-47%), between action hand-tool tasks and function tasks (range = 45-53%), and between action tool-tool tasks and associative tasks (48%). Double dissociations (see **Supplementary Material Table 1**) were found between function and associative tasks (Jarry et al., 2016, strong: P11 vs P12 and classical: P13 vs P14; Lesourd et al., 2019, strong: P10 vs P18 ; Osiurak et al., 2009, classical: P17 vs 19), action hand-tool and associative tasks (e.g., Osiurak et al., 2009; classical: P9 vs P10), action hand-tool and function tasks (Osiurak et al., 2009, classical: P5 vs P17) and action tool-tool and associative tasks (Lesourd et al., 2019, strong: P12 vs P17). Interestingly, in the only study that compared action tool-tool tasks and function tasks, dissociations between action tool-tool and function tasks were reported in only 24% of patients, and all had better performance in function tasks (Lesourd et al., 2019).

< Insert **Table 4** about here >

To summarize, a lesion within the left hemisphere of the brain significantly affected action tool tasks, more particularly action tool-tool compatibility tasks, and to a lesser extent function and associative tasks. Furthermore, while dissociations were observed in almost all tasks, we did not find any double dissociation between function and action tool-tool tasks, with the available data.

3.5. Summary of the main results

Results of activation and stimulation studies are summarized in **Figure 5**. If a brain region is engaged in a given task and if a stimulation in this brain area disrupts performance, then one may assume that this area is involved in task processing. Following this logic, areas SMG, IPS, LOTC and ATL play a key role in action tool knowledge, and function relations rely upon SMG, pMTG and ATL. Moreover, AG is involved in both action tool knowledge and function relations, frontal regions are involved in both action tool knowledge (premotor cortex) and associative relations (mPFC), and ventral temporal areas are involved in function

relations. As studies included in this review reported only activations in frontal areas for these tasks, we can only assume that these brain areas play a role in these relations. Concerning LBD patients' studies, action tool tasks were the most impacted followed by function and then associative tasks. Moreover, in action tool tasks, the difference between controls and patients were the most important in tool-tool compatibility compared to tool-hand compatibility tasks. Analysis of dissociations revealed that, except for action tool-tool compatibility versus function tasks, all other tasks may depend on distinct cognitive processes.

< Insert **Figure 5** about here >

4. Discussion

The aim of the present review was to provide a better understanding of the neural correlates of action tool (hand posture and kinematic components) and semantic tool (function and associative relations) knowledge. We examined activation, stimulation and brain-damaged patients' studies, and focused specifically on the left hemisphere, which is known to support production and comprehension of tool-related actions (Ishibashi, Pobric, Saito, & Lambon Ralph, 2016; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Reynaud et al., 2016; Reynaud, Navarro, Lesourd, & Osiurak, 2019). In the next sections, we will first discuss the role of brain regions involved in semantic tool and action tool knowledge. Second, we will discuss the particular case of action tool and function relations. Finally, we will examine several neurocognitive hypotheses which could explain the emergence of semantic tool and action tool knowledge in the brain.

4.1. Action tool knowledge relies upon posterior temporal regions, supramarginal gyrus and intraparietal sulcus

Action tool knowledge appears to rely upon a large brain network including temporal (LOTc and ATL) and parietal regions (IPL and IPS). These results are in line with the literature of apraxia that underlines the importance of the left parietal lobe in tool use skills (e.g., Goldenberg, 2009). Within the IPL, the SMG is thought to be a key region for action tool knowledge and is also considered as an integrative hub (i.e., SMG/PFt; Orban & Caruana, 2014). However, we found that all action tool tasks were not systematically impaired following virtual lesions in SMG, questioning the exact role of this parietal structure

in action tool knowledge (for a discussion see Lesourd, Osiurak, Navarro, & Reynaud, 2017). Specifically, SMG (PFt) was activated in tasks where participants had to judge hand-tool compatibility (Kleineberg et al., 2018), and tool-tool compatibility (Canessa et al., 2008). Virtual lesions located in PF, at the border of SMG/PFt, impaired only tool-tool compatibility (Andres et al., 2013; Pelgrims et al., 2011) but not hand-tool compatibility tasks (Pelgrims et al., 2011). However, the left SMG is involved in planning/executing object-related actions (Reynaud et al., 2016). A recent study found that virtual lesions in left SMG (PF/PFt) impacted the planning of functional grasps (hand-tool relations; Potok, Maskiewicz, Króliczak, & Marangon, 2019). Thus, one may ask why the virtual lesion made in SMG/PF did not impact the hand-tool compatibility task in Pelgrims et al (2011). This apparent discrepancy may be solved by assuming that the role of SMG in this particular case of hand-tool compatibility task may not be so critical. In this task, the hand and the tool are both displayed, and the participants can complete the task by matching the shape of the hand with the tool according to the available perceptual features (e.g., aperture of the hand, shape of the tool, etc.). Thus, the activation of motor representations may be less critical compared to production tasks or tool-tool compatibility tasks. Further studies may explore this hypothesis by comparing brain activations associated with hand-tool and tool-tool compatibility tasks in the left SMG. The left IPL (SMG) is tuned to process hand-tool relations (Buxbaum et al., 2007; Buxbaum, 2001; van Elk, 2014; Haaland et al., 2000), and it is also involved in the reenactment of hand motor representations (i.e., motor imagery; Pelgrims, Andres, & Olivier, 2009) and in the integration of these representations with the semantic tool knowledge represented in the temporal lobe (Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Sunderland, Wilkins, Dineen, & Dawson, 2013). This review also acknowledges the mandatory role of IPS, which is known to be involved in the planning of tool actions (Przybylski & Króliczak, 2017; Reynaud et al., 2016) and in the recognition of spatio-temporal errors during execution of object-related actions (Martin et al., 2017). Thus, judging if two tools share the same manner of manipulation, without actual production, will nevertheless activate motor representations in IPS (i.e., grasping component). We also found that performance in an action tool task could be facilitated following tDCS stimulation in ATL (Ishibashi et al., 2018), suggesting that this structure contributes to some extent to action tool knowledge. ATL is assumed to represent amodal semantic representations (Lambon Ralph et al., 2017), irrespective of domain-category (e.g., tools, animals, etc.) and it is therefore possible that accessing action tool representations may require semantic representations about tools. However, if a modulation of performance in an action tool task

was found with tDCS (Ishibashi et al., 2018), this was not the case with TMS (Ishibashi et al., 2011), questioning the exact role of ATL in action tool knowledge. One possible explanation is that tDCS is less focal compared to TMS (Lang et al., 2005; Nitsche et al., 2007), and thus stimulation of ATL *per se* was not responsible for the modulation of performance in the action tool task observed by Ishibashi et al. (2018). To sum up, action tool knowledge may require the functional coupling of temporal and parieto-frontal networks, as it is the case for the production of object-related actions (Hutchison & Gallivan, 2018).

We also examined the brain networks of two components of action tool knowledge, that is, hand posture and kinematics. First, fMRI studies showed that hand posture and kinematics could indifferently engage IPL/IPS or pMTG. However, stimulation studies showed that hand posture was impaired following virtual lesions in IPL (SMG) only for tool-tool compatibility but not for hand-tool compatibility (Andres et al., 2013; Pelgrims et al., 2011), and kinematics-related knowledge was impaired following virtual lesions of inferior LOTC (Perini et al., 2014). These results suggest that kinematics are preferentially processed in the inferior LOTC, whereas hand posture is preferentially processed in the IPL (SMG). We also reported that stimulations in pMTG and SMG during hand posture priming could impact a subsequent function task (De Bellis et al., 2018). Concerning studies in LBD patients, we observed a better performance in hand-tool compatibility tasks (in which patients have to select the correct postures among several postures) than in tool-tool compatibility tasks (in which patients have to decide if two tools are manipulated in the same manner). Differences in experimental tasks and cognitive load may explain this apparent dissociation. Indeed, in hand-tool tasks, visual cues are more important (e.g., position of the hand on the tool) and may have enabled the access to residual action tool knowledge, compared to action tool-tool tasks in which only the tools were displayed. In action tool-tool tasks, patients have to simulate both hand posture and kinematics associated with the two tools in order to compare them, which may require important working memory resources. By contrast, in the hand-tool tasks in which the correct postures appear among several distractors, patients can select their response by eliminating the least likely items (Lesourd et al., 2020). Another difference between action tool-tool tasks and hand-tool tasks is that action tool-tool tasks may depend more on kinematic components (e.g., a hammer is used with large oscillations of the arm) compared to action hand-tool tasks. Thus, LBD patients may be more impaired in action tool-tool tasks than in action hand-tool tasks because of task complexity or/and because they meet more difficulties to process the kinematic than the posture component of tool actions. In line with this hypothesis, Martin et al. (2017) reported slightly more difficulties in the

identification of kinematics errors (48%, $n = 47/98$) than hand posture errors (36%, $n = 35/98$) in LBD patients. However, in LBD patients, Voxel-Lesion Symptom-Mapping studies of brain correlates of hand posture and kinematics errors have shown inconsistent results. Martin et al. (2017) reported a dependency of hand posture and kinematics components on IPL and pMTG respectively, while Buxbaum et al. (2014) found the opposite pattern. Further studies are required to elucidate the neural correlates of hand-posture and kinematics in object-related actions.

4.2. Semantic tool knowledge relies upon temporal regions and angular gyrus

Semantic tool network is supported mainly by the temporal lobe, with brain areas distributed along the ventral and lateral visual stream, from visual associative regions (VVC) to more anterior parts of the temporal lobe (TE1a/TGd). We found that associative and function relations may rely upon distinct brain regions, that is, AG for associative relations and IPL/SMG for function relations. The role of AG in semantic knowledge retrieval have already been reported (Binder, Desai, Graves, & Conant, 2009), more specifically in thematic or combinatorial processing (Binder & Desai, 2011; Price, Bonner, Peelle, & Grossman, 2015). Other studies have shown that its involvement was modulated by task difficulty (Humphreys & Lambon Ralph, 2015); however, a recent work found an involvement of the AG in both the processing of thematic relations and the inhibition of irrelevant semantic information (Lewis et al., 2019). We also found that associative and function relations may rely upon common brain area, namely, the pMTG. Moreover, stimulation studies have reported that TMS to pMTG elicited the greatest disruption to weak association trials, whereas TMS to AG particularly disrupted the efficient retrieval of strong associations (Davey et al., 2015; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). Considering that pMTG is part of the semantic control network, according to the CSC model (Lambon Ralph et al., 2017), and given its involvement in both function and associative relations (but also action), we should expect pMTG activity to be more important for items that are not typically associated (function: saw and knife and action: key and screwdriver) compared to strong semantic associations (associative: hammer and nail). Further studies are needed to measure brain activity relative to action, function and associative conditions together. Concerning function relations, results showed that they were also disrupted following ATL stimulations, yet no stimulation data on associative relations were available in the present review. However, action relations could also be impacted following ATL

stimulations, which indicate that ATL may be involved in heteromodal conceptual representations. Associative relations also engaged the mPFC (Kleineberg et al., 2018), but the presence of this brain activation can be explained by the fact that the authors used a valuation task (i.e., what is the cost of this object?), and this kind of task classically involves mPFC (Domenech, Redouté, Koechlin, & Dreher, 2018). Thus, mPFC may not be a specific brain region supporting Semantic tool knowledge. Function relations are associated with activation in ventral temporal lobe (VVC), ATL (TE1a/TGd), and also pMTG (MST/TPOJ2) (Boronat et al., 2005; Canessa et al., 2008; Ebisch et al., 2007; Kellenbach et al., 2003). Moreover, stimulations in ATL (Ishibashi et al., 2011, 2018), pMTG and IPL (De Bellis et al., 2018) impacted behavioral performance in semantic tool tasks assessing function relations.

4.3. Where action tool knowledge meets semantic tool knowledge

4.3.1. *The particular case of action and function relations*

There is strong evidence in the literature that semantic tool knowledge (i.e., function relations) and action tool knowledge are supported by distinct neurocognitive processes (Buxbaum & Saffran, 2002; Chen et al., 2016; Garcea, Dombovy, & Mahon, 2013; Garcea & Mahon, 2012, 2019). For instance, neuropsychological dissociations have been reported between action tool and function knowledge (Garcea et al., 2013; Sirigu et al., 1991). In a fMRI study using MVPA, Chen et al. (2016) found greater action decoding compared to function in the left IPS, left vPMC, and right IFG while greater function decoding compared to action was found in the left parahippocampal gyrus. In the present review, we reported that function relations depended more on ATL than action tool knowledge whereas virtual lesions in IPS systematically impaired action tool knowledge but not function relations (Ishibashi et al., 2011, 2018).

In the present review, we found that function tasks and action tool tasks can be impacted following the same virtual brain lesions, that is, pMTG and IPL (SMG). In a priming experiment, De Bellis et al. (2018) asked participants to perform a function or an associative judgment task, while the pMTG or the SMG were stimulated during the prime (hand posture compatibility or not). The authors found that virtual lesions in pMTG, and to a lesser extent in SMG during the priming of a hand posture, impacted function judgment but not associative judgment. Second, in LBD patients, while we found double dissociations between action tool-tool tasks and associative tasks and between function and associative tasks, our analysis did not reveal any double dissociation between action tool-tool tasks and

function tasks. This result has to be taken carefully as few neuropsychological data were reported here.

One explanation is that judging function relations about tools may engage parietal regions only if a manipulation component is strongly associated with the function to be judged. In a fMRI-adaptation paradigm, Yee et al. (2010) found that adaptation in left IPS was predicted by the degree of function similarity between word pairs and was also predicted by the degree of manipulation similarity. However, as manipulation and function similarity were highly correlated together and function condition did not elicit any activation in this region in whole brain analysis, the authors argued that manipulation was more likely to account for this relationship. Further studies are needed to disentangle the role of parietal structures in function relations. For instance, one may hypothesize that in a function tool-tool compatibility task, we should observe a greater involvement of parietal structures if the function is associated with a high level of manipulability (e.g., knife and saw, cutting function) compared to a function associated with a low level of manipulability (e.g., match and light bulb, function to light up).

To sum up, these data question the nature of the links between function relations and action tool knowledge. If action tool knowledge and function relations are supported by independent systems, these systems are nevertheless mutually and preferentially interacting together. Retrieving action tool knowledge, and to a lesser extent function relations, should emerge from large-scale dynamic interactions between the fronto-parietal and temporal regions (Noppeney, 2008).

4.3.2. Task complexity or distinct neurocognitive processes?

We found a gradient between action (action tool-tool), function and associative tasks in LBD patients, in such a way that action tool-tool tasks were the most impaired followed by function and then associative tasks. This difference could be explained by variations in task difficulty rather than by the nature of the neurocognitive processes involved in these tasks. In LBD patients' studies, if control subjects succeed equally in terms of accuracy for action and function tasks, associative tasks appear easier (Bartolo et al., 2007; Lesourd et al., 2019). However, when difficulty was equally maintained across conditions (i.e., accuracy), Kalénine and Buxbaum (2016) found that both LBD patients and control subjects were slower to identify function than associative relationships. A similar result was found in healthy subjects between action and function matching tasks, where reaction times in the action condition were slower than in the function condition, after controlling for task difficulty (Canessa et al.,

2008; Garcea & Mahon, 2012). Moreover, fMRI studies which reported similar accuracies across conditions have also revealed greater changes in neural activity in IPL/IPS for action tool-tool compared to function tasks (Canessa et al., 2008), and for action hand-tool compared to associative tasks (Kleineberg et al., 2018). In summary, performance in action tool tasks as regards to semantic tool tasks is associated with slower reaction times coupled with greater changes in neural activity in IPL. These findings go against the task complexity hypothesis and confirm the involvement of specific neurocognitive processes underlying action tool representations.

4.4. Neurocognitive hypotheses of emergence and interactions of action tool and semantic tool knowledge

4.4.1. *The role of ATL and its relation with IPL*

We found that semantic tool and particularly function relations were depending on ATL. According to the CSC and hub-and-spoke model, ATL is an amodal representation hub whereas the spokes are modality-specific.

Behavioral studies found that RTs for function tool-tool tasks were similar for words and pictures whereas in action tool-tool tasks, words were judged slower than pictures (Garcea & Mahon, 2012; Ishibashi et al., 2011). Boronat et al. (2005) found greater percent BOLD signal change in action tool-tool compatibility condition, for pictures compared to words, in left IPL and left pMTG. In the present review, we reported that presenting either words or pictures or both engaged quite similar brain regions for action tool and semantic tool tasks, that is, ventrolateral/dorsolateral frontal cortex, left IPL and left pMTG (Boronat et al., 2005; Ebisch et al., 2007). Virtual lesion made in IPL during the presentation of tool words significantly slowed action tool-tool compatibility tasks but not semantic tool-tool compatibility tasks, whereas the reverse pattern was observed in ATL (Ishibashi et al., 2011).

Taken together these data confirm that semantic tool (function) knowledge contains amodal representation of concepts, stored in ATL, whereas posterior part of the brain is more involved in visual/action features, although these regions may be sensitive to words processing (Noppeney, Josephs, Kiebel, Friston, & Price, 2005; for a review see Culham & Valyear, 2006). In a recent sEEG study in humans, Aflalo et al., (2020) reported that action verbs and corresponding videos both yield activation in the posterior parietal cortex with longer latencies for action verbs. A possible explanation is that action verb activity in the

posterior parietal cortex originates from supramodal regions and automatically spreads to the posterior parietal cortex. This may explain why this region is involved in the processing of words that contain an action dimension (i.e., action verb, noun with a high dimension of manipulability; Saccuman et al., 2006).

The influence of ATL on IPL is far from being clear, and further studies should explore this relation. If action tool knowledge activation is triggered by early semantic tool activation, then we should observe early top-down influence on IPL coming from ATL.

4.4.2 LOTC/pMTG, an integrative hub?

In the present review we found that several brain regions were involved in both action and semantic tool knowledge, with a stronger involvement of the fronto-parietal network and the pMTG area for action tool knowledge (Canessa et al., 2008; Kellenbach et al., 2003; Kleineberg et al., 2018; Perini et al., 2014). This result indicates that some action and semantic tool tasks could share some commonalities in terms of neurocognitive processes. We found that virtual lesions in pMTG could modulate behavioral performance in all kinds of representations (i.e., action, function and associative), suggesting a key role of this brain region in action and semantic tool knowledge. The Dual Hub theory assumes that the pMTG supports mainly thematic relations (i.e., associative relations), however, we found that function and action relations were also supported by this brain region. The pMTG is part of LOTC, which is known to play a role in the perception of object-related actions (Wurm, Caramazza, & Lingnau, 2017), the conceptual processing of tools and actions (Kable & Chatterjee, 2006; Lingnau & Downing, 2015; Wurm & Caramazza, 2019), tool naming (Brambati et al., 2006), and the use of tools (Salazar-López, Schwaiger, & Hermsdörfer, 2016). LOTC also includes hand-selective representations that closely overlap with regions activated by tools (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012), suggesting that hand and object representations are tightly integrated (see 2AS+ model; Buxbaum, 2017). Moreover, LOTC/pMTG is also engaged in semantic control, according to the CSC (Jefferies et al., 2020; Noonan, Jefferies, Visser, & Lambon Ralph, 2013; Thompson, Robson, Lambon Ralph, & Jefferies, 2015). In broad terms, pMTG could be at the interplay between the semantic network and the tool use network (Lewis, 2006, p.224). While the pMTG is involved in a wide range of cognitive processes, each of which would refer to a single core-operation function (functional *polyhedron*; Genon, Reid, Langner, Amunts, & Eickhoff, 2018); one may also hypothesize that tool and action processing and semantic controlled

mechanisms may occupy similar neuroanatomy despite being computationally distinct (for a discussion see Jefferies, 2013).

However, while lesions occurring in pMTG have already been associated with apraxic-like deficits (Buxbaum et al., 2014; Kalénine & Buxbaum, 2016; Martin et al., 2017; Tarhan et al., 2015), it is unlikely that this brain region supports integration of both action and semantic tool features on its own. Indeed, it has been shown that left parietal lobe is critical for action tool representation (Goldenberg, 2009; Ishibashi, Pobric, Saito, & Ralph, 2016; Martin et al., 2017; Randerath, Goldenberg, Spijkers, Li, & Hermsdörfer, 2010; Reynaud et al., 2016, 2019; Salazar-López, Schwaiger, & Hermsdörfer, 2016).

4.4.3. The distributed hypothesis: the coupling between pMTG and IPL

Another hypothesis is that action tool and semantic tool tasks are supported by both common (i.e., pMTG and IPL) and distinct brain regions. Several studies reported that the production of object-related actions are supported by the exchange of information between the ventral and dorsal pathways (Bracci et al., 2012; Budisavljevic, Dell'Acqua, & Castiello, 2018; Hutchison & Gallivan, 2018; for a review see Milner, 2017). In a pantomime of tool use task, which requires the activation of action tool knowledge (Buxbaum, 2014; Buxbaum et al., 2007, 2005; Lesourd et al., 2019; Niessen et al., 2014), Garcea et al. (2018) reported an increase of functional connectivity between the left inferior LOTC, the left IPL and the left dPMC (see also Vingerhoets & Clauwaert, 2015).

While action tool knowledge is supported by ventro-dorsal pathway (i.e., SMG; Andres et al., 2013; Canessa et al., 2008; Kleineberg et al., 2018; Pelgrims et al., 2011), several studies also acknowledged the role of occipito-temporal regions (Almeida et al., 2013; Canessa et al., 2008; Chen, Garcea, & Mahon, 2016). It is therefore likely that action tool knowledge should also be supported by the coupling between ventral and dorsal pathways. For instance, in a fMRI study, Sim et al. (2015) showed hands performing an action as primes, followed by a manipulable target object which afforded similar actions to the prime. Using effective connectivity, the authors observed the functional influence of parietal regions on anterior temporal areas. Moreover, passively viewing images of manipulable tools is associated with an increase of connectivity between ventral and dorsal pathways (Almeida et al., 2013; Chen, Snow, Culham, & Goodale, 2018; Garcea et al., 2018). Finally, several studies also pointed out the structural connectivity existing between IPL and pMTG (Caspers et al., 2011; Vry et al., 2015).

Concerning semantic tool knowledge, ventral regions are typically involved in retrieving function relations (i.e., ATL and FG; Canessa et al., 2008; Chen et al., 2016; Ishibashi et al., 2011; Kleineberg et al., 2018). The present review also highlighted the role of pMTG (Andres et al., 2013) and AG which is located in the ventro-dorsal pathway for retrieving associative relations (Kleineberg et al., 2018; for a review see also Binder et al., 2009).

These data suggested that action tool and semantic tool knowledge may be retrieved by the way of mutual exchange between the ventral and the dorso-ventral pathways, in which pMTG and IPL represent key regions. The emergence of action tool and semantic tool knowledge could be achieved through three principles. First, ATL, an amodal representation hub, is involved in tool knowledge activation, and particularly in semantic tool knowledge. Second, several regional hubs are distributed across the brain (e.g., IPL) and support specific sources of information about tools/objects. However, it is not clear if these regional hubs only support modality-specific information. For instance, in left IPL, the integrative area aSMG/PFt receives inputs from aSMG/PF which stores mechanical knowledge, an abstract form of representation allowing us to understand physical interactions between tools and objects (Osiurak, 2014; Osiurak & Badets, 2016; Osiurak, Jarry, & Le Gall, 2010, 2011; Osiurak et al., 2020). Moreover, pMTG is also assumed to support abstract representations about actions (Lingnau & Downing, 2015; Wurm et al., 2017). Third, a coupling mechanism between regional hubs (under the potential influence of ATL) allows the integration of distinct representations about the same category (for a similar account see the *distributed domain-specific hypothesis*; Mahon & Caramazza, 2011).

5. Conclusion and future directions

In the present review, we found that action and semantic tool knowledge rely upon a large brain network including temporal and parietal regions. Semantic tool network includes primarily the ATL, the AG and the pMTG, whereas action tool knowledge network comprises the IPL, the IPS and the pMTG. Thus, this review acknowledges the role of temporal and parietal regions for processing semantic and action representations about tools. We also reported the existence of many different terms to name action tool and semantic tool knowledge in the literature, but also for the tasks that are used to assess these forms of knowledge. Multi-labelling of the same concept should be avoided, as this may lead to confusion. To conclude, we would like to stress that this present review may spur future

research in three directions. First, we reported that the processing of function and action relations could engage similar brain regions (pMTG/IPL), whereas associative relations engaged preferentially the AG. To our knowledge, no studies have directly tested action, function and associative relations in the same experimental design, which could be of great interest in the field of tool cognition. For instance, one may hypothesize that action and function relations are similar in terms of pattern of connectivity between temporal and parietal regions compared to associative relations. Second, the question of hand posture and kinematics still remains an open issue, as we found that both kinds of representations may tap into LOTC and IPL. Consequently, further studies should investigate specifically the neurocognitive bases of these two representations in both LBD and RBD patients (Voxel-Lesion Symptom-Mapping) and healthy subjects (fMRI/TMS) by means of similar judgment tasks taxing hand posture and kinematics. Furthermore, the analysis of functional connectivity between IPL and pMTG (Bracci et al., 2012) or the use of sensitive analyses in fMRI (i.e., MVPA; see for example Haynes, 2015) may shed a new light on the brain representations of hand postures and kinematics. Third, we restricted our work on the left hemisphere (see also Niessen et al., 2014) because RBD patients seem less affected than LBD patients (e.g., Randerath, Li, Goldenberg, & Hermsdörfer, 2009). However, the involvement of the right hemisphere, specifically the right pMTG has been reported in fMRI studies on tool use (Lewis, 2006; Reynaud et al., 2016), thus the impact of right-brain lesions, even moderate, deserves to be carefully documented in future works (Salazar-López, Schwaiger, & Hermsdörfer, 2016). Finally, we presented several neurocognitive models, which each captures a part of the data reported in the present review and more generally in the literature on the field. This work shed a new light on the critical role played by posterior parts of the brain (IPL, IPS and pMTG) in action tool and semantic tool knowledge.

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Appendix

Abbreviations of cerebral areas based on the Multi-modal parcellation of human cerebral cortex (Glasser et al., 2016).

MT+ complex and neighboring visual areas	PH LO1 LO2 LO3 MT MST	Area PH Area Lateral Occipital 1 Area Lateral Occipital 2 Area Lateral Occipital 3 Middle Temporal Area Medial Superior Temporal Area
Lateral temporal cortex	TGd PHT TE2a TE2p TF TE1a TE1p	Area TG dorsal Area PHT Area TE2 anterior Area TE2 posterior Area TF Area TE1 anterior Area TE1 posterior
Ventral stream visual cortex	FFC VVC	Fusiform Face Complex Ventral Visual Complex
Temporo-Parieto-Occipital Junction	TPOJ1 TPOJ2 TPOJ3 PSL	Area Temporo-parieto-occipital junction 1 Area Temporo-parieto-occipital junction 2 Area Temporo-parieto-occipital junction 2 Peri-Sylvian Language Area
Inferior parietal cortex	PGi PGs PGp PF PFt PFop IP0 IP1 IP2	Area PGi (Angular Gyrus) Area PGs (Angular Gyrus) Area PGp (Supramarginal gyrus) Area PF (Supramarginal gyrus) Area PFt (Supramarginal gyrus) Area PF opercular Area intraparietal 0 Area intraparietal 1 Area intraparietal 2
Superior parietal cortex	AIP LIPd	Anterior Intraparietal Area Area Lateral Intraparietal dorsal
Posterior cingulate cortex	31pd 7m	Area 31pd Area 7m
Anterior cingulate and medial prefrontal cortex	10v 8BM p32pr a24pr a32pr	Area 10v Area 8BM Area p32 prime Anterior 24 prime Anterior 32 prime
Orbital and Polar frontal cortex	10d a47r	Area 10d Area anterior 47r
Premotor cortex	6r 6a FEF	Rostral area 6 – inferior premotor Area 6 anterior – superior premotor Frontal Eye Field – superior premotor
Dorso-Lateral Prefrontal cortex	i6-8 8C	Inferior 6-8 transitional area Area 8C
Auditory Association cortex	A5 TA2	Auditory 5 Complex Area TA2
Posterior Opercular Cortex	FOP1 PFcm OP2-3 43	Frontal Opercular Area 1 Area PFcm Area OP2-3/VS Area 43

Insular and Frontal Opercular Cortex	FOP2 FOP4 FOP5 PoI1 PoI2	Frontal Opercular Area 2 Frontal Opercular Area 4 Frontal Opercular Area 5 Area Posterior Insular 1 Area Posterior Insular 2
Inferior Frontal Cortex	45 IFjp	Area 45 Area IFjp

Figures

Figure 1. These tasks propose either evaluation of tool-tool compatibility or hand-tool compatibility, in which the participants have to decide or match tools/objects according some specific characteristics: function (tools with the same purpose or not), associative (tools typically associated or not), hand posture (tools being grasped with the same hand posture), or kinematics (tools being manipulated in the same manner). In tool-tool (or object) compatibility tasks, the participants are presented with one or two tools whereas in the hand-tool compatibility tasks, the participants are presented with one tool and one or several hand postures. Semantic tool tasks include exclusively tool-tool compatibility tasks, whereas action tool tasks include both tool-tool and hand-tool compatibility tasks.

Figure 2. Activation sites reported in the present review are represented on a PALS-B12 left hemisphere (flat-map) atlas surface configuration (Van Essen, 2005). The parcellation is based on Glasser et al. (2016). For abbreviations and explanation, see the main text and Appendix. Each circle represents an activation site (non-continuous line: words, solid line: pictures, dashed line: words + pictures). On top left: activation sites for action tool>control contrasts are represented in blue. On bottom left: activation sites for semantic tool>control contrasts are represented in yellow. On the right: activation sites for: (1) semantic tool>action tool contrasts are depicted in green; and (2) action tool>semantic tool contrasts are represented in red. Each number refers to a specific study: (1) Boronat et al. (2005); (2) Kellenbach et al. (2003); (3) Ebisch et al. (2007); (4) Canessa et al. (2008); (5) Kleineberg et al. (2018); (6) Perini et al. (2014).

Figure 3. Stimulation sites are represented on a PALS-B12 left hemisphere (flat-map) atlas surface configuration (Van Essen, 2005). The parcellation is based on Glasser et al. (2016). For abbreviations and explanation, see the main text and Appendix. Each circle represents a stimulation site (non-continuous line: words, solid line: pictures). Stimulations were found mainly in inferior parietal lobe (IPL), in lateral occipito-temporal cortex (LOTC), intraparietal sulcus (IPS), and anterior temporal lobe (ATL). A sign “+” indicates that a brain stimulation at a given location (i.e., LOTC, IPL, IPS, ATL) and in a given task (i.e., action tool, function, associative) did not affect the behavioral performance, whereas the sign “-” indicates that the stimulation impaired the behavioral performance.

Figure 4. Each study, which may include several conditions or groups, is represented by a colored disk and the size of which depended on the number of patients included in the study. In the study of Buxbaum and Saffran (2002), no data for controls were available, thus mean raw scores of non-aprasic patients were used as controls for aprasic patients. A: Aprasic; NA: Non-Aprasic.

Figure 5. Schematic representation onto a 3D surface rendering of a MNI template of (1) cortical activation sites found in fMRI studies (specific contrast: e.g., action tool > semantic tool and non-specific contrast: e.g., action tool > control condition); and (2) brain stimulations (TMS/tDCS) which led to a behavioral deficit. MFG: middle frontal gyrus; IFG: inferior frontal gyrus; mPFC: medial prefrontal cortex; ATL: anterior temporal lobe; IPL/SMG: inferior parietal lobe/supramarginal gyrus; LOTC: lateral occipitotemporal cortex; FG: fusiform gyrus; AG: angular gyrus; IPS: intraparietal sulcus.

Fig.1.

Tasks classically used to assess action and semantic tool knowledge



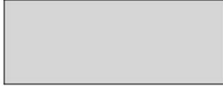
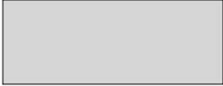


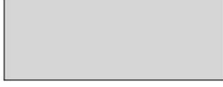
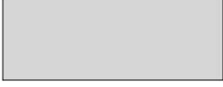






		Tool-tool compatibility		Hand-tool compatibility	
Semantic tool relations	function				
	associative				
Action tool relations	hand posture				
	kinematics			Does hammering need acceleration near the end of the downward movement?	

Fig.2.

Localization of fMRI activation sites

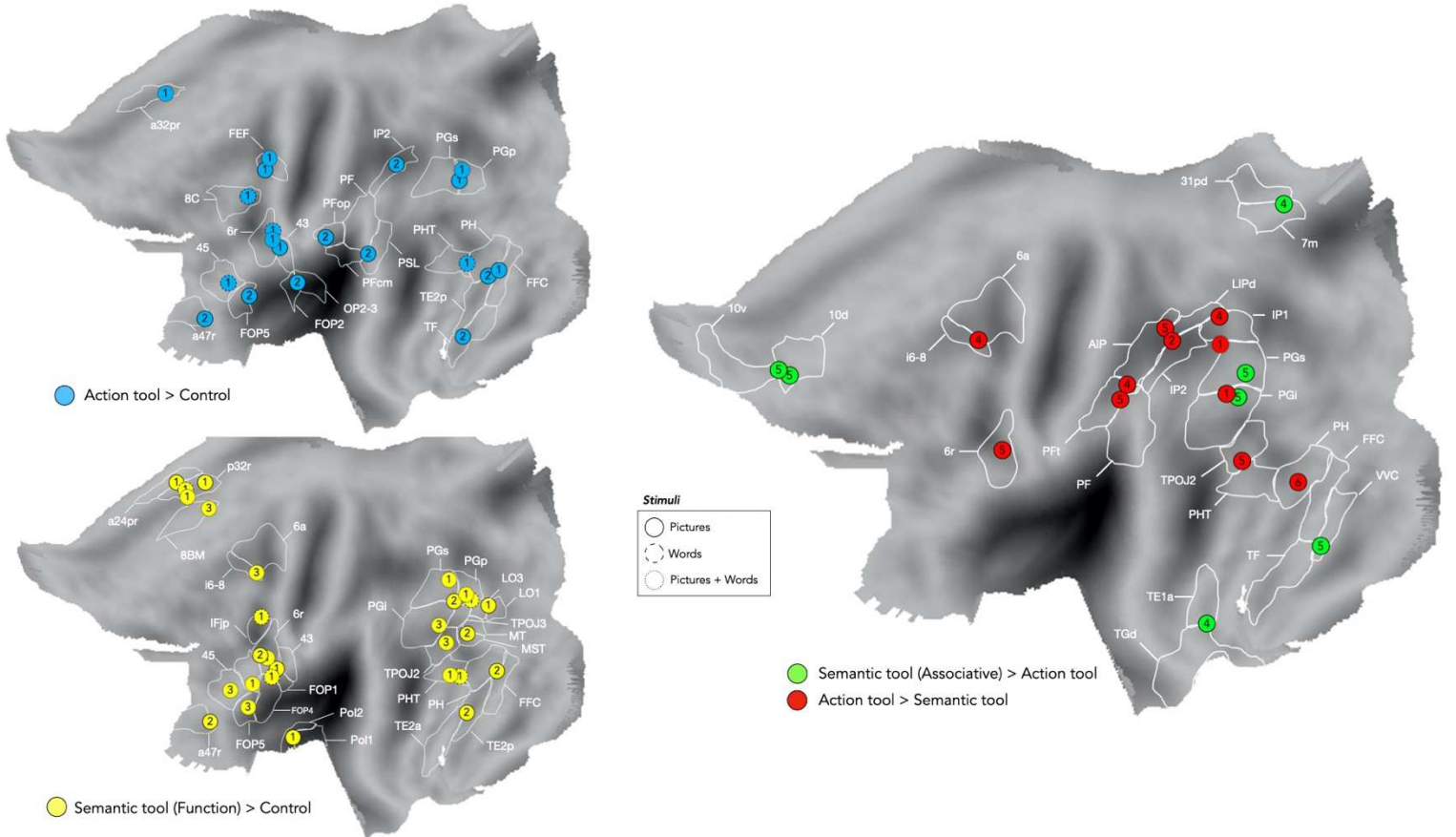


Fig.3.

Localizations of stimulation sites in TMS/tDCS studies

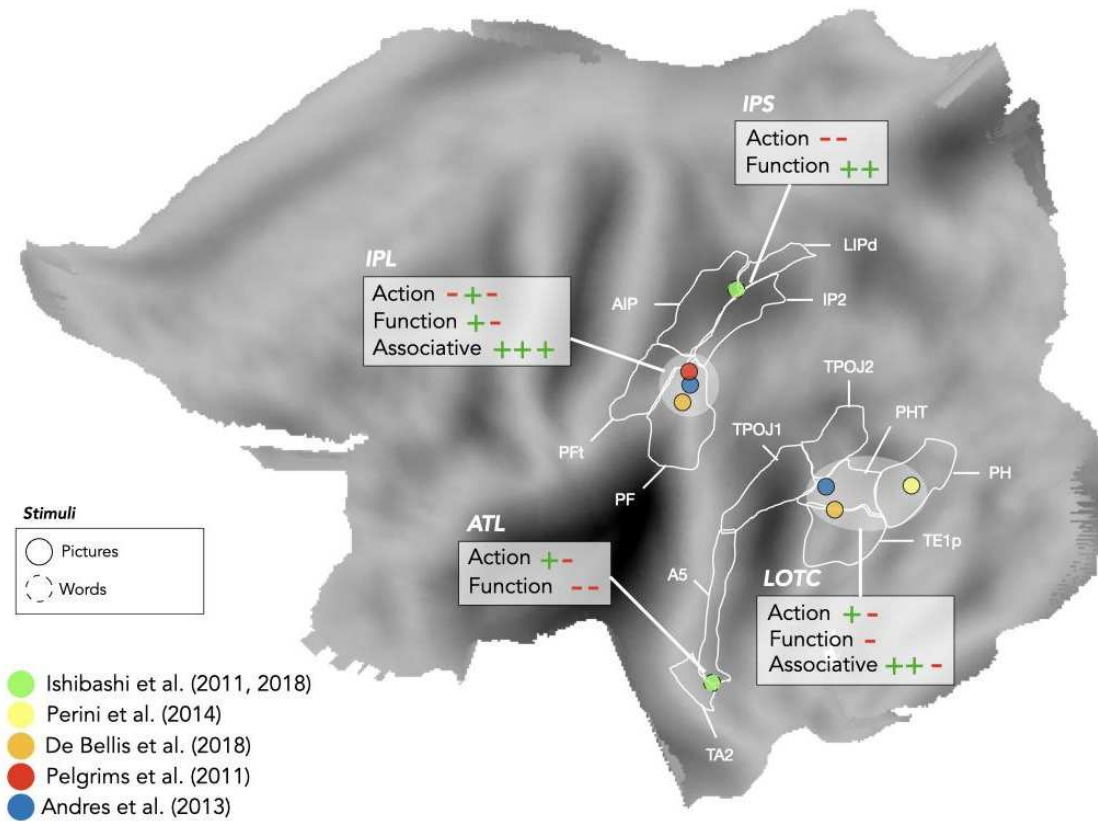


Fig.4.

Control-patient difference (%) for action tool and semantics tool tasks.

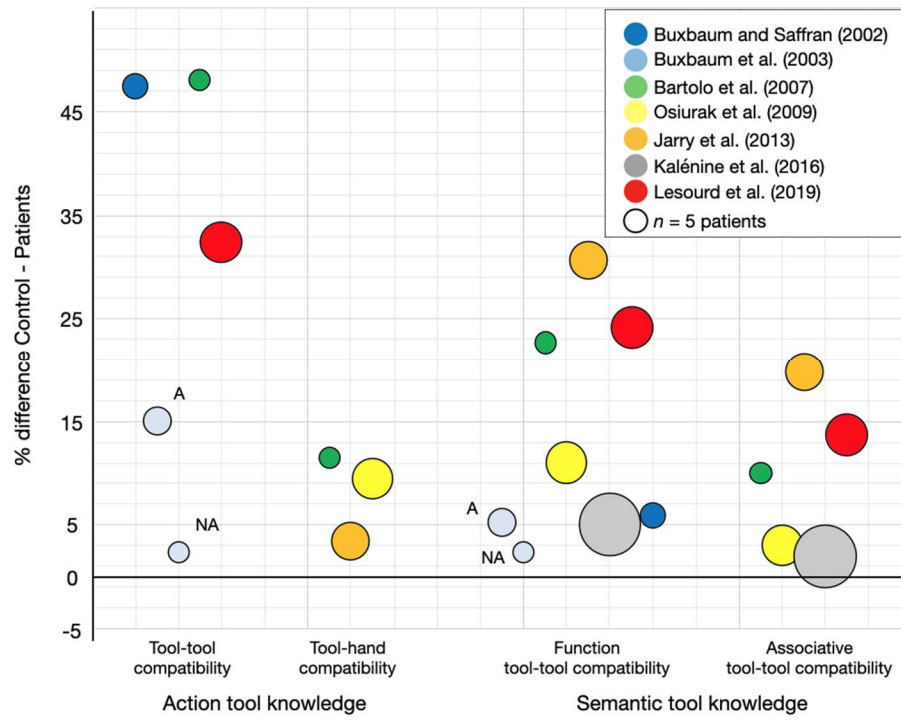


Fig.5.

Summary of the main results obtained from activation and stimulation studies

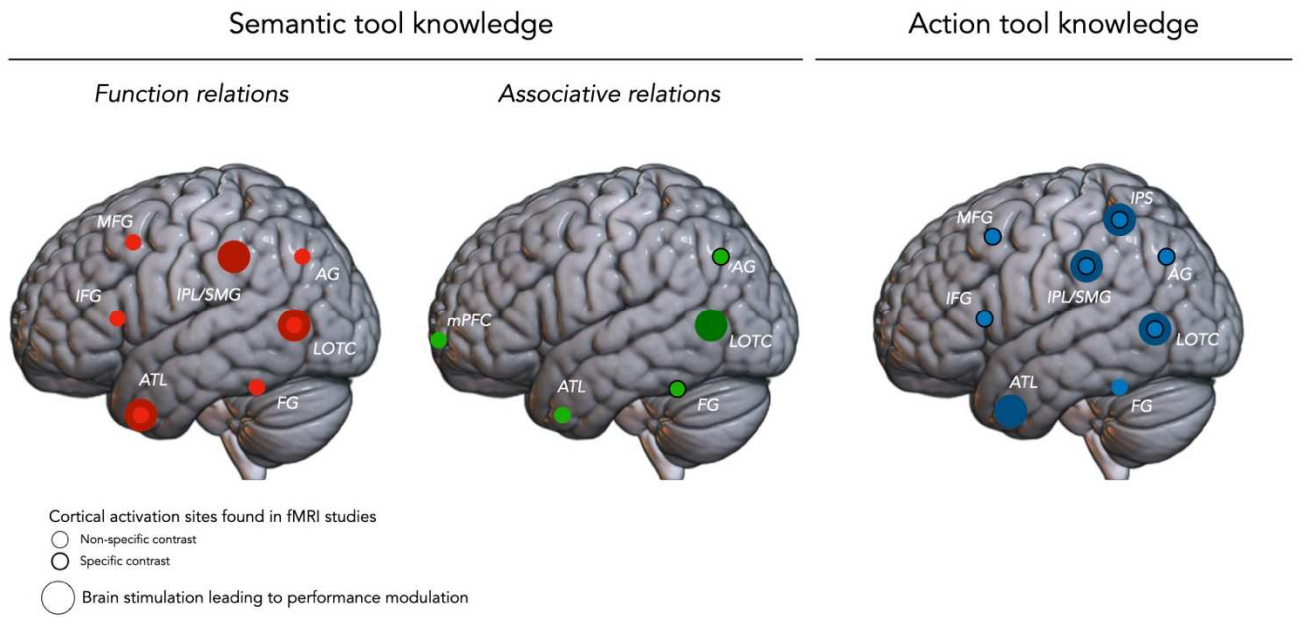


Table 1. Neurocognitive account of semantic and action tool knowledge

Brain regions	Semantic theories		Tool use theories	
	<i>CSC + Hub-and-spoke model</i>	<i>Dual Hub theory</i>	<i>Reasoning-based approach</i>	<i>2AS+</i>
IFG/MFG	Semantic control		Action control	Goal-relevant biasing signal
IPS			Production system (grasping component)	Grasping/reaching
IPL	Praxis spoke		Integrative process	Manipulation knowledge
AG	Automatic retrieval	Thematic hub		
LOTG/pMTG	Semantic control	Thematic hub		Visuo-kinesthetic representations Body and tool movements
FG/ITG	Visual spoke		Function/Associative relations	
ATL	Heteromodal conceptual representations	Taxonomic hub	Semantic reasoning	

CSC: Controlled Semantic Cognition; 2AS+: Two action systems plus

IFG/MFG: inferior frontal gyrus/middle frontal gyrus; IPS: intraparietal sulcus; IPL: inferior parietal lobe; AG: angular gyrus;

LOTG/pMTG: lateral occipitotemporal cortex/posterior middle temporal gyrus; FG/ITG: fusiform gyrus/inferior temporal gyrus;

ATL: anterior temporal lobe

Table 2. Overview of the neuroimaging studies considered in the present review

Study	Subjects' age (<i>n</i>)	Method	Task name	Instruction	Stimuli
Kellenbach et al. (2003)	27 (<i>n</i> = 9)	fMRI	Action knowledge Functional knowledge	Does using the object involve a twisting or turning action? Is this object used to attach or hold objects together?	Color photographs of manipulable and non manipulable tools One stimulus
Boronat et al. (2005)	23.1 (<i>n</i> =15)	fMRI	Manipulation Function	Are items related by manipulation? Are items related by function?	Words and line-drawing of manipulable and non-manipulable objects Pair of stimuli
Ebisch et al. (2007)	21.7 (<i>n</i> =14)	fMRI	Functional decision	Do the two items are functionally related?	Words and line-drawing of objects Pair of stimuli
Canessa et al. (2008)	24.6 (<i>n</i> =15)	fMRI	Action knowledge Function knowledge	Are these objects used with the same manipulation pattern? Are these objects used in the same context of use?	Photographs of manipulable objects Pair of stimuli
Perini et al. (2014)	27.7 (<i>n</i> = 24)	fMRI	Action task Location task	Detecting repetition of same action (1-back task) (i.e., rotate or squeeze) Detecting repetition of same location (1-back task) (i.e., kitchen or garage)	Picture of manipulable tools One item at a time
Kleineberg et al. (2018)	25.3 (<i>n</i> = 20)	fMRI	Manipulation knowledge Function knowledge task	Judging which hand posture best fit with the tool target Judging which recipient was functionally related with the target tool	Pictures of tools and recipients/hand postures One target and two items

Table 3. Overview of the stimulation studies considered in the present review

Study	Subjects'age (<i>n</i>)	Method	Task name	Instruction	MNI coordinates of stimulation sites
Ishibashi et al. (2011)	27.08 ± 7.02 <i>n</i> = 13	rTMS	Manipulation matching	Choosing among 3, the target that had the same way of manipulation as the probe	Left ATL: x = -51, y = 9, z = -21 Left IPL: x = -38, y = -44, z = 48
			Function matching	Choosing among 3, the target that had the same function as the probe	
Pelgrims et al. (2011)	26.1 ± 5.4 <i>n</i> = 16	rTMS	Hand configuration task	Deciding whether the same hand posture is normally adopted to use the two objects displayed on the screen	Left SMG: x = -59, y = -32, z = 46 Right SMG: x = 60, y = -28, z = 47
			Object-hand task	Deciding if a hand posture was compatible or not to use a tool	
			Contextual task	Deciding whether the two objects displayed on the screen are normally used in the same context	
Andres et al. (2013)	27.6 <i>n</i> = 16	rTMS	Hand configuration task	Deciding whether the same hand posture is normally adopted to use the two objects displayed on the screen	Left SMG: x = -60, y = -34, z = 46 Left pMTG: x = -60, y = -50, z = -1
			Contextual task	Deciding whether the two objects displayed on the screen are normally used in the same context	
Perini et al. (2014)	27.7 <i>n</i> = 24	rTMS	Action task	Detecting repetitions of the manipulation dimension (e.g., rotate or squeeze)	Left LOTC: x = -47, y = -68, z = -9
			Location task	Detecting repetitions of the location dimension (e.g., kitchen or garage)	
De Bellis et al. (2018)	24.0 ± 1.7 <i>n</i> = 27	rTMS	Taxonomic matching task	Identifying, among 3 objects, the 2 related objects (taxonomic relations) among 3 objects after functional, structural or pointing prime	Left SMG: x = -59, y = -36, z = 40 Left pMTG: x = -65, y = -49, z = -8
			Thematic matching task	Identifying, among 3 objects, the 2 related objects (thematic relations) among 3 objects after functional, structural or pointing prime	
Ishibashi et al. (2018)	22.3 <i>n</i> = 18	tDCS	Manipulation matching	Choosing among 3, the target that had the same way of manipulation as the probe	Left ATL [°]
			Function matching	Choosing among 3, the target that had the function as the probe	Left IPL [°]

rTMS: repetitive transcranial magnetic stimulation; tDCS: transcranial direct current stimulation; ATL: anterior temporal lobe; IPL: inferior parietal lobe; SMG: supramarginal gyrus; pMTG: posterior medial temporal gyrus

[°] Precise coordinates are not provided in Ishibashi et al. (2018), but as the same author conducted the studies in 2011 and 2018, we considered that the stimulation sites are identical in 2011 and 2018

Table 4. Overview of the LBD patients' studies considered in the present review

Study	Subjects'age (<i>n</i>)	Task name	Instruction	Lesion description
Buxbaum and Saffran (2002)	62.3 ± 11.1 (<i>n</i> = 13)	Manipulation	Selecting the two objects that shared the same manipulation among three (e.g., type-writer - piano)	apraxic (<i>n</i> = 7) F, P, T non-apraxic (<i>n</i> = 6) T
		Function	Selecting the two objects among three that shared the same purpose (e.g., radio - vinyl turntable)	
Buxbaum et al. (2003)	62.6 ± 9.8 (<i>n</i> = 14)	Manipulation	Forced choice of two objects among three that shared the same way to be held and used	apraxic (<i>n</i> = 9) T, P, F, SubC non-apraxic (<i>n</i> = 5) Cereb, F, T, P
		Function	Forced choice of two objects among three that shared the same possible function	
Bartolo et al. (2007) ^a	54.2 ± 9.6 (<i>n</i> = 5)	Object-manipulation	Matching two objects that have the same manner of manipulation (e.g., pipe - penny whistle) in the presence of a distractor (e.g., spoon)	F, T, P
		Object-function	Matching two objects that have similar function (e.g., jug - bottle) in the presence of a distractor (e.g., pot)	
		Object-relation	Matching two objects which functionally interact when used (e.g., teapot - cup) in the presence of a distractor (e.g., glass)	
		Pantomime recognition	Matching the pantomime executed by the examiner with the correct tools in presence of three distractors	
Osiurak et al. (2009)	58.2 ± 16.3 (<i>n</i> = 20)	Functional picture matching (associative)	Selecting among 4 objects the one (e.g., screw) which is associated with the target (e.g., screwdriver)	F, T, P, O, SubC
		Functional picture matching (categorical)	Selecting among 4 objects the one (e.g., belt) which is functionally equivalent with the target (e.g., pair of shoulder straps)	
		Gesture recognition	Selecting the photograph depicting the correct use of a tool among three representing the tool incorrectly oriented, inappropriately held or dangerously held	
Jarry et al. (2013; 2016) ^b	2013: 70.2 ± 10.3 (<i>n</i> = 16)	Functional association	Selecting from 4 objects, the one (e.g., nail) that is functionally associated with the target (e.g., hammer)	F, T, P, O, SubC
	2016: 68.2 ± 9.5 (<i>n</i> = 17)	Categorical association	Selecting among 4 objects the one (e.g., saw) which shares the same purpose as the target (e.g., axe)	
	Gesture recognition	Selecting the photograph depicting the correct use of a tool among four representing the tool incorrectly oriented, inappropriately held or dangerously held		
Kalénine et al. (2016)	57 ± 11 (<i>n</i> = 48)	Thematic relationship	Deciding which object of two is semantically related with the target (e.g., saw - wood)	MTG, STS, Pre/PostC, IPL, IFG, MFG
		Taxonommic relationship	Deciding which object of two is semantically related with the target (e.g., saw - drill)	
Lesourd et al. (2019)	65.2 ± 13.9 (<i>n</i> = 21)	Manipulation matching	Choosing two objects among three (e.g., slingshot, sword, bow) that required the same manner of manipulation	N/A
		Function matching	Choosing two objects among three (e.g., candle, cigarette, lamp) that could be used for the same purpose	
		Associative matching	Choosing among two objects (e.g., screw and nail), the one that is more likely to be used with the target (e.g., hammer)	

^a Six patients were initially included in Bartolo et al. (2007) but one patient had right lesion (case 6) and was excluded from the present review

^b One patient and 17 controls were added between Jarry et al. (2013) and Jarry et al. (2016)

F: frontal; P: parietal; T: temporal; SubC: Sub-Cortical; Cereb: Cerebellum; O: Occipital; MTG: Middle Temporal Gyrus; STS: Superior Temporal Sulcus; Pre/PostC: Pre- and Post-Central gyrus; IPL: Inferior Parietal Lobe; IFG: Inferior Frontal Gyrus; MFG: Middle Frontal Gyrus; N/A: Not Available

Table 5. Patients impairments and dissociations according to Crawford and Garthwaite's (2005, 2007)

	Per cent of patients showing a deficit ^a				Per cent of dissociations ^b					
	Action		Function	Associative	Action TT	Action TT	Action TT	Action HT	Action HT	Function
	Tool-tool	Hand-tool	Tool-tool	Tool-tool	Action HT	Function	Associative	Function	Associative	Associative
Bartolo et al. (2007)	5/5 (100)	2/5 (40)	5/5 (100)	4/5 (80)	na	na	na	na	na	na
Osiurak et al. (2009)	-	8/20 (40)	12/20 (60)	7/20 (35)	-	-	-	9/20 (45) A>F: 7/9 F>A: 2/9	2/20 (10) A>Ass: 1/2 Ass>A: 1/2	8/20 (40) F>Ass: 1/8 Ass>F: 7/8
Jarry et al. (2016)	-	4/17 (25)	10/17 (59)	9/17 (53)	-	-	-	9/17 (53) A>F: 8/9 F>A: 1/9	6/17 (35) A>Ass: 6/6 Ass>A: 0/6	8/17 (47) F>Ass: 4/8 Ass>F: 4/8
Lesourd et al. (2019)	17/21 (81)	-	12/21 (57)	14/21 (67)	-	5/21 (24) F>A: 5/5 A>F: 0/5	10/21 (48) A>Ass: 6/10 Ass>A: 4/10	-	-	6/21 (29) F>Ass: 5/6 Ass>F: 1/6

Action TT: action tool-tool compatibility tasks; Action HT: action hand-tool compatibility tasks; A: action; F: Function; Ass: associative
na: not available

^a The presence of a deficit is attested according to the Crawford-Garthwaite Bayesian test for single-case analysis (2007).

^b The presence of a dissociation is attested according to the Revised Standardised Difference Test (Crawford and Garthwaite, 2005)