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Got it! Understanding the concept of a tool

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ABSTRACT

Understanding the function of a tool is an essential step in learning to use a tool. This aspect of interaction with tools has hitherto been neglected. Unlike acquiring the expertise in handling a new tool, which involves practice, understanding its function usually only requires a single observation of the tool being used. The present study uncovers the neural areas involved in this transient understanding effect as a left-lateralized pattern involving prefrontal and mediotemporal areas. We suggest that activation in this network reflects the conceptual encoding of the function of new tools as it is independent from the well-known tool-related networks. We demonstrate that understanding the function of a new tool does not rely on known semantic or motor networks involved in processing tool use.

Introduction

The human ability to skilfully manufacture and manipulate complex tools is a feature that sets us apart from other animals. In contrast to the simple tools used by other species, the customized specificity of manmade tools reflects a deep understanding of the physics of the body and the environment (Johnson-Frey, 2004). Even if tools and tool use are based on physical principles, it is not always obvious, when coming across a new tool, what it is used for and how to use it. However, it is usually sufficient to see a tool used once within its usual action context to grasp the concept of how to use it.

Imagine seeing for the very first time in your life an ancient board bender, as used for manufacturing of wooden barrels. The first impression is of a peculiar, heavy kind of fork. However, seeing it only once in action as it bends hot boards to shape a barrel makes the purpose of this tool immediately apparent. This phenomenon is instantaneous and extremely strong. The effect is a sudden comprehension of the general idea of physical properties and mechanisms of a tool and also about its context, e.g., the manipulated object. This "understanding of a tool" as we see it is a pure conceptual or semantic phenomenon and does not include the acquisition of skilful manipulation abilities.

Although the acquisition of conceptual knowledge is a fundamental component of tool use learning, this understanding effect has never been investigated, as previous studies on novel tools have only concentrated on the factor of skill or acquisition of proficiency (Imamizu et al., 2000; Tamada et al., 1999; Creem-Regehr and Lee, 2005; Creem-Regehr et al., 2004) or on the aspect of familiarity (Vingerhoets, 2008), but not on the understanding of the tool's function.

Several functional imaging studies (Canessa et al., 2008; Boronat et al., 2005; Shmuelof and Zohary, 2005) as well as a detailed review (Lewis, 2006) describe at least two dissociable factors regarding human tool use including (1) skills for dexterous tool use and (2) semantic knowledge, integrating the knowledge of a tool with the knowledge of the action to be performed (Lewis, 2006; Johnson-Frey, 2004). These two factors can also be distinguished on a neural basis. The tool use motor network is reported to include the dorsal and ventral premotor cortex, the inferior and superior parietal lobe, as well as the posterior mediotemporal gyrus and the inferior temporal cortex (Chao et al., 1999; Moll et al., 2000; Chao and Martin, 2000). The semantic network includes parts of the inferior frontal gyrus, the fusiform gyrus, and again the posterior mediotemporal gyrus and inferior temporal cortex (Lewis, 2006; Martin and Chao, 2001; Chao et al., 1999).

Another important distinction between networks is also the differentiation between object or tool manipulation and tool use. Johnson and Grafton (2003) described two networks. Sensorimotor transformations involved in 'acting on' or manipulating objects are supposed to occur in bilateral organized parietofrontal circuits, whereas 'acting with' or using tools is supported by a left-lateralized system, involving the inferior parietal lobule and medial frontal gyrus (Johnson and Grafton, 2003). This distinction between manipulation and function is also apparent in patient studies (Buxbaum and Saffran, 2002; Buxbaum et al., 2003; Goldenberg and Spatt, 2009). Patients with apraxias, which concern both sides of the body, although they are caused by unilateral, predominantly left-sided, brain lesions, are

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typically more impaired with skills involving object use, although they are surprisingly accurate when grasping and manipulating familiar objects on the basis of their perceptual properties, even when failing to use such objects appropriately (Johnson-Frey, 2004; Buxbaum et al., 2003; Goldenberg, 2009).

Therefore, these two factors should also be dissociable in regard to the learning of tool use; in other words, the acquisition of proficiency in manipulation of a special tool (skill) should be separable from the acquisition of knowledge about a tool (understanding).

Only a few studies have already investigated the acquisition of proficiency in manipulating novel tools. Imamizu et al. (2000) reported changes in cerebellar activity reflecting a newly acquired internal model of a tool (a computer mouse with novel rotational information). Subsequent work with the same task revealed an increased connectivity of the cerebellum with the pars opercularis and pars triangularis in the inferior frontal gyrus (Tamada et al., 1999). Creem-Regehr and colleagues assigned a special function to a set of novel objects and investigated the processing of those by comparing them to a set of novel objects without previously trained function. They report an activation of the ventral premotor cortex (vPMC) associated with the novel objects with learnt function when they are simply observed, and an increased activation for the novel objects with learnt function in dorsal premotor cortex (dPMC), vPMC, supplementary motor area (SMA), insula, cerebellum, and posterior parietal cortex, when subjects were asked to imagine grasping the tools (Creem-Regehr and Lee, 2005; Creem-Regehr et al., 2004).

However, understanding of the concept precedes any exercise. This present study was designed to investigate the neural mechanisms underlying this outstanding aspect of learning novel tool use. Therefore, we opted for a task, which is primarily designed to provoke the understanding of a tool's concept. To this end, we used a carefully selected set of commonly unknown tools and explained their function to the subjects by showing them in their usual action context.

Based on the previous findings describing a left-hemispheric dominance for tool use as opposed to object manipulation, we hypothesize that the acquisition of conceptual knowledge about tools is also represented in a neural system within the left cerebral hemisphere that is (at least) partly dissociable from other networks subserving tool processing.

Materials and methods

Subjects

Twenty-six healthy right-handed volunteers underwent successful data acquisition. Twenty subjects (10 females, 21–35 years of age, average 26.6 ± 3.5 years) who passed the behavioural cutoff of 15 reported ‘understandings’ of an ‘unknown tool’ were included in the fMRI analyses. All subjects had normal or corrected-to-normal vision. Each subject gave written informed consent, and the study was approved by the local ethics committee.

Stimuli

A set of 100 tools taken from internet pages (special handicraft pages, ancient tools, hobby tools) was rated on the extent of familiarity (25 additional subjects). All tools were clearly recognized as tools. The 30 most unknown (> 80% non-familiar) were selected and complemented by a set of 30 well-known tools. Every one of these tools was then processed into two stimuli, using the software program blender as 3D animation application (http://www.blender.org/). Examples of these stimuli are included as supplementary material. Every animated stimulus had a duration of 3.7 seconds. All animations were optimized in a pilot study (20 additional subjects) until subjects reported understanding the action of unknown tools in at least 25 out of 30 cases and ceased to report any confusing details in animations of tools they knew.

Experimental design

The experiment consisted of 60 trials (30 known tools and 30 unknown tools). Two example trials are depicted in Fig. 1. First, the tool was demonstrated in a simple rotation (demo), after which the subject was asked for a familiarity decision (known vs. unknown). Second, the same tool was presented in the usual action context (action) followed by the question for comprehension (understood vs. not understood). Subjects were asked to press the button only after the presentations, but without any limit in response time.

This resulted in a 2×2 factorial design with the factors known/unknown (according to the answers given) and action/demo (fixed). All pairs of stimuli were presented in a randomized order. A variable onset delay of every stimulus in relation to the acquisition time (0, 470, 940, 1410, or 1880 ms) produced an oversampling of the actual image acquisition time of 2350 ms by a factor of 5, consequently leading to an acquisition sampling rate of 470 ms. All stimuli were displayed with VisuaStim VGA goggles (Resonance Technology Inc.), and responses were collected with a custom-made 4-button button box.

To verify the self-reported understanding of a tools action, subjects were asked to complete an unheralded questionnaire after the scanning session. This questionnaire contained static pictures of the tools and the subjects were asked to either name the tool (if known) or describe the function as accurately as possible. This questionnaire was rated by two independent raters, and the tool's function was considered as being ‘understood’ if the subject was able to meaningfully describe the physical principle applied and the objects involved.

Image acquisition

The experiment was carried out on a 3-T MRI scanner with a 12-channel head coil (Siemens TRIO, Erlangen, Germany). Thirty-six transversal slices (216 mm FOV, 72×72 matrix, 3 mm thickness, no spacing) covering the whole brain were acquired using a fast-gradient echo EPI sequence (TR 2350 ms, TE 30 ms, 80° flip angle). One functional run with on average 857 T2* scans (the number of volumes

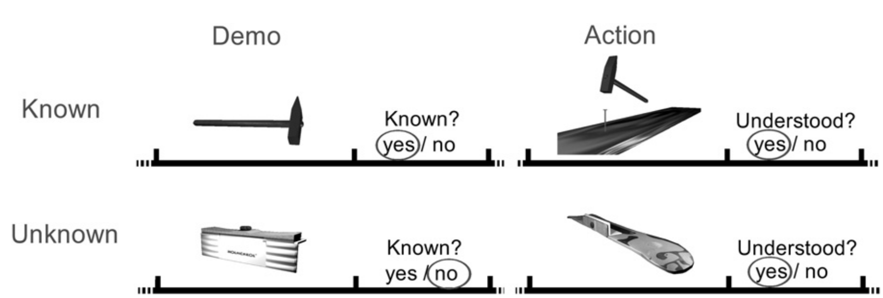

Fig. 1. Experimental design. Two example trials are depicted. First, the tool was demonstrated in rotation (demo), after which the subject was asked for a familiarity decision (known vs. unknown). Second, the same tool was presented in action (action) followed by the question for comprehension (understood vs. not understood).

actually acquired depended on the individual response times) was performed, with each scan sampling over the 36 slices. Before the functional run, an anatomical T1 image (256 mm FOV, 256 × 192 matrix, 240 slices, 1 mm thickness, 50% spacing, TR 2300 ms, TE 2.98 ms) was acquired applying an MPRAGE sequence.

Image analysis

Data analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.90, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Functional data were motion-corrected using MCFLIRT (Jenkinson et al., 2002). To correct for the temporal offset between the slices acquired in one scan, a Fourier-space time series phase shifting was applied. Non-brain voxels were removed using BET (Smith, 2002). To correct for large drifts, a temporal high-pass filter (Gaussian-weighted least-squares straight-line fitting) with a cutoff frequency of 1/128 Hz was used for baseline correction of the signal. Spatial smoothing using a Gaussian kernel of FWHM 9 mm as well as mean-based intensity normalization of all volumes by the same factor was applied to the functional data. To align the individual functional data slices onto the MNI 3D stereotactic coordinate reference system, a rigid linear registration with 6 degrees of freedom (3 rotational and 3 translational) was carried out using FLIRT (Jenkinson and Smith, 2001).

Statistical analysis

The first 5 volumes of each subject's scan were removed to allow for full T1 saturation. Time series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich et al., 2001).

From the 2 × 2 design (Fig. 1), four conditions were created: known_demo, known_action, unknown_demo, and unknown_action. From these conditions, four effects of interest were estimated. First, the main effect of familiarity of a tool was estimated from the difference between known tools and unknown tools in the demonstration condition. Second, the main effect of tool use that is areas that are more activated by viewing a known tool in action as compared to the demonstration only of this object. The other two effects of interest were interactions that were estimated by comparing the action effects from known tools (known_action > known_demo) to the action effect from unknown tools (unknown_action > unknown_demo). This results in the effect of recognising tool use (recognition effect) in contrast to the effect of understanding tool use (understanding effect). We chose to contrast the interactions to concentrate on the moment of seeing the use instead of only seeing the tool. Thus, we removed the observation related activation by subtracting the demo condition first, thereby removing as much activation as possible linked to what happened in the task before that very moment.

The second-level analysis was carried out using FLAME (FMRIB's Local Analysis of Mixed Effects; Beckmann et al., 2003; Woolrich et al., 2004). FMRI data postprocessing was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.90, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Z (Gaussianized T/F) statistic images were thresholded using GRF theory-based maximum height thresholding with a (corrected) significance threshold of $P = 0.05$ (Worsley, 2001).

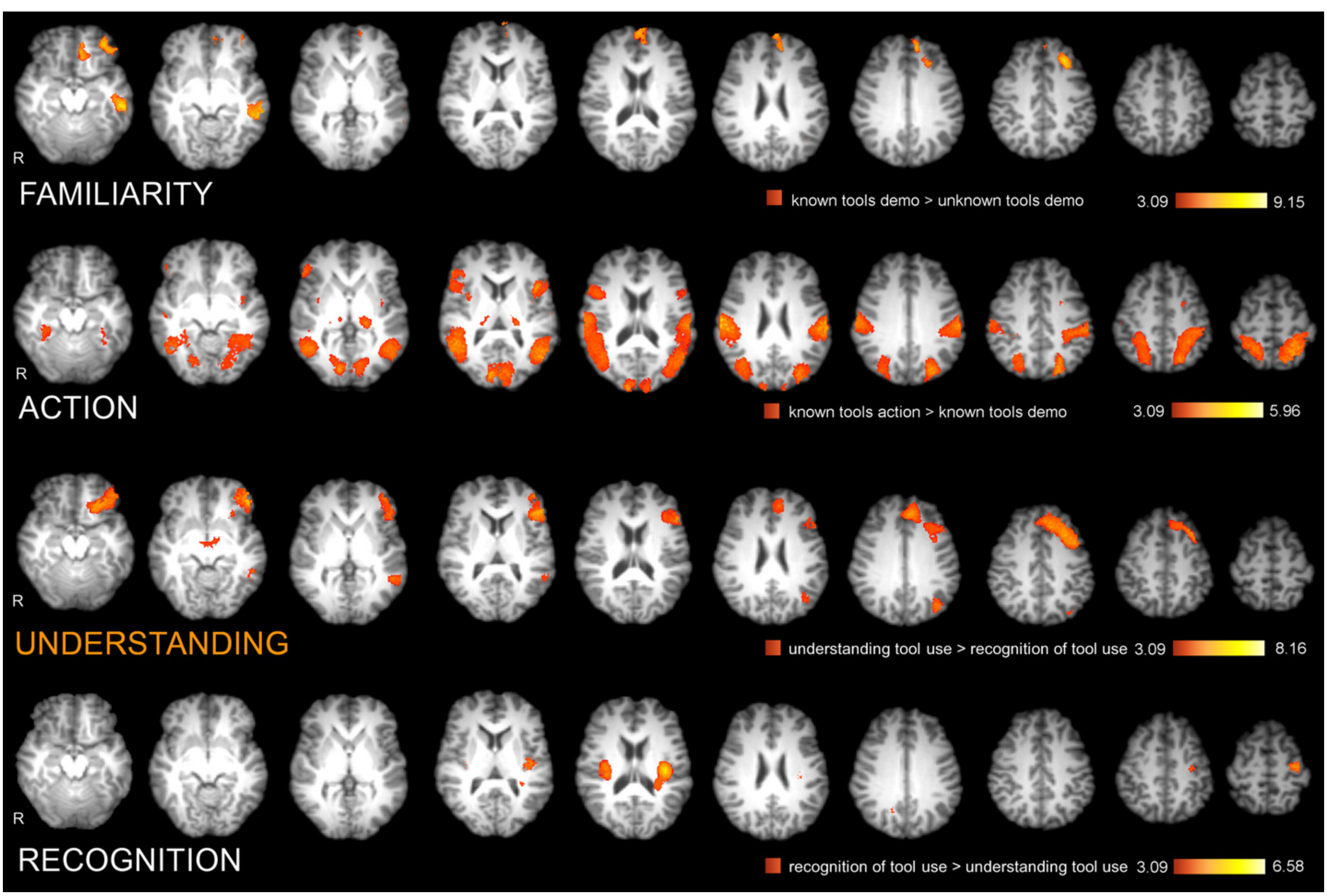

Fig. 2. Familiarity effect: areas activated more by viewing known tools than by viewing unknown tools. Action effect: viewing of tool use as compared to viewing only the tool. Understanding effect: areas that are activated more by an understanding of how to use a previous unknown tool than by recognising a known tool being used (from top to bottom). Recognition effect: areas that are activated more by the recognition of tool use than by understanding. Images display z-scores, thresholded at $P < 0.05$ (corrected), rendered upon axial slices at $Z = (-17, -08, +01, +10, +19, +28, +37, +46, +55)$.

Results

Behavioural results

On average, subjects reported knowing 32.75 (±3.7) tools out of the set of 60. On the other hand, 26.9 (±3.8) tools were reported to be unknown. After the presentation of an unknown tool, subjects reported in 21.7 (±4.6) cases that they understood the action (81%). After the presentation of a known tool, subjects had the possibility to report a false alarm, i.e., the tool was mistaken, or they felt irritated by the presented action. This happened in 1.1 (±1.2) cases on average. These trials were excluded from the analysis.

In the unheralded questionnaire after scanning, subjects were able to describe the 'understood' tools correctly in 79.4% of the cases. These descriptions included the physical principle and the objects involved. Six subjects were able to explain 100% of the understood actions correctly.

fMRI results

As explained in the methods section, from the 2×2 design (please refer to Fig. 1) four conditions were created: known_demo, known_action, unknown_demo, and unknown_action. From these conditions, four effects of interest were estimated, which are displayed in Fig. 2.

The top row illustrates the FAMILIARITY effect (known_demo>unknown_demo). This effect displays areas that are more activated, when a known tool is seen as compared to the demonstration of an unknown tool. The activation describes a left-hemispheric frontotemporal pattern, including areas in the middle and superior temporal gyri, the frontal pole, and the frontal medial cortex.

The second row of Fig. 2 shows the main effect ACTION (known_action>known_demo). Areas that are more activated while seeing a known tool in an action context as compared to a simple rotation include areas in the occipital pole and bilateral in the opercular part of the inferior temporal gyrus. More posterior and superior, a bilateral pattern is displayed in the somatosensory cortices with the local maximum in the postcentral gyri, along the intraparietal sulcus, and in the temporo-occipital part of the middle temporal gyrus (posterior to the activation in the familiarity effect). Subcortically, there is strong activation in the thalamus.

The most important contrast of our study, the UNDERSTANDING effect in the third row, shows areas that are more activated by seeing a previously unknown tool's action for the first time, while understanding it, as compared to the observation of an already known tool in action (unknown_action–unknown_demo>known_action–known_demo). The activation sites of this entirely left-hemispheric effect comprise a large activation of the lateral and medial prefrontal cortices with local maxima reaching from the frontal orbital cortex and the frontal pole, over the pars triangularis of the inferior frontal gyrus, the middle frontal gyrus, up to the medial superior frontal gyrus. This widespread prefrontal activation is again complemented by an activation in the middle temporal gyrus anterior to the activation cluster in the action effect and posterior to the activation in the familiarity effect.

The opposite effect of this interaction, the RECOGNITION effect, is displayed in the last row. It shows areas that are more activated by processing the action of a known tool than of an unknown tool (known_action–known_demo>unknown_action–unknown_demo) and reveals a bilateral activation in the anterior insula, which is complemented by an activation in the precentral gyrus.

Local maxima of the four contrasts are given in Table 1.

Table 1
Local maxima of the four contrasts.

Contrast		Coordinates (MNI)			Z-max
		x	y	z	
Familiarity	L. middle temporal gyrus	−56	−29	76	5.91
	L. superior frontal gyrus	−26	28	44	5.76
	L. frontal medial cortex	−8	34	−15	5.06
	L. frontal pole	−11	49	38	5.02
Action	R. postcentral gyrus	64	−14	29	8.20
	L. postcentral gyrus	−62	−19	26	7.96
	R. occipital pole	10	−89	6	8.08
	L. intraparietal sulcus	−30	−48	58	7.59
	R. intraparietal sulcus	29	−44	58	6.01
	L. thalamus	−20	−29	3	6.62
	R. thalamus	19	−30	6	6.23
	L. middle temporal gyrus	−49	−62	7	6.53
	R. middle temporal gyrus	51	−53	10	6.36
	L. inferior frontal gyrus (p. op.)	−46	17	9	6.41
	R. inferior frontal gyrus (p. op.)	52	18	15	6.19
Understanding	L. frontal pole	−4	41	−8	7.25
	L. inferior frontal gyrus (p. triang.)	−50	26	13	6.99
	L. frontal orbital cortex	−33	30	−21	6.41
	L. middle frontal gyrus	−30	22	47	6.38
	L. superior frontal gyrus (medial)	−6	40	43	6.32
	L. middle temporal gyrus	−55	−48	0	5.34
Recognition	L. anterior insula	−37	−19	18	6.37
	R. anterior insula	35	−19	20	5.03
	L. precentral gyrus	−34	−17	62	4.73

MNI coordinates, maximum z-score of the local maxima for the four effects: main effect familiarity (known_demo>unknown_demo), main effect action (known_action>known_demo), interaction effect understanding (unknown_action–unknown_demo>known_action–known_demo), and interaction effect recognition (known_action–known_demo>unknown_action–unknown_demo).

Discussion

In the present study, we could, for the first time, identify a left-hemispheric activation pattern engaged in coding the moment of understanding of the use of a tool. This understanding effect is an important step in learning the concept of novel tools and precedes any experience and practice. The activation sites (left prefrontal and left mediotemporal) we identified for the task of understanding the concept of a tool largely differ from previously described networks of tool use and tool use learning.

Understanding tool use

The understanding effect presents a network of areas that are activated in trials where subjects reported that they understood the purpose of a previously unknown tool after it was presented in action. The self-reported understanding of a tool's concept, which was used to define the conditions for the evaluation, could be validated by the unheralded questionnaire after scanning. Although subjects were not told they would be asked to explain the tools after scanning, they were able to describe it correctly it in eight out of ten cases. This finding implies that understanding the concept of a tool needs requires only one presentation of the tool in its action context to acquire a general knowledge about the physical principles applied and the object included. This might be linked to the simplicity of the task as all tools were easily recognizable as tools and also all objects included were prototype objects. However, it is also possible that the advanced imitation capabilities of the healthy human subject facilitate this quick understanding.

The pattern identified for the understanding effect is left-lateralized, involving mainly prefrontal areas as well as inferotemporal and parietal areas.

Instead of reflecting the activation sites of consolidated conceptual and semantic knowledge, the understanding of tool use utilizes several sites of the motor–skill network as described in Lewis meta-analysis (Lewis, 2006), especially a widespread activation in the left-hemispheric frontal lobe, with foci in the middle frontal gyrus (MFG, lateral BA 8), the pars triangularis of the inferior frontal gyrus (IFG, BA 45), but also in the posterior middle temporal gyrus. This activation is shared with two other contrasts, i.e., the action contrast and the familiarity contrast. However, the activation maxima lie slightly apart; the maximum in the understanding contrast is located in between the activation cluster in the action effect and the activation in the familiarity effect. This could indicate that the understanding process needs to integrate information concerning both the action, as coded in the action effect, and the object, as described by the familiarity effect, thus engaging a region between these two maxima.

The pMTG is reported to play a large role in processing action information and action understanding, as well as in the integration of visual and sensorimotor attributes of tools (Martin et al., 1996; Johnson-Frey et al., 2005; Beauchamp et al., 2004). It has been shown that lesions of the left pMTG can lead to poor linguistic and semantic knowledge for tools, yet spares the ability to manipulate tools (Damasio et al., 1996; Lauro-Grotto et al., 1997). Although subjects did not report any naming strategies when asked after the experiment, this activation in the current context indicates that they might have implicitly used semantic categories as 'as pliers' or 'hammer-like.' This is also reflected by the descriptions in the questionnaire. Alternatively, there could be a functional specificity along the posterior mediotemporal gyrus, with action knowledge about tools more posterior and language-related tool knowledge more anterior, as this could also be assumed from the distributed maxima between contrasts.

More generally, the left medial temporal lobe has been implicated in associative memory encoding (Vandenberghe et al., 1996; Achim et al., 2007). Moreover, this region is also implicated during novelty detection and has its activity correlated with subsequent recognition performance (Stark and Okado, 2003). Also implicated in novelty detection is the lateral prefrontal cortex (PFC, Kishiyama et al., 2009).

Interestingly, this finding could be more specified by a study of Luo et al. (2004), who directly attributed the activation of the left lateral PFC to a provoked *Aha!* reaction when subjects were asked to solve ambiguous sentences. Even more closely related to our study are the findings of Qiu et al. (2010), who identified a left inferior and middle frontal activation to be involved in breaking a mental set and forming novel associations. However, the activation patterns associated with these tasks are not sufficient to completely explain the understanding effect as only one aspect of a general process of rapid understanding or problem solving. Luo et al. (2004) identified the anterior cingulate gyrus, the left insula, the left superior/inferior/middle frontal gyri, the inferior temporal gyrus, and the precuneus as relevant for understanding, whereas Qiu et al. (2010) described an involvement of the precuneus, the left inferior/middle frontal gyrus, the inferior occipital gyrus, and the cerebellum. Common to all three patterns are therefore only the left prefrontal regions, thus possibly mediating the other areas like the pMTG in integrating visual and sensorimotor information.

The strong involvement of the prefrontal cortex in tool use understanding shows the importance of left prefrontal cortex in tool use and tool use (re-)learning. Nevertheless, this aspect has mostly been neglected in apraxia research, as there is a long-standing tradition in clinical neuropsychology, which maintains that left parietal lesions are a main cause for limb apraxia (Goldenberg, 2009). Still, Goldenberg et al. (2007) explored patients with frontal brain damage (and dysexecutive syndrome) in various tests of tool use; however, they could only identify a difference in multistep actions between patients and healthy control subjects. They did not differ in a novel tool task, functional associations, or pantomime of object use. Interestingly, only one patient of their sample presents a left-hemispheric lesion of the lateral prefrontal cortex in vicinity to the maxima identified in the understanding effect, thereby possibly explaining, why this group performed rather well in the novel tool task. This finding is supported by the more recent study of Goldenberg and Spatt (2009), who describe a general loss in performance in apractic patients when their lesions expand to prefrontal areas, as well as a correlation between lesion size in the left middle frontal and precentral gyri with the use of novel tools (in the same task as 2007).

Altogether, the frontotemporal activation found in our study could indicate that understanding a new tool use involves the creation of new knowledge about this tool based on associative memory encoding under strong involvement of prefrontal regions.

The strict laterality of the understanding network is another interesting finding of this study. First, it seems to be clearly connected to previous findings, which suggest a laterality for 'acting with' or using tools as opposed to 'acting on' or manipulating objects (Johnson and Grafton, 2003). Johnson and Grafton argue that this 'acting with' system represents schemata for skilled tool use that have been acquired over a longer period of time. The here identified pattern suggests, that already the understanding of a concept of a tool is processed with left-hemispheric dominance, even before any skill or proficiency of use is achieved. And second, the laterality reflects the laterality in apraxias, which is predominantly a symptom of left brain damage, although some symptoms of apraxia can also occur after right brain damage (Goldenberg, 2009). Together with the activation pattern, this might suggest that there are at least two different reasons for a failure in tool use after left brain damage: the loss of the 'acting with' schemata for skilled tool use, or the inability to (re-)understand the concept.

Demarcation from other tool use networks

Equally important are areas from the reported motor–skill network that are *not* active during the understanding of tool use. This includes the inferior parietal lobule (IPL). The IPL plays a crucial role in apraxia, as an injury in the left IPL may cause severely impaired tool use (Heilman et al., 1982; Buxbaum and Saffran, 2002; Buxbaum et al., 2003). The patients, however, tend to retain an understanding of the function of a tool (Buxbaum and Saffran, 2002). This backs our finding that the IPL is not crucial for understanding tool use.

The presentation of known tools as compared to unknown tools (familiarity effect) causes activation in the left inferior temporal cortex, in the lateral superior frontal gyrus, and medial in the frontal pole and frontal medial cortex. Thus, it partly replicates the findings of Vingerhoets (2008), who also reports a left-hemispheric activation pattern, including the inferior parietal lobe, for the comparison of known tools to unknown tools. However, the study of Vingerhoets does not report any activation in frontal regions. These findings could therefore be discussed as being due to the task. As subjects were asked to give an explicit response to their knowledge of the tool, we suggest that the frontal activation is connected to working memory processes during the retrieval of stored knowledge. Interestingly, we were also able to identify a large activation in the posterior part of the middle temporal gyrus, anterior to the site identified in the action effect. The presence of a posterior midtemporal activation in the familiarity contrast coupled with the absence of such an activation in the understanding contrast supports the idea that this area plays a role in categorization of objects according to their physical and semantic properties (Chao et al., 1999), instead of conceptual properties regarding their use.

The estimated action effect shows activation that is related to the observation of a previously known tool in its action context as compared to the pure observation of the tool rotating. The identified pattern of activations describes typical activation sites for observation of motion or observation of tool use. These include areas in the posterior parietal cortex, which has been suggested to be selectively activated by the retrieval of knowledge about a tool action, rather than by passive viewing (Kellenbach et al., 2003; Vingerhoets, 2008) but also the pars opercularis of the inferior frontal gyrus (Iacoboni et al., 1999), and the posterior middle temporal gyrus, both of them also present in the tool use network described by Lewis (2006). Moreover, the pattern also includes areas that are normally used for object and tool handling, as it includes vast portions of the inferior and superior parietal lobe, as well as the hand areas of the somatosensory cortex and the thalamus. The pronounced activation in motor regions as compared to the findings from Lewis' meta-analysis could be explained by the fact that the pure demonstration and recognition of the tool has been subtracted from the observation of action, thus emphasizing the role of action observation areas (Buccino et al., 2001). Another possible explanation is that subjects were asked to press the "not understood" button after seeing a tool in action when they misunderstood, e.g., if the action was not the one they expected, or if they realized they had misidentified the tool in the demo condition. To solve the issue of a correct tool handling, they might have imagined using the tool properly, thus also causing motor activation.

That neither the perception of an action, nor (un)familiarity can explain the perception of tool use is also demonstrated by the unique activation pattern of the recognition effect. The recognition effect is derived from the interaction between the presentation and the previous knowledge of a tool, i.e., it displays areas that are active when subjects recognize the typical action of a normal tool. The activations pattern is formed by an activation of the sensorimotor hand area in the dominant (left) hemisphere and a bilateral activation of the anterior insula. Both of these areas have been reported in connection with different kinds of embodiment. An example of PCG involvement in the perception of action as opposed to the pure perception of an object has been given by Liljeström et al. (2008). The anterior insula has been reported in connection to the sense of agency. Interestingly, this activation is rather related to seeing oneself as the cause of an action rather than being aware that an action is caused by somebody else (Farrer and Frith, 2002). The theory of embodied semantics for actions proposes that the sensorimotor areas used for producing an action are also used for the conceptual representation of an action (Aziz-Zadeh and Damasio, 2008). In this context, this would suggest that the perception of an action performed any time in the task also has a resonant effect on areas that are normally activated while consciously experiencing oneself as a cause of an action, thereby helping to understand the action. The identified activation in the sensorimotor areas in the recognition contrast demonstrates the tight connection between perceiving an action and executing it; the missing activation of these areas in the understanding contrast on the other hand emphasizes the role of personal motor experience, which seems to be needed for such an activation to appear on a simple perception, because in case of understanding, the subjects never actually touched or used the tools (as opposed to the recognition case). Hence, the interaction contrasts would propose two things. First, the acquisition of knowledge about tool use is distinguishable from stored knowledge about tool use. And second, while the encoding of new information strongly relies on working memory areas such as the prefrontal cortex, the actual storage of information is more closely related to executional sensory and motor areas.

In summary, we could, for the first time, identify an activation pattern engaged in coding the moment of understanding the use of a tool. Very similar to other described tool use networks, this network is strictly left-hemispheric. The sites activated during this moment of understanding form a unique pattern that differs largely from other networks devoted to processing tools and emphasizes the role of the left prefrontal cortex in tool use learning.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.03.050.

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