

Functional Interactions during the Retrieval of Conceptual Action Knowledge: An fMRI Study

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Abstract

■ Impaired retrieval of conceptual knowledge for actions has been associated with lesions of left premotor, left parietal, and left middle temporal areas [Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., & Damasio, A. R. Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology*, 409–432, 2003]. Here we aimed at characterizing the differential contribution of these areas to the retrieval of conceptual knowledge about actions. During functional magnetic resonance imaging (fMRI), different categories of pictograms (whole-body actions, manipulable and nonmanipulable objects) were presented to healthy subjects. fMRI data were analyzed using SPM2. A conjunction analysis of the neural activations elicited by all pictograms revealed ($p < .05$, corrected) a bilateral inferior occipito-temporal neural network with strong activations in the right and left fusiform gyri. Action picto-

grams contrasted to object pictograms showed differential activation of area MT+, the inferior and superior parietal cortex, and the premotor cortex bilaterally. An analysis of psychophysiological interactions identified contribution-dependent changes in the neural responses when pictograms triggered the retrieval of conceptual action knowledge: Processing of action pictograms specifically enhanced the neural interaction between the right and left fusiform gyri, the right and left middle temporal cortices (MT+), and the left superior and inferior parietal cortex. These results complement and extend previous neuropsychological and neuroimaging studies by showing that knowledge about action concepts results from an increased coupling between areas concerned with semantic processing (fusiform gyrus), movement perception (MT+), and temporospatial movement control (left parietal cortex). ■

INTRODUCTION

In 1870, Finkelnburg defined asymbolia as “a partial or complete loss of the ability to comprehend and express concepts by means of acquired signs.” He presented five cases of aphasic patients who also showed nonverbal symbolic impairments (e.g., for signs, notes, money, rituals, or conventions). One patient (case II) exhibited, in addition to her aphasia, impaired pantomime performance on verbal command (e.g., making the sign of a cross) but preserved imitation abilities (Duffy & Liles, 1979), whereas another global aphasic patient (case V) showed a pantomime agnosia (Rothi, Mack, & Heilman, 1986). Finkelnburg concluded that asymbolia was the underlying cause of these symptoms. Liepmann (1908), in contrast, considered apraxia to be a disorder of skilled movements and argued that apraxia might be more apparent with symbolic gestures because they have to be performed solely from memory without any help from sensory information present during the manipulation of objects (see also Goldenberg, Hentze, & Hermsdörfer, 2004).

Thus far, lesion studies failed to provide a clear answer to this debate (Varney, 1982). Early studies (Goodglass & Kaplan, 1963) showed that the gestural ability was not related to the severity of aphasia when auditory comprehension was controlled for. In contrast, Kertesz and Hooper (1982) found that apraxia correlated with severity of aphasia and, in particular, with comprehension deficits. However, the same group reported dissociations between aphasia and apraxia (Kertesz, Ferro, & Shewan, 1984): Six severely aphasic patients did not suffer from apraxia. In contrast, all patients with severe apraxia ($n = 40$) also showed severe aphasia (Kertesz et al., 1984). Recently, using multidimensional scaling in 40 patients with left brain damage, Goldenberg, Hartmann, and Schlott (2003) failed to reveal a close clustering of deficits in pantomime, imitation, drawing, and language tests (Goldenberg et al., 2003). Similarly, Saygin, Wilson, Dronkers, and Bates (2004) showed that in left-hemisphere-injured patients, “action comprehension deficits in the linguistic and non-linguistic domains were not tightly correlated.”

Nevertheless, studies concerned with the retrieval of action knowledge independent of actual motor performance can help to disentangle the relationship between impaired conceptual knowledge for actions and other forms of symbolic impairments. For example, damage to

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inferior occipito-temporal areas can lead to a dissociation between impaired recognition of line drawings of objects and preserved recognition of action drawings and pantomimes (Ferreira, Ceccaldi, Giusiano, & Poncet, 1998; Schwartz, Barrett, Crucian, & Heilman, 1998). These findings suggest that at least partially separable neural networks underlying the processing of action and object stimuli may exist, a notion which, on a more general level, is consistent with the dual-route hypothesis (Goodale & Milner, 1992) or the idea that conceptual knowledge is mediated by neural networks that depend on sensorimotor attributes of the presented information (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005).

One group lesion study further explored knowledge of action concepts by evaluating attributes of pictured actions. In that study, the authors distinguished between the retrieval of conceptual knowledge (recognition) and lexical retrieval (naming) and proposed “that action concepts embody knowledge about the behaviours of entities, especially animate entities such as people and animals, but also inanimate entities such as tools and vehicles” (Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). These action concepts not only contribute to the planning of movements but also to the recognition of movements made by others (Buccino et al., 2001). The highest lesion overlap in patients with impaired retrieval of conceptual knowledge for actions was found in the left premotor cortex, the left parietal cortex, and in the white matter underneath the left MT+. In contrast, impaired lexical retrieval of action knowledge was associated with left frontal opercular lesions (Tranel, Adolphs, Damasio, & Damasio, 2001).

In this study, we aim to disentangle the specific contribution of the areas subserving the retrieval of conceptual knowledge about actions as implicated by the abovementioned lesion study (Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). We refer to action concepts as knowledge about complex actions that contributes to the recognition of actions. To identify the neural correlates of action knowledge, we compared neural activity elicited by retrieving the meaning of action pictograms to the neural activity elicited by retrieving the meaning of pictograms not associated with actions. Pictograms are visual symbols that are void of any spoken or written information. Their meaning is either related to the employed image or to a related concept (Kitagami, Inoue, & Nishizaki, 2002). The action pictograms employed in this study showed biological movements which represented different kinds of sports. To access the meaning of an action pictogram, knowledge about the illustrated movement had to be retrieved. Additionally, pictograms of different kinds of objects were employed. We separated pictograms of small, manipulable objects from large, nonmanipulable objects, as nonmanipulable objects were not expected to lead to any implicit action-related processing. With

respect to manipulable objects, it is still a matter of debate whether action knowledge is a prerequisite for the recognition of manipulable objects (Gerlach, Law, Gade, & Paulson, 2002; Chao & Martin, 2000). Thus, we presented different categories of black and white pictograms to healthy volunteers during functional magnetic resonance imaging (fMRI): whole-body actions, manipulable and nonmanipulable objects (see Figure 1). During scanning, subjects were asked to indicate via button press whether they knew the meaning of the pictogram. For the processing of pictograms, irrespective of content, we expected activation of a network of bilateral occipito-temporal and left frontal brain areas, comparable to activations observed in studies of semantic retrieval with verbal stimuli (Noppeney, Phillips, & Price, 2004). Due to its importance in object recognition, especially higher-level shape processing (Kourtzi & Kanwisher, 2001), the lateral occipital complex of the ventral stream was expected to be activated by pictograms of manipulable and nonmanipulable objects (Grill-Spector, Kourtzi, & Kanwisher, 2001). Furthermore, additional activations of dorsal stream areas (premotor and parietal cortex) could occur during processing of manipulable object pictograms (Beauchamp, Lee, Haxby, & Martin, 2002; Chao & Martin, 2000). Processing of action pictograms was expected to activate area MT+, as Kable et al. (2005) and Kable, Lease-Spellmeyer, and Chatterjee (2002) found differential activation of human MT+ triggered by action pictures versus object pictures in a picture–word matching task. Furthermore, we expected action pictograms to lead to left parietal cortex activation, an area recently shown to be involved in retrieving knowledge about manipulative actions (Boronat et al., 2005).

Finally, we were interested in assessing possible changes of connectivity within the neural network subserving the processing of action and object pictograms.

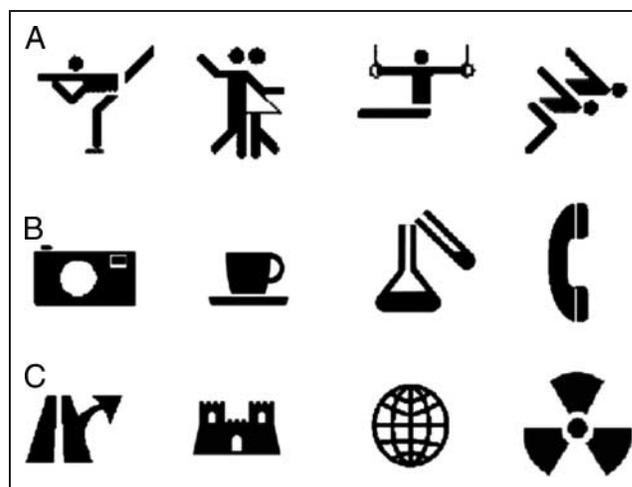


Figure 1. Examples of pictogram stimuli: (A) action pictograms, (B) manipulable objects, and (C) nonmanipulable objects.

We accordingly employed a design which allowed us, by the analysis of psycho-physical interactions, to investigate changes in the coupling between areas involved in the processing of pictograms in general, and, more importantly, with regard to the purpose of this study, the areas specifically engaged in the retrieval of conceptual knowledge about actions.

METHODS

Subjects

Twelve healthy, right-handed volunteers (5 women, 7 men; mean age ($\pm SD$) 25 ± 5 years) participated in this fMRI experiment. Handedness was assessed using the German version of the Edinburgh Handedness Inventory (mean laterality quotient = +84, $SD = 16$) (Oldfield, 1971). No subject had any history of neurological or psychiatric illness. Informed written consent was obtained from all subjects who were naïve to the purpose of the experiment. The study was approved by the local ethics committee and was conducted in accordance with the Declaration of Helsinki.

Experimental Design

In this blocked fMRI experiment, we used three different categories of pictograms as stimuli (C1–C3) and simple geometric objects for control (C4). Because comparisons with a “resting state” can lead to artificial task-dependent deactivations (McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003), we introduced the control condition (C4) with comparable visual input, response selection, and identical motor responses to Conditions 1–3, but without processing of complex pictograms (i.e., only squares or circles were shown). Stimuli were presented using Presentation 0.76 (Neurobehavioral Systems, California) software and projected on a screen from a distance of 29 cm to the subject through a mirror fixed to the head coil. Subjects were allowed to move their eyes to avoid an interaction of the neural mechanisms underlying covert attention with the neural processes of interest (Fink, Dolan, Halligan, Marshall, & Frith, 1997).

The stimuli used were pictograms symbolizing (a) whole-body actions (C1), (b) manipulable objects (C2), (c) nonmanipulable objects (C3), or (d) squares/circles (C4, for control) (see Figure 1). Pictograms are graphical symbols frequently used at public facilities, such as public transportation, sports venues, or commercial facilities, and represent either a concept or an object by illustration (see, e.g., www.ecomo.or.jp/symbols_english/symbol_index2.html). A standard set of pictograms is defined in the international standard *ISO 7001: Public Information Symbols*. They can be an effective means of providing important information without language. All pictograms used in this study were black on a white

background. For the action condition (C1), sport-related pictograms were used (Figure 1A). For the manipulable objects condition (C2), pictograms of man-made artifacts were shown, some of which were tools (Figure 1B). For the nonmanipulable objects condition (C3), large entities such as buildings, vehicles, but also pictograms depicting animals (e.g., indicating a farm) or static humans (e.g., indicating a restroom), were used (Figure 1C). For control (C4), squares and circles were presented to the subjects (8 squares, 2 circles per block in random order).

The central projection of the stimuli on the white screen subtended a vertical and horizontal visual angle up to 5.4° . Stimuli were shown for 2400 msec. The interstimulus interval was jittered and was either 300, 600, or 900 msec, during which a blank screen was shown. The stimuli were grouped according to the condition of interest in blocks of 30 sec, each consisting of 10 stimuli. The blocks were separated by a 20-sec baseline (blank screen), which was followed by an instruction of 5 sec announcing the upcoming condition. In C1 to C3, subjects indicated by button presses whether they knew the meaning of the symbol. In C4, subjects indicated by button presses whether a square was presented. Subjects responded by pressing two keys with either the index or middle finger of their right/left hand indicating “yes” with their index and “no” with their middle finger. In half of the trials, subjects used their right hand, in the other half, subjects used their left hand.

fMRI images were acquired during two sessions of 15 min each. This experiment consisted of 32 blocks, yielding a total of eight blocks (80 trials) per condition. Conditions were presented in counterbalanced order within and between subjects, and trials within a block appeared in a randomized order. Prior to the experimental session, subjects were informed that they had to fill in a questionnaire afterward, in which they should name the presented symbols. These questionnaires consisted of all 240 presented pictogram stimuli. Subjects were asked to describe each symbol’s meaning in one word.

Behavioral Data Analysis

Reaction times were acquired during scanning. The questionnaires filled in by the subjects after scanning were tested for omissions and errors. Repeated-measures analysis of variance (ANOVA) in SPSS was used for the analysis of the behavioral data.

Structural and Functional Magnetic Resonance Imaging

fMRI images were acquired on a Siemens Sonata 1.5-T whole-body scanner with echo-planar imaging (EPI) capability using the standard radio-frequency head coil. Multislice T2*-weighted echo-planar images were obtained from a gradient-echo sequence with the fol-

lowing parameters: echo time (TE) = 66 msec, repetition time (TR) = 2.5 sec, flip angle = 90°, field of view (FOV) = 200 mm, slice thickness = 4 mm, interslice gap = 0.4 mm, in-plane resolution = $3.125 \times 3.125 \text{ mm}^2$. The 24 slices were aligned to the AC–PC line. To obtain anatomical images at high resolution, a T1-weighted MP RAGE (magnetization-prepared, rapid acquisition gradient echo) sequence was used (TE = 3.93 msec, TR = 2.2 msec, inversion time TI = 1200, flip angle 15°, FOV = 240 mm, slice thickness = 1.5 mm, matrix = 180×256 , number of sagittal slices = 128).

Image Processing

After applying standard procedures for image realignment, slice timing, normalization (voxel size $3 \times 3 \times 3 \text{ mm}$), and smoothing, data were analyzed with Statistical Parametric Mapping software SPM2 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk) using a random effects analysis. After spatial transformation, the functional data were smoothed with a Gaussian kernel of 8 mm to reduce the variance due to anatomical variability. The time series were high-pass filtered (with a cutoff frequency of 1/128 Hz) to remove low-frequency artifacts. We included six head movement parameters as regressors to control for movement-related variance. The different conditions were modeled as box-car functions convolved with the canonical synthetic hemodynamic response function in SPM2. Specific effects were tested by applying appropriate linear contrasts to the parameter estimates for each condition, resulting in a *t* statistic for each voxel. An activation cluster was considered significant when it passed a threshold of $p < .05$, corrected at the cluster level (with $p < .001$ uncorrected at the voxel level).

For the conjunction analysis, a one-way ANOVA in SPM2 and the revised test proposed by Nichols, Brett, Andersson, Wager, and Poline (2004) with a voxel level threshold of $p < .05$, familywise error (FWE) corrected (no cluster threshold possible in a conjunction analysis), were applied. Only clusters extending to a size of at least 20 voxels are reported. The conjunction analysis of all three pictogram conditions > control was calculated to reveal common activations across the different categories of pictograms. The contrasts manipulable objects > nonmanipulable objects and nonmanipulable objects > manipulable objects were used to test for differences between the processing of the two object categories. The contrast action pictograms > objects (manipulable and nonmanipulable combined) was calculated to look for action-specific activations.

Finally, psycho-physiological interactions (PPIs) (Friston et al., 1997) were calculated for the two largest clusters (right and left fusiform gyrus) elicited by pictogram processing (irrespective of pictogram type as revealed by the conjunction analysis). The coordinates of the voxels of maximal activation intensity in the contrast pic-

tograms > control for the group (i.e., in the right and left fusiform gyrus) were used in the contrast pictograms > control at the single-subject level. A sphere of 4 mm radius was centered at the nearest local maximum. The mean-corrected blood oxygen level-dependent signal time course from this sphere was then used as the physiological factor. The psychological factor was a vector coding for the main effect of symbol category (2 for action symbols, –1 for manipulable objects, –1 for nonmanipulable objects) convolved with the hemodynamic response function. The PPI was then computed as the element-by-element product of the physiological and the psychological vectors. For each subject, we created a new statistical model containing the PPI as regressor and the psychological and the physiological vectors as covariates of no interest. Subjects' specific contrast images were then entered into random effects group analyses. The statistical threshold was again set at $p < .05$, corrected at the cluster level (with $p < .001$ uncorrected at the voxel level).

RESULTS

Behavioral Data

The action pictograms evoked significantly longer reaction times than the (manipulable and nonmanipulable) object pictograms and the control condition [mean RT in msec \pm SD: actions 1176 msec \pm 281 msec, objects 1082 msec \pm 270 msec, control 610 \pm 106 msec; $F(2, 10) = 28.55, p < .05$].

The analysis of the questionnaires showed a significant effect of condition [mean error rate in % \pm SD: actions: 5 \pm 3%, objects: 2 \pm 2%, $F(2, 10) = 9.72, p < .05$] as significantly more action pictograms were misinterpreted compared to the (manipulable and nonmanipulable) object conditions. The rate of omissions was not significantly different between conditions (mean rate of omissions in % \pm SD: actions 2 \pm 2%, objects 2 \pm 3%).

Neural Activations

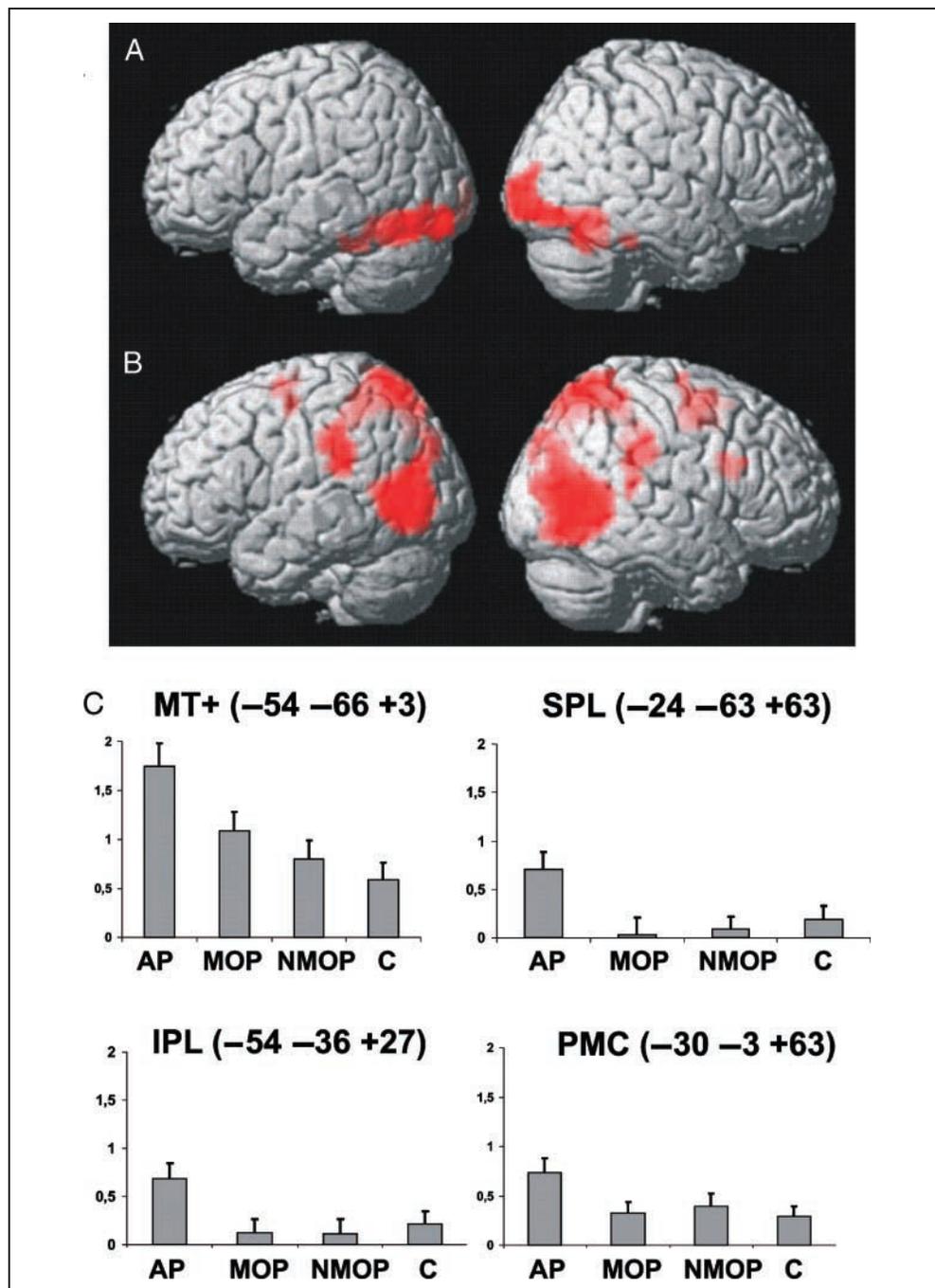
Retrieval of Pictogram Meaning

The retrieval of pictogram meaning (i.e., pictograms representing both actions and objects, manipulable as well as nonmanipulable) contrasted to the control condition (squares, circles) revealed (as depicted by the conjunction analysis) bilateral activation of the inferior occipito-temporal cortex including the fusiform gyrus (see Figure 2A).

The contrasts manipulable objects > nonmanipulable objects and nonmanipulable objects > manipulable objects led to no significant differential activations. Thus, the two object conditions were collapsed in all subsequent analyses.

The contrast action pictograms > object pictograms revealed differential activations in the superior temporal sulcus, extending into the human motion-sensitive area

Figure 2. Neural activations related to the processing of pictograms in general (A) and of action pictograms specifically (B) as well as the mean signal changes for the four experimental conditions in the main areas of the left hemisphere (C). (A) Retrieving the meaning of object and action pictograms (each pictogram type contrasted to the control condition in a conjunction analysis) activated the inferior occipito-temporal cortex, including the fusiform gyrus bilaterally. (B) The neural activations associated with processing of action pictograms (contrasted to object pictograms) included the human MT+ bilaterally, the superior and inferior parietal cortices bilaterally, and the premotor cortex bilaterally. (C) Mean signal change in the left MT+ ($-54, -66, +3$), left superior parietal lobe (SPL; $-24, -63, +63$), left inferior parietal lobe (IPL; $-54, -36, +27$), and left premotor cortex (PMC; $-30, -3, +63$) for the action pictograms (AP), pictograms of manipulable (MOP) and nonmanipulable objects (NMOP), and the control condition (C, geometric shapes), respectively.



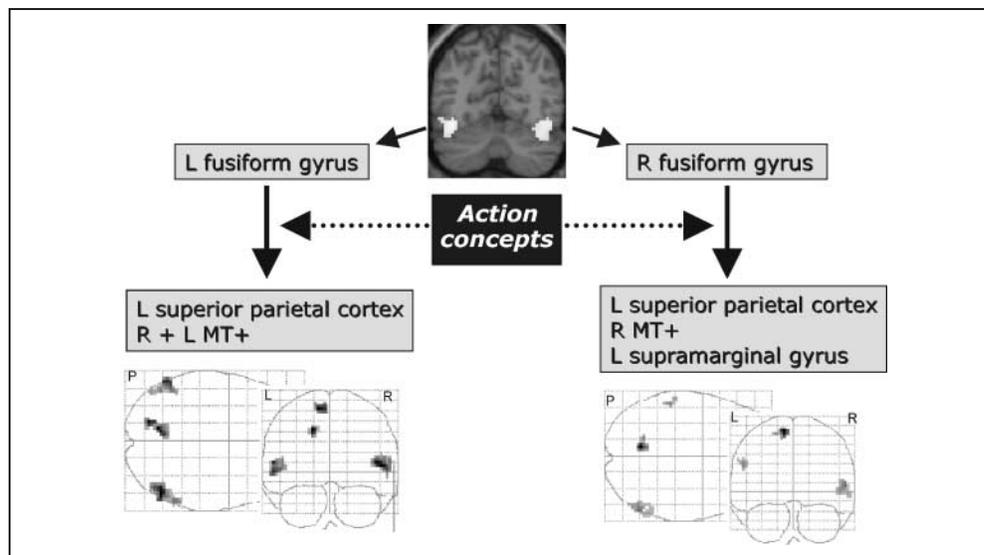
MT+ (Malikovic et al., 2007; Zeki et al., 1991), in the superior and inferior parietal cortex, and the premotor cortex bilaterally (see Figure 2B). With the exception of area MT+, these areas did not show differential activations between the object and control conditions (see Figure 2C). The reverse contrast (object pictograms > action pictograms) showed no significant differential activations.

Psycho-physiological Interactions

The activation peaks of the two largest clusters in the right ($+45, -60, -15$) and left ($-39, -72, -15$) fusiform

gyrus (as revealed by the conjunction analysis of pictogram processing irrespective of category) were chosen for the analysis of PPIs. We tested for possible functional interactions of the left and right fusiform gyri with other brain regions that may critically depend on the category of the processed pictogram. For the right fusiform gyrus ($45, -60, -12$), significant context-dependent contributions during the processing of action pictograms were found in the right middle temporal (MT+; $57, -66, 6$; $Z = 3.91$), the left superior parietal ($-9, -63, 66$; $Z = 4.6$), and the left inferior parietal cortex, including the left supramarginal gyrus, ($-54, -33, 30$; $Z = 3.67$; all

Figure 3. Psycho-physiological interactions. During processing of action pictograms, the right fusiform gyrus showed significant interactions with the left superior and inferior parietal cortex (supramarginal gyrus) and right MT+, whereas the left fusiform gyrus significantly interacted with the left superior parietal cortex and MT+ bilaterally.



$p < .05$, corrected) (see Figure 3). No significant PPIs were found during the processing of pictograms representing objects (for manipulable and nonmanipulable objects combined, as no significant differential activations for the two object categories had been observed, see above).

For the left fusiform gyrus ($-42, -69, -15$), significant context-dependent contributions during the processing of action pictograms were found in the right and left middle temporal (MT+; $51, -66, 6$; $Z = 4.4$; $-57, -63, 9$; $Z = 4.22$) and the left superior parietal cortex ($-12, -69, 63$; $Z = 4.43$; all $p < .05$, corrected) (see Figure 3). No significant changes in the contribution of the left fusiform gyrus were observed during the object conditions.

DISCUSSION

The aim of this study was to explore further the contribution of the areas involved in the neural network that underlies the retrieval of conceptual action knowledge as triggered by action pictograms. Pictograms are symbols which represent a concept by illustration. In order to recognize the meaning of a pictogram, knowledge about the underlying concept is a prerequisite. We explored the brain areas differentially recruited during the processing of action, but not object pictograms. To achieve this, we first detected by a conjunction analysis the neural network that was active during all pictogram conditions, and then looked for differential activations during the processing of action pictograms (relative to the processing of object pictograms). Finally, using psycho-physical interactions, we explored enhanced neural interactions between areas generally involved in semantic processing of pictograms and the network supporting

action concept retrieval (specifically) triggered by action pictograms.

Processing of pictograms irrespective of pictogram type (actions as well as manipulable and nonmanipulable objects) led to activations in the inferior occipito-temporal cortex bilaterally, as determined by a conjunction analysis. The peak activations within the large occipito-temporal clusters were located in the right and left fusiform gyri. These areas have previously been associated with semantic retrieval of word stimuli (Noppeney et al., 2004; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001) and with semantic memory in general (Martin & Chao, 2001).

The retrieval of action concepts triggered by action pictograms compared to the processing of the meaning of object pictograms activated a neural network consisting of MT+, the superior and inferior parietal cortex, and the premotor cortex bilaterally. Thus, areas concerned with movement perception (Assmus et al., 2003; Zeki et al., 1991) and execution (Hermsdorfer et al., 2001) were also active during the processing of static action pictograms (Kourtzi & Kanwisher, 2000). That the retrieval of action and object concepts, which contribute to the recognition of the respective pictograms, may rely on differential neural substrates is supported by neuropsychological single-case studies of dissociations between action and object recognition deficits (Magnie, Ferreira, Giusiano, & Poncet, 1999; Ferreira et al., 1998; Schwartz et al., 1998). Furthermore, investigating the neural responses to overt motion of humans and (manipulable) objects, Beauchamp et al. (2002) found segregated responses to human and object stimuli in the posterior temporal cortex.

A possible confound in the comparison between action and object pictograms is the fact that only the former stimuli included human-like forms engaged in whole-body actions. The perception of humans (Saxe,

Jamal, & Powell, 2006) and inferring intentions from human actions (Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004) activates, at least in part, areas that we also found for the categorical comparison between the processing of action and object pictograms. It should be noted, however, that Saxe and coworkers used pictures of real humans, whereas we used pictograms of sportive whole-body actions. Because our study design did not contain person-without-action pictograms, we cannot differentiate whether activity in, for instance, the posterior temporal cortex, found in the current study, represents conceptual knowledge about human actions, perception of humans per se, or a combination thereof. This is an interesting question for further studies possibly using parametric designs in which the amount of implied (human) action is systematically varied.

For the categorical comparison between the processing of action and object pictograms, the two object pictogram types were collapsed, as the differential contrasts between the manipulable and the nonmanipulable object conditions revealed no significant differences. The lack of differential neural activations for manipulable and nonmanipulable object pictograms was somewhat unexpected considering previous studies, which point to an important role of action knowledge in the processing of manipulable objects (and tools) (Grezes & Decety, 2002; Chao & Martin, 2000; Tranel, Damasio, & Damasio, 1997). A possible explanation for this negative result could be related to the task used in our study: Subjects were required to retrieve the meaning of the object pictograms, but not to categorize them. In fact, Gerlach et al. (2002) found activation of the left premotor cortex only during categorization of tools, but not during the mere naming of tools. Further evidence that processing of object stimuli is influenced by the respective task requirements is provided by a study of Valyear, Culham, Sharif, Westwood, and Goodale (2006), in which the perception of an identical object differentially activated dorsal or ventral stream areas depending on whether subjects processed the object's orientation (implicitly activating the appropriate grasp for the object) or its identity. Therefore, the lack of dorsal stream activations when processing pictograms of manipulable objects (compared to nonmanipulable object pictograms) could be due to the fact that our subjects were instructed not to consider the actions related to the respective objects, but only to retrieve the meaning of the object pictograms. The differential neural systems for nouns and verbs (Damasio & Tranel, 1993) may provide another explanation for the lack of difference between the manipulable and nonmanipulable object conditions. Because all objects are denoted by nouns, the retrieval of the pictogram meaning may have (implicitly) activated the neural representations of verbs (for action pictograms) and nouns (for both the manipulable and the nonmanipulable object conditions). This interpretation would be consistent with the notion "that noun-verb

dissociations reflect salient differences in the neural representation of objects and actions" and "that the brain distinguishes between nouns and verbs on the basis of semantics (meaning)" (Shapiro et al., 2005, p. 1058).

The right and left fusiform gyri, the areas maximally activated in the conjunction analysis of processing of all pictogram types, were chosen as the seeds for the analysis of PPIs. This analysis tested whether any region throughout the whole brain showed context-dependent changes in coupling with the right and left fusiform gyri. Interestingly, only during the retrieval of conceptual action knowledge triggered by action pictograms were significant PPIs detected. These PPIs consisted of an increased coupling between the fusiform gyri and the middle temporal cortex (MT+) bilaterally as well as the left superior and left inferior parietal cortex. Thus, the areas revealed by the PPI analysis were parts of the larger network determined by the categorical comparison of action versus object pictogram processing, which additionally included the right superior and inferior parietal cortex and the bilateral premotor cortex. Taken together, our data suggest that within a larger network concerned with the processing of action stimuli, the retrieval of conceptual action knowledge is realized by an increased coupling between areas concerned with semantic processing (fusiform gyrus), perception of movement (MT+), and temporo-spatial movement control (left parietal cortex).

Our findings are in good accordance with neuropsychological studies: Patients with impaired knowledge for actions showed a lesion overlap in the white matter underneath the left MT+, in the left parietal cortex, and in the left premotor/prefrontal cortex (Tranel et al., 2003). The authors proposed that, "when we evoke the concept of an action, we activate collections of sensory and motor patterns in cerebral cortices appropriate to represent pertinent features of the concept." The human MT+ is known to be engaged not only in overt motion processing (Zeki et al., 1991) but also in processing implied motion from static images (Kourtzi & Kanwisher, 2000; Peigneux et al., 2000). Therefore, the bilateral activation of MT+ in the current study is likely to represent the implied motion related to the retrieved action concepts. Activation of MT+ during access of action knowledge has already been shown in previous neuroimaging studies (Kable et al., 2002). Kable et al. (2002) compared conceptual matching of actions to conceptual matching of objects, and found activations in occipito-temporal regions near MT+. Kable et al. concluded that regions around MT+ process both conceptual and perceptual features of motion.

The importance of the left parietal cortex in the control of complex action is undisputed (Liepmann, 1905). Although the left inferior parietal cortex is involved in temporo-spatial movement control (Assmus, Marshall, Noth, Zilles, & Fink, 2005; Assmus et al., 2003; Weiss et al., 2001; Poizner et al., 1998; Liepmann, 1905), the

left superior parietal cortex contributes to the internal representations used for the control of actions (Wolpert, Goodbody, & Husain, 1998). Thus, activation of the left parietal cortex during the retrieval of action concepts is likely to represent aspects of higher motor control. Furthermore, this finding corresponds well to neuropsychological studies, which demonstrate the importance of the left parietal cortex for gesture recognition (Varney & Damasio, 1987; Ferro, Martins, Mariano, & Caldas, 1983). Based on the results of their Gesture Recognition Test in 65 patients with left hemisphere lesions, Ferro et al. (1983) suggested that gestures are represented at the conceptual-symbolic level in the (left) parietal cortex. With respect to our results of the analysis of PPIs, it is noteworthy that Varney and Damasio (1987) suggested that the supramarginal, rather than the angular, gyrus is involved in pantomime recognition.

Taken together, the analysis of the PPIs revealed that both semantic areas (fusiform gyrus) and areas concerned with the perception (MT+) and control of actions (left parietal cortex) are involved in accessing conceptual action knowledge. Our results are in line with conclusions drawn by Buxbaum, Schwartz, and Carew (1997) concerning the role of the semantic system for object use. The authors hypothesized that the execution of complex goal-directed movements is facilitated by a linkage between semantic and sensorimotor information about objects. On the other hand, preserved sensorimotor experiences triggered by object use may support recognition of (manipulable) objects even in severe semantic agnosia (Magnie et al., 1999). By showing that accessing conceptual information about motion attributes activates the middle temporal cortex (MT+), Kable et al. (2005) also supported the view that “conceptual knowledge is instantiated by distributed neural regions partially organized along sensorimotor lines.”

In summary, we found that knowledge about action concepts is retrieved by the interaction between areas engaged during semantic processing and a network of sensorimotor areas. With respect to the clinical observations made by Finkelnburg (1870) concerning asymbolia, our data suggest that patients suffering from a disconnection syndrome between semantic and sensorimotor brain regions are likely to show deficits in the understanding and expression of symbolic actions.

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