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Perceiving and naming actions and objects

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Neuropsychological studies have suggested differences in the cortical representations of verbs and nouns. Assessment of word-class specific deficits often relies on picture naming with different sets of images used for action and object naming. Such a setup may be problematic in neuroimaging studies, as the perception of the image and the actual differences in retrieving verbs or nouns become intertwined. To address this issue, we investigated how different sets of images affect the pattern of activation in action and object naming. In the present fMRI experiment, healthy volunteers silently performed both action and object naming from action images, and object naming from object-only images. A similar network of cortical areas was activated in all three conditions, including bilateral occipitotemporal and parietal regions, and left frontal cortex. With action images, noun retrieval enhanced activation in bilateral parietal and right frontal cortex, areas previously associated with visual search and attention. Increased activation in the left posterior parietal cortex during this condition also suggests that naming an object in the context of action emphasizes motor-based properties of objects. Action images, regardless of whether verbs or nouns were named, evoked stronger activation than object-only images in the posterior middle temporal cortex bilaterally, the left temporo-parietal junction, and the left frontal cortex, a network previously identified in processing of action knowledge. The strong influence of perceptual input on neural activation associated with noun vs. verb naming can in part explain discrepancies in previous lesion and functional neuroimaging studies on the processing of nouns and verbs.
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Introduction

The apparent differences in the neural representation of nouns and verbs have been studied extensively in patients with brain damage (McCarthy and Warrington, 1985; Zingeser and Berndt,

1990; Caramazza and Hillis, 1991; Bird et al., 2000; Arevalo et al., 2007). Some aphasic patients display difficulty in processing verbs, while they are still able to process nouns. In others, the pattern is reversed (Zingeser and Berndt, 1990; Daniele et al., 1994). The existence of patients in whom focal brain damage is combined with selective impairments of grammatical categories has led to the suggestion that there are distinct cortical areas for processing verbs and nouns (Damasio and Tranel, 1993). Lesion data has implied a link between left frontal areas and verb processing, whereas noun processing seems to depend on the integrity of left temporal areas (Damasio and Tranel, 1993; Daniele et al., 1994). In some cases, however, deficits in verb processing are associated with lesions involving the left parietal cortex (Silveri and Di Betta, 1997), whereas frontal damage may also lead to deficits in processing nouns (Shapiro et al., 2000). There are also clear differences in the exact nature of processing deficits as production and comprehension deficits with nouns and verbs do not always co-occur (Caramazza and Hillis, 1991; Silveri and Di Betta, 1997).

Several alternative explanations have been proposed for category-specific dissociations. According to one account, nouns and verbs are distinguished in the brain on the basis of their semantic properties, nouns typically referring to objects and verbs to actions (McCarthy and Warrington, 1985; Damasio and Tranel, 1993). In this view, semantic information is stored in distributed networks in the cortical areas that are active during perception (Warrington and Shallice, 1984; Martin and Chao, 2001). For instance, words could be organized according to sensorimotor dimensions such as manipulability. The observation that tool processing (Damasio et al., 1996; Martin et al., 1996, Valyear et al., 2007) and action word processing (Martin et al., 1995; Kable et al., 2002) engage similar regions supports this notion. Nouns and verbs also differ in terms of semantic variables such as imageability (Bird et al., 2000), which may account for differential disruptions in some patients (Luzzatti et al., 2002).

Alternatively, selective impairments may reflect the differential syntactic structure of verbs and nouns. In this view, category-specific disruptions are caused by selective damage to areas specifically involved in processing the grammatical categories of verbs or nouns

(Caramazza and Hillis, 1991; Shapiro et al., 2000). Dissociations in processing verbs or nouns may indeed stem from impairments in the ability to carry out morphological transformations. For example, some patients with difficulties in verb or noun naming show difficulties in using pseudowords as members of that category as well (Shapiro et al., 2000). Thus, whether grammatical class, semantic properties, or both, serve as the organizational principle of lexical information remains unclear.

Neuroimaging studies addressing noun versus verb processing have yielded rather inconsistent results. Interpretation of the results is difficult, as a large variety of experimental tasks have been employed, in both production (e.g. Shapiro et al., 2005) and comprehension (e.g. Perani et al., 1999; Vigliocco et al., 2006), including overt and covert picture naming (Martin et al., 1995; Saccuman et al., 2006), lexical (Perani et al., 1999) or semantic judgments (Tyler et al., 2001) on words or pictures, and morphological transformations on words (Shapiro et al., 2005). Some studies have not found any differences between noun and verb processing and have instead shown that the same (distributed) cortical network is activated for nouns and verbs in semantic categorization and lexical decision tasks (Tyler et al., 2001) as well as in picture naming (Sörös et al., 2003). Other studies have shown that while there is considerable overlap between cortical activations evoked by noun and verb processing, such overlap is not complete. Stronger activation related to verbs has been found in a network including left premotor areas and left middle temporal lobe in lexical decision (Perani et al., 1999), verb generation (Warburton et al., 1996), and picture naming (Martin et al., 1995), but there is less evidence for a clear double dissociation between objects and actions in functional neuroimaging studies.

Lately, focus has been on determining whether grammatical class or semantics is the main organizational principle of lexical knowledge. A semantic distinction is emphasized by studies indicating, e.g., that while responses to verbs or nouns do not differ, words can be distinguished along sensorimotor dimensions (Vigliocco et al., 2006) or according to manipulability (Saccuman et al., 2006). Other results suggest that differences between the word classes emerge when words are inflected (Tyler et al., 2004; Longe et al., 2007) or produced in the context of short phrases (Shapiro et al., 2005, 2006), thus stressing the importance of grammatical class in the neural organization of words.

Here, we studied how the properties of the visual image (depicting/ not depicting action) and the required task (action/object naming) influence brain activation in picture naming. We focus on confrontation naming as it is the task that is most directly comparable to studies on aphasic patients. In behavioral studies, actions and objects are typically named from completely different sets of pictures. For experiments accessing the underlying neural processes, such a setup is problematic as it is difficult to match the stimuli even for visual complexity. Identical stimuli for naming nouns and verbs, depicting an action and an object/subject, have previously been used in one fMRI (Hernandez et al., 2001) and one MEG experiment (Sörös et al., 2003). In both studies, healthy subjects showed quite similar activation patterns for action and object naming. However, the spatiotemporal sequence found in the MEG study, involving the left dorsal premotor cortex (Sörös et al., 2003), differed from the typically reported left temporal and left ventral premotor cortex activation in MEG studies in which objects have been named from object-only images (Salmelin et al., 1994; Levelt et al., 1998; Vihla et al., 2006). Comparison of the overall distribution of activation between fMRI/ PET experiments on picture naming is less feasible as the focus has usually been on specific contrasts. The variability of these findings, and of those listed above, raises the question of how much of the

observed noun/verb dissociation derives from the level of perception and conceptual analysis versus the level of name retrieval.

In the present fMRI experiment, healthy subjects were asked to silently name actions and objects that were presented as simple line drawings. We used two sets of pictures, one depicting actions performed on/with objects (cf. Hernandez et al., 2001; Sörös et al., 2003) and the other displaying only the objects. Subjects named both actions and objects from the action images, and objects from the object images. Actions were not named from pictures with isolated objects, as this task would require the subject to make inferences about the actions, a process not required in object naming. This design addresses the following questions: (i) Do action and object naming activate different cortical regions when the stimulus is identical? (ii) How does the content of the image (with/without action) modulate the brain correlates of object naming?

Materials and methods

Subjects

Fifteen healthy right-handed subjects (7 females, 8 males; ages 19–32 years; mean age 25 years) participated in the study. All subjects were native Finnish speakers. Informed consent was obtained from all subjects, in agreement with the prior approval of the Helsinki and Uusimaa Ethics Committee.

Stimuli and experimental procedure

The task was to silently name actions or objects from simple line drawings (Fig. 1). Two sets of images were used, each with 100 scenes. *Action* images illustrated a simple event (e.g. to write with a pen) whereas *object-only* images consisted of objects from the same images when the action had been dissolved into arbitrary lines in the background, in order to keep the visual complexity of the image unchanged. The action images were derived, for the most part, from a previous MEG study (Sörös et al., 2003). The corresponding object and action words were mostly of medium to high frequency in the Finnish language. The naming consistency for objects and actions from action images was evaluated by six graduate students. A scene was excluded when fewer than five subjects named the intended noun or verb. Images of the type 'dog barks' in which the agent was the only depicted 'object' (11 in total in the previous set) were replaced with new ones.

The verb and noun corresponding to one image always had different word stems. The Finnish word frequency values were derived from a massive newspaper corpus with 22.7 million word tokens using a computerized search program (Laine and Virtanen, 1999). The cumulative stem frequency value (including all the inflectional variants of a word stem) varied from 0.6 to 581.5 per million words for the nouns (mean±standard deviation (SD); 63.2±108.3), and 1.4 to 1330.5 per million words for the verbs (131.2±249.6) There was no significant difference in the cumulative stem frequency between verbs and nouns (Mann–Whitney U test, $P=0.082$, n.s.). The word length was 3–9 letters/phonemes for the nouns (5.5±1.3) and 4–10 letters/ phonemes for the verbs (6.9±1.4). The number of syllables was 1–4 for both verbs (2.3±0.6) and nouns (2.3±0.5). There was a significant difference in word length in letters/phonemes ($P<0.05$) but not in the number of syllables ($P=0.239$, n.s.).

The experiment consisted of three conditions: (i) action naming from action images (Act), (ii) object naming from action images (ObjAct), and (iii) object naming from object-only images (Obj).
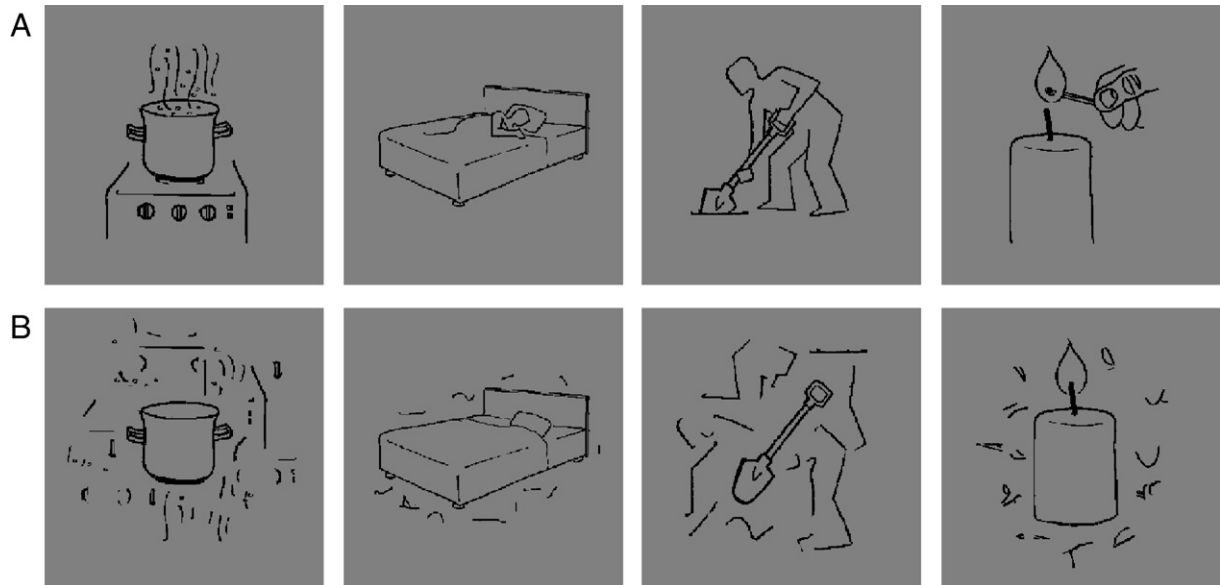
Fig. 1. Examples of stimuli. A) Action images. B) Object-only images. Both actions (Act) and objects (ObjAct) were named from action images, and objects (Obj) from object-only images.

Task periods (30 s) and rest periods (21 s) alternated in a block design. There were two sessions, each lasting about 13 min. The rest period was indicated by the word LEPO ('rest') shown on the screen during the entire rest period. At the end of the rest period, the word changed to ESINE ('object') or TEKEE ('does') to prompt the subject to name either nouns or verbs during the ensuing task period. Within each task period, 10 images were shown (duration 300 ms, interval 1.8–4.2 s). Each condition (Act, ObjAct, and Obj) was repeated in five blocks per session in a randomized order. The same pictures were used for the ObjAct and Act conditions, but the presentation order was balanced so that half of the pictures were novel and half had been seen before in the other condition.

The pictures were projected onto a screen from behind the MRI scanner, and the subject viewed the pictures via a mirror, positioned above the head coil. In order to avoid movement artifacts the participants were instructed to name the actions or objects silently. Subjects were asked to keep their eyes straight ahead during the rest condition and not to move during the experiment. Before the scanning sessions the subjects performed a practice block in front of a computer to ensure that they had understood the instructions. After the scanning session the subjects briefly reported on their performance in the scanner.

Data acquisition and analysis

MR images were acquired using a Signa VH/i 3.0 T MRI scanner (GE Healthcare, Chalfont St Giles, UK) and a quadrature transmitting-and-receiving head coil. A single-shot gradient-echo echo-planar imaging (GRE-EPI) sequence was used for acquiring the functional imaging data (TR=3 s, TE=32 ms, flip angle=90°). The cerebrum was covered with 39 oblique axial slices, measured in an interleaved order. The matrix size was 64×64, with in-plane resolution 3.4 mm× 3.4 mm (7 subjects) or 3 mm×3 mm (8 subjects). The slice thickness was 3 mm with no spacing between the slices. Anatomical images were acquired using a standard T1-weighted 3D SPGR sequence.

The analysis was performed using statistical parametric mapping (SPM2; Wellcome Department of Cognitive Neurology, London,

UK) and Matlab (The MathWorks, Inc, MA, USA). The first four volumes of the functional images were discarded in order to eliminate the T1 saturation effects. All images were realigned to the first volume to correct for head motion, and were corrected for movement by susceptibility artifacts (Andersson et al., 2001). The anatomical images were coregistered with the mean image of the functional series. All images were spatially normalized to the MNI template image (2 mm isotropic voxels) and smoothed with an 8-mm full-width at half-maximum isotropic Gaussian kernel. The data were high-pass filtered with a cut-off frequency of 1/510 Hz to reduce the effect of slow drifts. Serial correlations were compensated for by using a first-order autoregressive model to pre-whiten the data.

Statistical parametric maps (SPMs) were calculated using the general linear model (Friston et al., 1995). Regressors for the three naming conditions and for the rest condition were entered into the design matrix and convolved with a canonical hemodynamic response function. Nine different contrasts were evaluated using t statistics, three contrasts comparing the naming tasks to rest (Act/ObjAct/ Obj>Rest), and six contrasts comparing all task conditions: object and action naming from the same set of pictures were compared (ObjAct>Act and Act>ObjAct), and object naming from object-only pictures was contrasted with object naming from action pictures (Obj>ObjAct and ObjAct>Obj) and with action naming (Obj>Act and Act>Obj). The contrast images were entered into a random-effects group level analysis and were corrected for false discovery rate (FDR, $P<0.001$ in task-rest contrasts; $P<0.01$ in task-task contrasts) (Genovese et al., 2002), with a minimum cluster size of 20 voxels. Results are reported in MNI coordinates as given by SPM2. Anatomical regions were identified using an automated anatomical labeling method by Tzourio-Mazoyer et al. (2002).

Results

Task versus rest

A similar network of cortical areas was activated in all three conditions, including bilateral occipitotemporal and parietal regions,
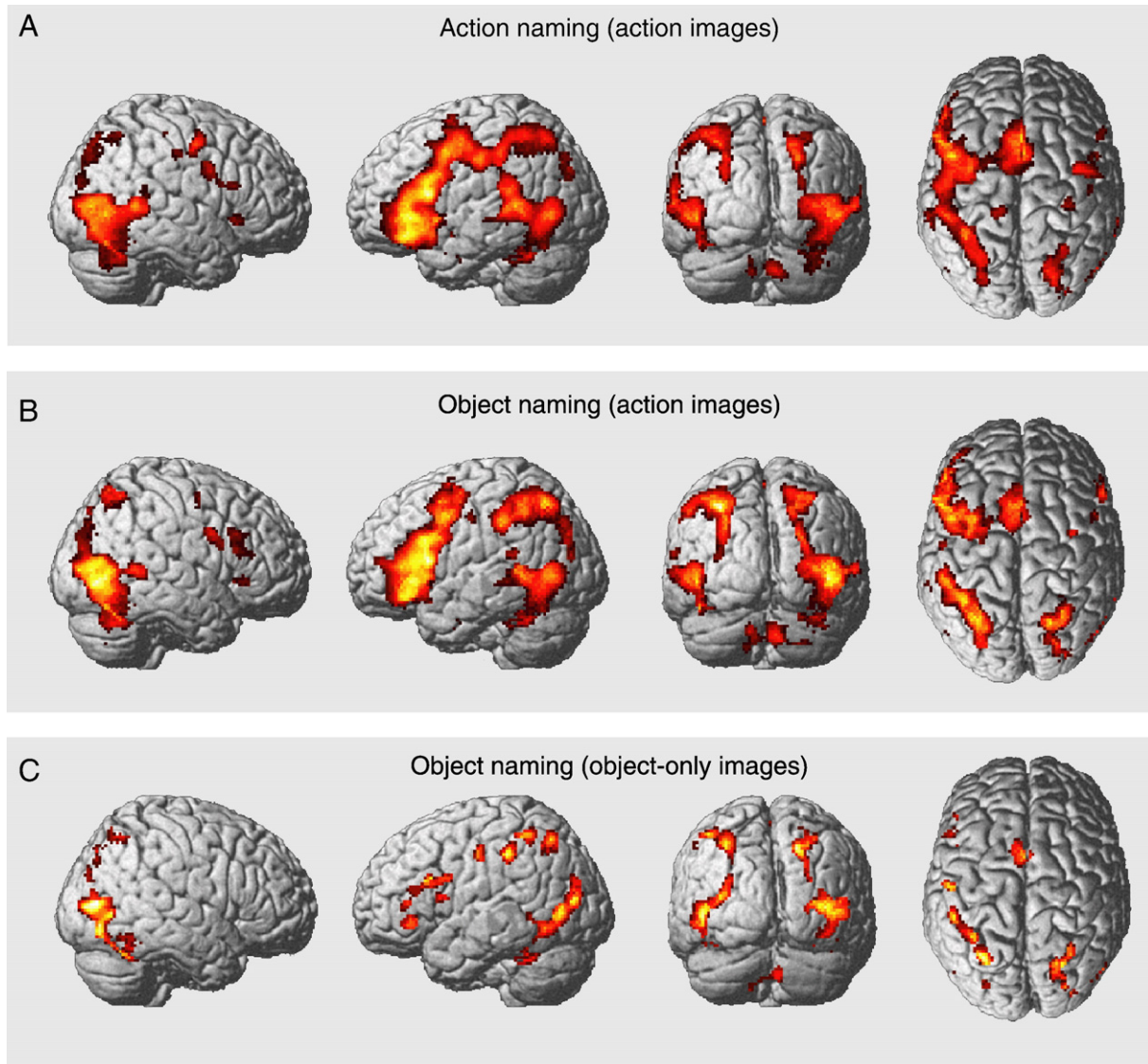
Fig. 2. Comparison of naming tasks against resting baseline. A) Act>Rest, B) ObjAct>Rest, C) Obj>Rest. The results are shown at a significance level of $P<0.001$, corrected for false discovery rate.

and left frontal cortex. Fig. 2 provides an overview of the results using an FDR threshold of $P<0.001$. For brevity, Table 1 lists the activation maxima for each task against the rest condition using a strict threshold (corrected for family-wise error, $P<0.05$). The occipitotemporal cortex and the fusiform gyrus were activated bilaterally in all conditions. When actions or objects were named from action images (Act and ObjAct) the activation additionally encompassed the left posterior middle temporal cortex. Activation was seen in the left inferior frontal gyrus in all tasks. In both action and object naming from action images (Act and ObjAct) the activation centered in the operculum of the inferior frontal gyrus and extended superiorly to include the precentral gyrus (BA 6) and anteriorly to BA 47. The frontal activation was less pronounced when objects were named from object-only images (Obj), mainly encompassing the inferior frontal region (BA 44/47). The supplementary motor area was activated in all conditions, with activity spreading inferiorly to the cingulate gyrus, although in naming objects from object-only images (Obj) this region did not

reach the strict threshold required for listing in Table 1. Bilateral activations of the superior and inferior parietal lobules extending into the precuneus were detected in all three conditions. All three tasks activated the cerebellum bilaterally. Activation in the hippocampus or parahippocampal gyrus was also seen. In general, naming objects from object-only images evoked less extensive activations, but a slightly lower threshold revealed activations in the same cortical regions as in the other conditions.

Comparisons between task conditions

Fig. 3 gives an overview of the three contrasts among tasks that displayed significant differences (see Table 2 for a detailed listing of areas). When objects and actions were named from exactly the same stimuli, object naming (ObjAct>Act, Fig. 3A) was accompanied by enhanced activation in the inferior and superior parietal lobules bilaterally (BA 7/40) and in the right middle frontal gyrus (BA 8/9). Naming actions did not evoke significantly stronger

Table 1
Comparison against resting baseline

Anatomical region	MNI coordinates			Brodmann area	T value
	x	y	z		
Act>Rest					
L. cerebellum/fusiform gyrus	−34	−50	−26	37	15.5
L. cerebellum	−28	−34	−28		9.2
L. fusiform gyrus/ parahippocampal gyrus	−34	−20	−24	20	9.0
L. middle occipital gyrus	−48	−72	−2	19/37	13.3
L. inferior occipital gyrus	−46	−62	−12	19/37	10.9
L. inferior parietal lobule/ postcentral gyrus	−50	−22	40	3	11.2
L. inferior parietal lobule	−40	−48	58	40	8.6
L. superior temporal gyrus	−58	−36	18	22/40	10.0
L. middle temporal gyrus	−66	−38	6	22	9.9
L. middle temporal gyrus	−50	−42	6	22	9.5
L. inferior frontal gyrus, opercularis	−46	14	14	44	13.4
L. inferior frontal gyrus, triangularis	−46	32	−2	45/47	12.5
L. inferior frontal gyrus, orbitalis	−44	34	−16	47	9.9
L. insula	−30	28	0	13	9.9
L. precentral gyrus	−48	4	44	6	11.9
L. precentral gyrus	−40	−4	56	6	8.9
L. insula	−36	6	−4	13	8.8
L. hippocampus	−36	−14	−14		12.2
R. inferior occipital gyrus	42	−76	−8	19	10.2
R. middle occipital gyrus	36	−80	6	19	10.2
R. middle temporal gyrus	50	−68	0	37	10.5
R. middle temporal gyrus	50	−74	10	19/39	8.7
R. middle temporal gyrus	64	−48	8	21	9.0
R. fusiform gyrus	44	−52	−20	37	10.4
R. cerebellum	40	−58	−30		8.5
R. precentral gyrus	50	−6	50	4	8.8
R. supplementary motor area	2	6	62	6	11.7
L. supplementary motor area/ cingulate gyrus	−4	18	46	32	11.7
R. hippocampus	36	−18	−12		8.5
R. hippocampus	36	−6	−24		8.5
ObjAct>Rest					
L. superior parietal lobule	−32	−62	48	7	14.1
L. middle occipital gyrus	−48	−72	−2	19/37	11.3
L. cerebellum/fusiform gyrus	−34	−50	−26		11.1
L. inferior occipital gyrus	−46	−64	−12	19/37	10.4
L. inferior parietal lobule	−48	−34	38	40	8.4
L. fusiform gyrus	−44	−48	−22	37	8.4
L. fusiform gyrus	−42	−46	−24	37	8.2
L. middle temporal gyrus	−44	−50	4	39	9.7
L. inferior frontal gyrus, triangularis	−48	34	8	45	10.7
L. inferior frontal gyrus, opercularis	−46	14	12	44	10.5
L. inferior frontal gyrus, triangularis	−56	16	2	45	9.2
L. inferior frontal gyrus, triangularis	−44	12	26	9	9.7
L. inferior frontal gyrus, orbitalis	−34	30	−8	47	9.7
L. precentral gyrus	−50	4	46	6	8.8
L. supplementary motor area	−6	16	50	32	10.3
L. supplementary motor area	−8	6	60	6	9.6
R inferior occipital gyrus	40	−74	−4	19/37	12.5
R. middle occipital gyrus	36	−86	6	19	10.1
R. middle temporal gyrus	50	−74	10	19/39	8.8
R. superior parietal lobule	28	−60	50	7	11.4
R. superior parietal lobule	18	−66	60	7	8.3
R. fusiform gyrus	38	−48	−20	37	11.2
R. inferior temporal gyrus	46	−64	−10	19/37	9.8
R. cerebellum	40	−58	−28		9.7

Table 1 (*continued*)

Anatomical region	MNI coordinates			Brodmann area	T value
	x	y	z		
Obj>Rest					
L. middle occipital gyrus	−48	−72	−2	19/37	11.6
L. cerebellum/fusiform gyrus	−32	−50	−24		9.0
L. cerebellum/fusiform gyrus	−34	−40	−28		8.5
L. superior parietal lobule	−30	−62	46	7	10.2
L. inferior parietal lobule	−48	−36	42	40	8.5
L. inferior frontal gyrus, opercularis	−42	12	12	44	9.2
L. inferior frontal gyrus, orbitalis	−34	32	−4	47	8.6
R. fusiform gyrus	38	−48	−20	37	13.0
R. middle occipital gyrus	40	−84	4	19/37	10.6
R. precuneus	20	−70	46	7	9.4
R. superior parietal lobule	28	−58	48	7	8.6
R. middle occipital gyrus	34	−88	8	19/37	8.5

Significant at $P<0.05$, corrected for family-wise error (FWE).

activation (Act>ObjAct) in any part of the network, although a small (k=9) cluster in the left anterior temporal lobe survived a lower threshold ($P<0.05$, corrected for false discovery rate). Naming objects from the images with action context compared to naming the same objects from object-only images (ObjAct>Obj, Fig. 3B) resulted in significantly stronger activation in a large mostly left-lateralized network, including the precentral gyrus (BA 6/9), the inferior frontal gyrus (pars opercularis and triangularis), the inferior and superior parietal lobules (BA 7/40), and the posterior middle temporal gyrus. Naming actions compared to naming objects from object-only images (Act>Obj, Fig. 3C) revealed enhanced activation in the left supramarginal gyrus (parieto-temporal junction; BA 40), left and right posterior middle temporal cortex, left precentral gyrus and superior medial frontal gyrus. In addition, activation was observed bilaterally in the anterior temporal lobe, bordering the frontal lobe. Thus, the contrasts ObjAct>Act and ObjAct>Obj showed overlapping activation bilaterally in the inferior and superior parietal lobules as well as in the right middle frontal gyrus, as shown in Fig. 4 (red). Overlap in activation between contrasts Act>Obj and ObjAct>Obj was seen bilaterally in the posterior middle temporal gyrus, in the left supramarginal gyrus, and in the left precentral gyrus and medial frontal gyrus (Fig. 4, blue).

One would intuitively expect differences in the Act>Obj condition in the left inferior frontal cortex as well, as the contrast ObjAct>Obj (Fig. 3B) indicated activation of the left inferior frontal cortex whereas the contrast ObjAct>Act did not (Fig. 3A). At the individual level, 10 out of 15 subjects showed activation of the inferior frontal lobe in the contrast Act>Obj (uncorrected, $P<0.001$) but, at this threshold level (FDR, $P<0.01$), the effect did not reach significance in the group analysis. When the threshold was slightly relaxed (FDR, $P<0.05$) the activation encompassed both the anterior temporal lobe and the inferior frontal region. There were no areas with stronger activation to naming objects from object-only pictures than to naming objects or actions from the action pictures (Obj>ObjAct, Obj>Act) even when the threshold was lowered.

Discussion

Our goals were to investigate whether different cortical regions are activated when actions or objects are named from identical
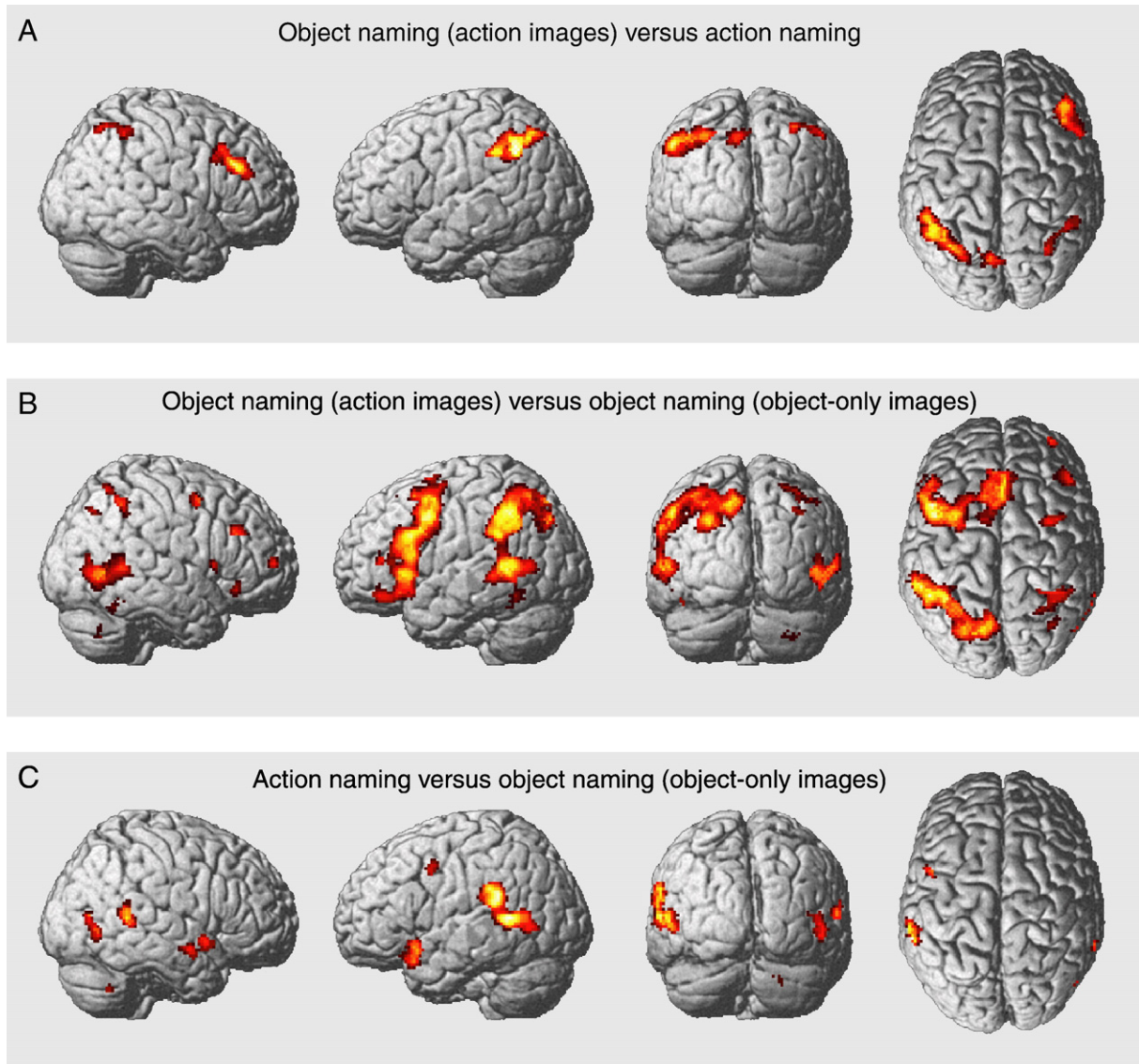
Fig. 3. Comparisons between conditions. The results are shown at a significance level of *P*<0.01, corrected for false discovery rate. Only the contrasts that revealed significant activation are shown here: A) ObjAct>Act, B) ObjAct>Obj, C) Act>Obj.

images, and how the content of the image (depicting/not depicting action) affects the brain correlates of naming. Our results indicate that action and object naming engage a common cortical network, but that the provided input (action pictures, object-only pictures) and the requested output (verb, noun) influence the level of activation in a subset of areas within that network.

Overall, naming actions and objects relative to fixation activated a cortical network which included left inferior frontal and dorsal premotor areas, bilateral occipitotemporal cortex and parietal cortex. This pattern of activation is broadly consistent with previous reports of areas activated in fMRI/PET experiments on picture naming (Price et al., 1996, 2005; Murtha et al., 1999; Abrahams et al., 2003). In addition, MEG studies on picture naming have shown that activation propagates from the occipital cortex to parietal and temporal and further to frontal regions (Salmelin et al., 1994; Levelt et al., 1998; Sörös et al., 2003). These regions are typically involved in a wide range of linguistic tasks, including tasks tapping semantic and phonological processing and

verbal working memory (Vandenberghe et al., 1996; Cabeza and Nyberg, 2000; Bookheimer, 2002; Jobard et al., 2003).

We found that when the stimulus was the same (action image), noun retrieval enhanced activation of the right frontal and bilateral parietal cortex. The stronger activation in naming objects from pictures with action context, relative both to naming actions from the same images and to naming objects from object-only pictures, suggests involvement of additional task-specific processes. The results could be interpreted in two ways: on one hand, the activation pattern may reflect a visual search for task-relevant objects (Nobre et al., 1997; Corbetta and Shulman, 1998), or a shift of attention towards such items (Beauchamp et al., 2001) when objects are named within an action scene. On the other hand, there is usually a right-hemisphere dominance for such visuospatial shifts (Nobre et al., 1997), whereas in our study the parietal activation was more pronounced in the left hemisphere. The left posterior parietal cortex appears to be involved in explicit retrieval of actions associated with

Table 2
Direct comparisons between tasks

Anatomical region	MNI coordinates			Brodmann area	T value
	x	y	z		
ObjAct>Act					
L. inferior parietal lobule	−50	−38	38	40	8.16
L. inferior parietal lobule	−50	−54	48	40	7.42
L. superior parietal lobule	−30	−66	52	7	7.40
L. precuneus	−12	−66	44	7	6.58
R. middle frontal gyrus	42	34	30	9	7.86
R. middle frontal gyrus	48	20	42	8	6.52
R. superior parietal lobule	34	−64	56	7	7.36
R. inferior parietal lobule	46	−48	54	40	5.95
ObjAct>Obj					
L. precentral gyrus	−44	6	38	9/6	8.54
L. inferior frontal gyrus	−30	8	26	6	8.10
L. supplementary motor area	−10	18	50	32	7.97
L. inferior frontal gyrus, triangularis	−44	22	26	46	7.14
R. middle cingulum	10	30	36	9/32	7.11
L. supplementary motor area	−12	2	68	6	6.82
L. inferior frontal gyrus, triangularis	−54	26	2	45	6.75
L. inferior frontal gyrus	−30	36	10	10	5.78
L. insula	−30	26	0	13	5.08
L. putamen	−20	12	8		4.83
L. superior parietal lobule	−14	−74	48	7	8.74
L. inferior parietal lobule	−50	−50	42	40	8.68
L. inferior parietal lobule	−36	−52	42	40	6.64
L. middle occipital gyrus	−26	−76	38	19	7.70
L. supramarginal gyrus	−56	−40	30	40	7.32
L. middle temporal gyrus	−46	−50	6	39	7.45
L. middle temporal gyrus	−62	−48	6	21	7.26
R. middle frontal gyrus	34	56	8	10	9.17
R. inferior frontal gyrus	46	30	30	9	6.57
R. precentral gyrus	32	0	50	6	5.73
R. inferior frontal gyrus, opercularis	52	14	8	44	5.07
R. inferior frontal gyrus, orbitalis	54	28	−10	47	4.69
R. postcentral/inferior parietal lobule	26	−46	42	7	5.81
R. inferior parietal lobule	40	−50	50	40	5.18
R. superior parietal lobule	26	−60	60	7	4.98
R. superior occipital gyrus	34	−72	46	7	4.98
R. middle temporal gyrus	62	−52	10	22	5.94
R. middle temporal gyrus	48	−68	0	37	5.70
R. fusiform gyrus	42	−50	−22	37	6.33
R. cerebellum	32	−66	−38		4.96
Act>Obj					
L. supramarginal gyrus	−56	−42	26	40	9.56
L. middle temporal gyrus	−62	−50	8	21	9.16
L. superior temporal pole	−46	18	−22	38	7.81
L. superior medial frontal gyrus	−4	18	42	32	6.72
L. precentral gyrus	−52	6	44	6	5.97
R. middle temporal gyrus	60	−48	12	22	7.35
R. inferior temporal gyrus	54	−66	−4	19/37	6.38
R. cerebellum	36	−58	−42		7.20
R. insula	46	8	−8	13/38	6.78
R. anterior superior temporal gyrus	50	−2	−14	38	6.30

Activations are listed at a significance threshold of *P*<0.01, corrected for false discovery rate. Only clusters with more than 20 voxels are listed. The table shows at most 7 local maxima, located more than 12 mm apart.

manipulable objects, as suggested by neuroimaging (Kellenbach et al., 2003) and lesion data (Buxbaum et al., 2000, 2005), and in answering questions concerning object manipulation (Boronat et al., 2005). Another interpretation would thus be that naming objects in an action context triggers access to knowledge about how objects are used to a greater extent than when naming the same objects in isolation. These interpretations are not mutually exclusive; the observed activations could reflect both types of processes. It is worth noting that our study contained all types of objects and was thus not optimal for identifying activation related to manipulability as such.

In our study, the only activation that appeared to be specifically associated with name (verb) retrieval was the anterior superior temporal lobe. This region was more strongly activated in naming actions from action images than in naming objects from object-only images. However, the activation was not particularly strong or robust (only a few subjects showed activation in the single-subject data). When the stimulus was the same (action image), retrieval of a verb vs. a noun revealed activation in the left anterior superior temporal lobe only after lowering the significance threshold. While this region has typically not been associated with verb processing, verb-specific activation was reported in lexical decision (Perani et al., 1999). Sentence processing activates the anterior temporal lobe more than word lists (Humphries et al., 2006), suggesting that this region is involved in syntactic processing (Perani et al., 1999). In the present data set, the anterior temporal activation could thus reflect higher syntactic complexity associated with verbs than nouns. Given the low level of statistical significance, however, any interpretation must be treated with caution.

In object naming, the content of the picture (with/without action) had a pronounced effect on neural activation. These activations could be separated into two sets of regions, those that were sensitive to the task, i.e., specific to naming objects in the context of action (as discussed above), and those that were sensitive to the stimulus type, i.e., activated specifically by the action images. Action images, regardless of whether verbs or nouns were named, evoked stronger activation than object-only images in posterior middle temporal cortex bilaterally, in the left parieto-temporal junction (supramarginal gyrus), and in the left frontal cortex. Our results thus suggest that the content of the stimulus modulated activation in this cortical network. The results are in line with previous studies showing that these regions are involved in processing action knowledge. The left posterior middle temporal cortex (LPMT) has been implicated in a large number of studies on verb processing (e.g. Martin et al., 1995; Perani et al., 1999; Kable et al., 2002; Davis et al., 2004). LPMT is activated when action is observed (cf. Grezes and Decety, 2001), or implied in static pictures (Kourtzi and Kanwisher, 2000). LPMT is also more active for tools than for animals (Damasio et al., 1996; Martin et al., 1996; Chao and Martin, 2000; Devlin et al., 2002). Importantly, action-related processing in the LPMT is not specific to the visual modality, but it responds also to semantic decisions on auditory action words (Noppeney et al., 2005) and when listening to action-related sentences (Tettamanti et al., 2005), implying a more general role for the LPMT in action knowledge. Neuroimaging studies have also implicated the left premotor cortex in processing verbs (e.g. Perani et al., 1999; Shapiro et al., 2006) and tools (Damasio et al., 1996; Martin et al., 1996; Valyear et al., 2007). The anterior intraparietal cortex, close to the parieto-temporal junction, is activated by written and spoken action words in semantic decision tasks (Noppeney et al., 2005). In addition, cortical stimulation mapping of the left supramarginal gyrus can disrupt verb production (Corina et al., 2005). Our data indicate that these regions are

Overlap between contrasts ObjAct > Act and ObjAct > Obj
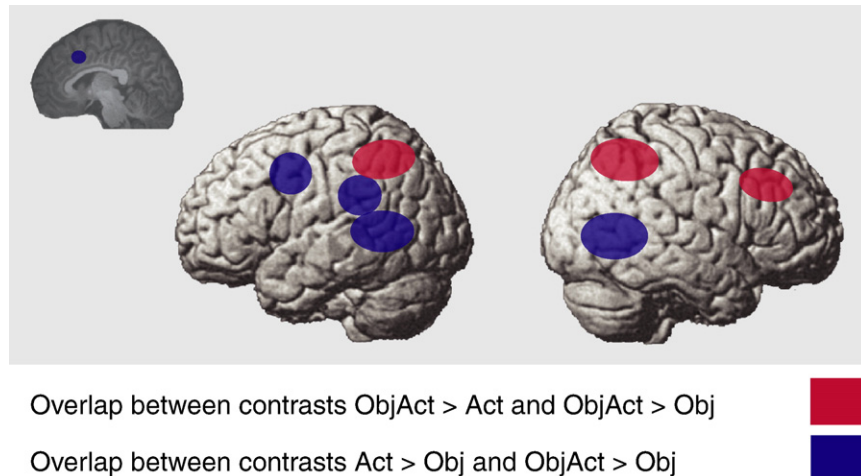
Overlap between contrasts Act > Obj and ObjAct > Obj

Fig. 4. Schematic overview showing overlap in activation between contrasts comparing object naming from action images to action naming or to object naming from object images (ObjAct>Act/Obj, red), and overlap between contrasts comparing action or object naming from action images to object naming from object-only images (Act/ObjAct>Obj, blue).

automatically activated by observation of action, regardless of whether the task is to name the action or the object.

For the activation in the left inferior frontal gyrus there are also other possible interpretations. The left inferior frontal gyrus has been reported to be involved in a variety of tasks, and it is also believed to play a more executive role in semantic retrieval. For example, this region has been associated with control of semantic analysis (Roskies et al., 2001; Wagner et al., 2001). Its activation has been proposed to reflect higher selection demands (Thompson-Schill et al., 1997), a hypothesis that would seem to agree with the present finding of stronger activation when naming either objects or actions from action images than when naming objects from object-only images.

The activation patterns in our study thus seem to be related primarily to differences in stimulus properties and perception, and not to differences between the two grammatical categories in name retrieval. The only activation that appeared to be more specifically associated with name (verb) retrieval was the somewhat elusive involvement of the anterior superior temporal lobe. We found no regions specific to nouns as a grammatical category. Our results agree with a recent study showing that when naming events either as verbs or nouns from identical images (Siri et al., 2008), no differences were found between verbs or nouns as grammatical categories. Similarly, in a picture naming task (Saccuman et al., 2006), no significant differences were found between verbs and nouns, whereas manipulable, compared to non-manipulable, actions and objects elicited activation in a fronto-parietal cortical network. Vigliocco et al. (2006) also found no effect for grammatical class in listening to verbs or nouns, whereas motor words activated the left precentral gyrus and sensory words the left inferior temporal and left inferior frontal regions. These studies have been taken to indicate that semantic features, rather than grammatical class, serve as organizational principles of words. We further show that the context in which the items are presented is essential.

In lesion studies, preserved ability to name nouns and impaired ability to name verbs, or vice versa, is typically determined by naming actions from action pictures and objects from object-only pictures. Based on the present study, those tasks do evoke different activation patterns (Fig. 3C). However, the differences do not seem

to be linked to computations specific to grammatical category or verb/noun retrieval, per se, but rather to differential processing of the content of the image. It is certainly plausible that damage to the areas that have been associated with action perception and comprehension in this and other studies, including the left frontal and inferior parietal cortex and bilateral posterior middle temporal cortex, could result in impaired production of verbs. For example, left frontal damage is often associated with selective damage to verb processing (cf. Shapiro and Caramazza, 2003). Based on the present study we would further predict that object naming from those same action images would be impaired as well but could be better preserved for object-only images. Nevertheless, it is important to keep in mind that the activation patterns in a healthy and lesioned human brain may not be directly comparable. In an MEG study of picture naming, Sörös et al. (2003) found that the cortical routes of activation for object and action naming converged in healthy subjects, but they diverged for an anomic patient who had more difficulties in object naming. Moreover, the activation chains for both object and action naming deviated from those of the healthy controls, even though for the latter task (relatively well-preserved action naming) the activation patterns were closer to normal. This suggests that even the patient's relatively more spared action naming was neurally implemented in a qualitatively different way.

In conclusion, our results converge with previous evidence (Hernandez et al., 2001; Sörös et al., 2003; Siri et al., 2008), showing that retrieval of verbs and nouns in the healthy human brain using identical stimuli in a picture naming task engages a similar distributed cortical network, as measured with BOLD fMRI. Importantly, however, the content of the image (action vs. object only) had a pronounced effect on the activation in parts of that network that have previously been implicated in processing of action knowledge. Furthermore, object naming in the context of action revealed additional activations, both in comparison to verb retrieval from the same set of images, and in comparison to noun retrieval from images not depicting action, suggesting that attention may be more directed towards motor-based properties of objects when they are presented not as single entities but as part of images that also depict the relevant action.

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