Distinct Cortical Areas for Names of Numbers and Body Parts Independent of Language and Input Modality

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Some models of word comprehension postulate that the processing of words presented in different modalities and languages ultimately converges toward common cerebral systems associated with semantic-level processing and that the localization of these systems may vary with the category of semantic knowledge being accessed. We used functional magnetic resonance imaging to investigate this hypothesis with two categories of words, numerals, and body parts, for which the existence of distinct category-specific areas is debated in neuropsychology. Across two experiments, one with a blocked design and the other with an event-related design, a reproducible set of left-hemispheric parietal and prefrontal areas showed greater activation during the manipulation of topographical knowledge about body parts and a right-hemispheric parietal network during the manipulation of numerical quantities. These results complement the existing neuropsychological and brain-imaging literature by suggesting that within the extensive network of bilateral parietal regions active during both number and body-part processing, a subset shows category-specific responses independent of the language and modality of presentation. © 2000 Academic Press

INTRODUCTION

The goal of the present work is to examine whether the semantic representations of numbers and body parts are associated with partially distinct cortical territories. Clinical and cognitive neuropsychology studies associate semantic deficits in both domains to lesions coarsely localized to the left parietal lobe (McCarthy and Warrington, 1990). Furthermore, patients with left inferior parietal lesions often exhibit simultaneous deficits for numbers and body parts (Benton, 1992; Gerstmann, 1940). Such an association of neuropsychological deficits is however notoriously ambiguous, and has been the subject of much debate. It might suggest that there is a shared substrate for numbers and body parts in the left parietal region, perhaps based on a common functional system for spatial representation and manipulation (Gerstmann, 1940) or on the crucial role that finger counting plays in numerical development (Butterworth, 1999). However, it might also reflect the existence of distinct regions that merely happen to be promiscuous and are therefore frequently affected simultaneously by cerebral dysfunction (Benton, 1961; Benton, 1992).

In support of the latter interpretation, number and body part deficits, although frequently associated, can be at least partially dissociated in brain-lesioned patients (Benton, 1961; Critchley, 1953). Some patients exhibit selective deficits in understanding body part names and particularly in locating them in space, a deficit known as autotopoagnosia (Goodglass and Budin, 1988; Ogden, 1985; Shelton *et al.,* 1998; Sirigu *et al.,* 1991; Suzuki *et al.,* 1997). Other patients exhibit a selective deficit in understanding numerals, associated with severe acalculia (Cipolotti *et al.,* 1991; Dehaene and Cohen, 1997). Selective preservation of numbers is also on record (Thioux *et al.,* 1998).

Neuropsychological studies are inherently limited in their localizing ability because brain lesions tend to be large, do not respect functional boundaries, and are further complicated by subsequent brain reorganization processes. In the present study, we therefore sought to bring neuroimaging evidence from normal subjects to bear on the issue of the dissociability of number and body part representations in the cortex.

Previous imaging studies of numbers and body parts. Some previous brain-imaging experiments have studied body-part and number processing circuits, though without comparing them directly in similar tasks and in the same subjects. As for body parts, a few studies using only nonverbal tasks requiring internal manipulations of the body in space have revealed a network comprising intraparietal, precentral, and mesial prefrontal components, with greater activity in the left hemisphere (Bonda *et al.,* 1995; Bonda *et al.,* 1996; Parsons *et al.,* 1995). As for numbers, the internal

manipulation of numerical quantities relies on areas located in the banks of the intraparietal sulcus, where activation can be identified whenever subjects perform various calculation and approximation tasks with Arabic numerals (Chochon *et al.,* 1999; Dehaene, 1996; Dehaene *et al.,* 1999; Dehaene *et al.,* 1996; Pesenti *et al.,* 2000; Pinel *et al.,* 1999; Roland and Friberg, 1985; Rueckert *et al.,* 1996). This system is bilateral, although it activates with a right-hemispheric lateralization when subjects are engaged in a number comparison task (Chochon *et al.,* 1999).

Criteria for semantic-level category specificity. The present work aims at extending those imaging results by examining whether a subset of those areas qualifies as a category-specific semantic system showing specialization either for numbers or for body parts. In neuropsychology, two criteria are used to define semantic-level category-specific deficits. First, the patient's impairment must be significantly more severe for a given category of items than for another. Second, this dissociation must hold across a variety of task contexts (Caramazza, 1998; Caramazza and Shelton, 1998; Warrington and Shallice, 1984). The logic behind this operational definition is that semantic representations are functionally located at an abstract level common to multiple word listening, speaking, reading, or picture identification contexts. Patient E.W. (Caramazza and Shelton, 1998), for instance, was strikingly more impaired for the category of animals than for any other conceptual category. The deficit was attributed to a high-level loss of abstract semantic knowledge about animals because the dissociation was observed with a wide variety of tasks tapping comprehension and production, with both auditory and visual inputs and with verbal and nonverbal stimuli.

Similar criteria can be used to identify semantic representations using brain-imaging techniques. Many of the initial brain-imaging studies of category-specific systems were open to various stimulus artifacts because they used only a single modality of stimulus presentation, for instance pictures of animals versus pictures of tools (Damasio *et al.,* 1996; Dehaene, 1995; Martin *et al.,* 1995; Martin *et al.,* 1996; Moore and Price, 1999; Perani *et al.,* 1995). A few imaging studies, however, used several tasks and/or modalities of input to authenticate abstract semantic representations. Petersen *et al.* first demonstrated that the same left inferior frontal area could be activated by both auditory and visual words when subjects generated semantic associates of those words or when they categorized them as dangerous animals (Petersen *et al.,* 1988). Two more recent functional imaging studies also used distinct modalities of input in order to identify a common network of semantic areas distributed in the left temporal, parietal and frontal lobes (Chee *et al.,* 1999; Vandenberghe *et al.,* 1996).

In those papers, however, the possibility that part of this network was organized categorically was not studied. It is only very recently that the existence of category-specific brain regions has been probed more systematically with a variety of input modalities (Cappa *et al.,* 1998; Chao *et al.,* 1999; Gorno-Tempini *et al.,* 1998; Perani *et al.,* 1999). For instance, Gorno-Tempini *et al.* (1998) varied both stimulus type (written words or pictures) and category (person or nonperson) to identify a left anterior temporal area activated specifically when knowledge of famous people is retrieved and equally accessible by word and by picture stimuli. Likewise, Chao *et al.* (1999) report categorical differences in posterior temporal lobe activity induced by tools and by animals, whether presented as written words or as pictures. Some studies have also demonstrated category-specific activations independent of the tasks performed (Cappa *et al.,* 1998; Chao *et al.,* 1999; Perani *et al.,* 1999).

Outline of the present study. In the present work, a similar strategy is used to examine the semantic representation of numbers and body parts. We test the existence of distinct category-specific semantic networks for number and body part names by presenting the words in two different modalities (written or spoken words) and in two different languages (French or English) in bilingual subjects. Areas are reported only if they fulfill three criteria. First, the area must show significantly more activation to one semantic category of words than to another. Second, this advantage for one category over the other must be found whether words are presented visually or auditorily, indicating an amodal level of representation. Third, this advantage must also be found whether words are presented in the subject's first language or in a second language, indicating that it occurs at a language-independent level of representation.

Ideally, it would be desirable to add yet a fourth criterion, the presence of reliable category specificity regardless of the semantic task performed. Here, however, limits on experimental duration led us to study a single task which was selected to be as similar as possible in both categories. In both cases, subjects were shown a single word and were asked to judge its relation to a fixed reference by pressing one of two response keys. Furthermore, number and body part names were matched as much as possible for frequency and word length. Thus, the task inputs and outputs were highly similar. The nature of the comparative relation being probed, however, varied with the category being tested (above or below the shoulders for body parts; larger or smaller than 12 for numbers). The ability to locate parts of the body is thought to rely on an abstract internal representation of the body in space, the "body schema," which seems to be the level of representation which is impaired in cases of autotopoagnosia with left

parietal lesions (Goodglass and Budin, 1988; Ogden, 1985; Shelton *et al.,* 1998; Sirigu *et al.,* 1991; Suzuki *et al.,* 1997). We therefore expected a left parietal activation, together perhaps with precentral and mesial prefrontal activations as observed during nonverbal internal manipulations of the body in space (Bonda *et al.,* 1995; Bonda *et al.,* 1996; Parsons *et al.,* 1995). Contrariwise, larger-smaller number comparison is thought to depend on a sense of numerical quantities and their proximity and distance relations on an internal semantic space, the mental "number line" (Dehaene, 1992; Gallistel and Gelman, 1992). In agreement with the proposed localization of this quantity system (Dehaene and Cohen, 1995) and with previous brain-imaging experiments (Chochon *et al.,* 1999; Dehaene, 1996), areas showing greater activation during number comparison were expected to be found in the intraparietal sulcus, particularly in the right hemisphere.

Note, finally, that given the neuropsychological literature, we expected such areas to be seen against a large backdrop of areas common to both tasks, particularly in the left parietal lobe. The present design, however, focused exclusively on the identification of areas showing activation differences between numbers and body parts. We were able to identifiy areas of common activation, but our design could not distinguish which were related to a common semantic system and which merely reflected the shared sensory, attentional, and motor requirements of the two tasks.

METHODS

Subjects

The experiments were approved by the regional ethical committee, and all subjects gave written informed consent to participate. In experiment 1, subjects were five male native French speakers, aged between 27 and 50 (mean 37 years), who had learned English as a second language. In experiment 2, subjects were three females and three males, aged between 23 and 35 (mean 27 years). Half the subjects had French as their first language and English as a second language, while the converse was true for the remaining subjects. In both experiments, the second language had been learned at school after the age of 7.

Task

We implemented a $2 \times 2 \times 2$ design in which modality, language, and category were varied orthogonally. In different blocks, names of numbers and of body parts were presented in either French or English and in either the visual or the auditory modality. Response times were recorded from word onset via two buttons, one in each hand. With numerals, the sub-

jects' task was to press one key if the target number was larger than or equal to 12 and the other key otherwise. With body parts, subjects pressed one key if the part was higher than or on the same level as the shoulders when a person is standing and the other key otherwise. The behavioral data of one subject in experiment 1 were lost due to computer failure.

Stimuli

Written words were presented for 500 ms in upper case, centered on screen, and subtended 1° vertically and up to 5° horizontally. Spoken words were recorded by a fluent French-English bilingual, digitized at 22 kHz, and presented through a PC-compatible computer sound board and MR-compatible piezo-electric headphones inserted in a noise-protection helmet. Nineteen words with translation equivalents in French and English were selected in each category (numbers: 1, 2, 3, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 20, 30, 40, 50, 60; body parts: hand, head, arm, mouth, nose, leg, stomach, finger, shoulder, elbow, tongue, ear, hair, cheek, thumb, hip, thigh, jaw, ankle). Analyses of variance were conducted to examine possible differences in lexical frequency, number of letters, and number of syllables in the stimuli. The number of letters was well matched ($P > 0.19$ for effects of language, category, and their interaction). Numerals were slightly more frequent than body parts ($F(1,72) = 4.25$, $P = 0.043$), but this was true only for English words ($F(1,36) = 5.79$, $P = 0.021$), not for French words ($F < 1$). Finally the number of syllables did not differ across categories or across languages ($P > 0.13$), though a category by language interaction indicated that numerals had more syllables than names of body part in English ($F(1,36) = 5.96$, $P = 0.020$), but not in French ($F < 1$).

Experimental Design

In experiment 1, stimuli were presented at a rate of one item every 2.5 s. Stimuli were presented in blocks of 18 trials with a fixed modality, language, and category. At the beginning of each block, during the acquisition of the first three brain volumes (15 s), a written sentence in the subject's first language warned the subjects of the nature of the upcoming task (e.g., "you are going to see number words in English"). Then, nine brain volumes (45 s) were acquired while subjects performed the specified task. Blocks were arranged pseudo-randomly in runs consisting of an initial rest period, four blocks, and a final rest period (run length = 6 min). Three subjects participated in six runs, and two subjects in four runs.

In experiment 2, stimuli were presented at a rate of one item every 12 s. Stimuli were presented in short blocks of six such 12-s trials, preceded by a 12-s written instruction as above, for a total block length of 84 s. All subjects participated in three runs, each consisting of

eight pseudo-random blocks with all combinations of modality, language, and category (run length = 11 min, 12 s).

Functional Imaging

We used a 3-Tesla Bruker whole-body magnetic resonance imaging system. In experiment 1, 20 5-mm-thick axial slices were obtained with a T2*-weighted gradient echo, echoplanar imaging sequence (matrix = 64×64, repetition time of 5 s), using blood oxygen level-dependent contrast. The 20 slices were acquired as two groups of 10 with a within-group interslice interval of 115 ms. The two groups were separated by a silent period lasting 1350 ms, during which the words were presented, thus ensuring good comprehension. Seventy-two brain volumes were acquired consecutively for each run (12 images for each of six blocks). The first three images of each run were not included in the analysis. In the second experiment, 18 6-mm-thick axial slices were obtained using the same sequence, but with a shorter repetition time (TR) of 2 s (equal interslice intervals of 111.1 ms). Although each trial corresponded to six repetition cycles, fMRI images were acquired only during the last five cycles. During the first cycle, excitation gradients were maintained, but read-out gradients were omitted, thus leaving a quasisilent period of 2 s, during which the target word was presented. Then 336 brain volumes were acquired consecutively for each run (42 images in each of eight blocks). The first six images of each run were not included in the analysis. In both experiments, high resolution anatomical images (gradient echo, inversion recovery, matrix = $128 \times 128 \times 256$, field of view $192 \times 256 \times 256$ mm) were also acquired.

Statistical Analysis

All analyses were performed with Statistical Parametric Mapping, Version 96 (SPM96; http://www.fil.ion.bpmf.ac.uk/spm). For each subject, anatomical images were transformed stereotactically to Talairach coordinates using the standard template of the Montreal Neurological Institute. The functional scans, corrected for subject motion, were then normalized using the same transformation and smoothed with a Gaussian spatial filter to a final smoothness of about 14 mm. In experiment 1, all images from the five subjects were analyzed together. The data from each run were modeled using the general linear model with separate functions modeling the hemodynamic response to each experimental block, the rest period, and the instructions. Covariates were used to model long-term signal variations (temporal cutoff 240 s) and overall differences between runs. Contrasts probed the main effects of each variable (language, modality, and category), as well as the effect of category within each language and each language condition. Regions are reported only if

they showed a main effect of category (voxelwise $P < 0.0001$, corrected for multiple comparisons to $P = 0.05$) as well as a category effect within each modality and language (voxelwise $P < 0.05$ for each of four tests).

In experiment 2, because of the larger number of images, we first averaged the data across the six subjects to yield three average runs. In each run, each of the eight types of events was modeled by a Gaussian function with a peak delay of 6 s and a standard deviation of 2 s. Covariates modeled long-term signal variations (temporal cutoff 240 s) and differences between runs. Contrasts were as above, except that the following thresholds were used: main category effect, voxelwise $P < 0.001$, corrected for multiple comparisons to $P < 0.5$; masked by four subcomparisons, voxelwise $P < 0.05$.

RESULTS

Brain imaging. Our first experiment used a blocked design with a fast (2.5-s) interstimulus interval. Four brain regions showed significantly greater activation for body parts than for numerals, irrespective of modality and language (Table 1). These were located in the left intraparietal sulcus, left precentral sulcus, left mesial frontal gyrus, and left dorsolateral prefrontal cortex (Fig. 1). Conversely, four other regions showing greater activation for numerals were found in the right intraparietal sulcus/inferior parietal lobule, right supramarginal gyrus (close to the postcentral gyrus), right precuneus, and left supramarginal gyrus/insula.

Our second experiment, with six new subjects, was a replication using an event-related design to monitor the temporal profile of the hemodynamic response on each trial. For body parts versus numerals, three of the four regions observed in experiment 1 were replicated: left intraparietal sulcus, left precentral sulcus, and mesial frontal gyrus (the latter activation now straddled across the midline and could not be reliably associated with one hemisphere or the other). In those regions, the maxima for experiments 1 and 2 were within 1–1.5 cm of one another (Table 1), and the active clusters showed a considerable amount of overlap (Fig. 1). The left dorsolateral prefrontal activation found in experiment 1 was not replicated. Conversely, for numerals versus body parts, two active clusters were observed in the right parietal lobe, in regions coarsely homologous to those observed in experiment 1: the intraparietal sulcus and the postcentral sulcus (Fig. 2). A third focus of activation was found in the right anterior insula, a location which was not activated in experiment 1. Note, however, that in experiment 1 a large cluster of activity was found in the left insular/supramarginal region. At a lower threshold (10^{-3}, uncorrected), two small foci of greater activation for numerals were also detected in this region in experiment 2 (left supramarginal gyrus, coordinates $-63, -27, 17$,

TABLE 1

Coordinates and Z Scores of Peaks Showing Greater Activation for Numbers or Body Parts
Irrespective of Language and Input Modality

			Experiment 1							
			Body parts					Numerals		
x	y	z	Z score	Location	x	y	z	Z score	Location	
−39	−63	45	5.21	Left IPS	30	−54	60	5.69	Right IPS/SPL	
−51	9	42	4.83	Left PrCS	54	−42	33	4.93	Right SMG/PoCS	
−6	18	51	5.79	Left MFG	9	−45	33	5.51	Right PreCu	
−48	45	21	6.37	Left DlPFC	−45	−9	18	4.73	Left SMG/Ins	

			Experiment 2							
			Body parts					Numerals		
x	y	z	Z score	Location	x	y	z	Z score	Location	
−36	−69	45	5.24	Left IPS	18	−39	48	4.07	Right IPS/PoCS	
−45	15	42	3.79	Left PrCS	60	−21	36	3.66	Right PoCs	
6	27	48	4.57	Midline MFG	39	9	18	4.03	Right Ins	

Note. Abbreviations: IPS, intraparietal sulcus; PrCS, precentral sulcus; MFG, medial frontal gyrus; DlPFC, dorsolateral prefrontal cortex; SPL, superior parietal lobule; SMG, supramarginal gyrus; PoCS, postcentral sulcus; PreCu, Precuneus; Ins, Insula. Note that the anatomical labels are based on full cluster extent rather than peak location.

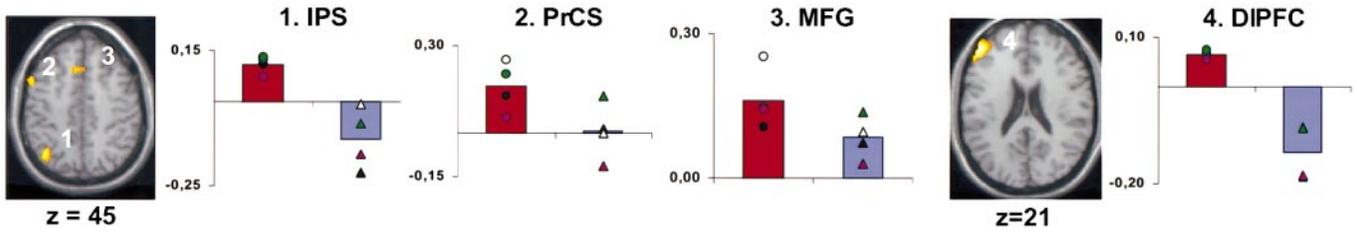Z score = 4.04; left insula, coordinates −42, 3, 21, Z score = 3.90).

The temporal profiles of the active regions are shown in Figs. 1 and 2. In all regions, the curves diverge sharply for numerals versus body parts, and this divergence shows a similar time course whether the words are spoken or written, and presented in French or in English. All clusters show a phasic peak 5–7 s after the onset of the word stimulus, a delay compatible with known hemodynamics. In most case, the preferred category evokes a transient increase in activation above the baseline level. The only exception is a cluster in the right intraparietal/postcentral sulcus, which exhibits a signal decrease selectively for body parts. In all other clusters, a tonically elevated activation level in favour of the preferred category is also visible throughout the epoch. Since subjects were asked to concentrate on a given category of words for six trials in a row, top-down attentional effect may have caused this tonic bias.

The above analyses focused on the differences in activation between numbers and body parts. Yet as noted in the introduction, previous neuropsychological and imaging evidence suggest that numbers and body part processing may share a vast set of common areas in the bilateral parietal lobes. To test this, we examined parietal activation common to numbers and body parts relative to rest ($P < 0.001$, corrected). This was feasible only in experiment 1, in which a distinct resting period was available. To remove modality- and language-specific effects, we also required that this difference relative to rest remained significant at $P < 0.05$ in a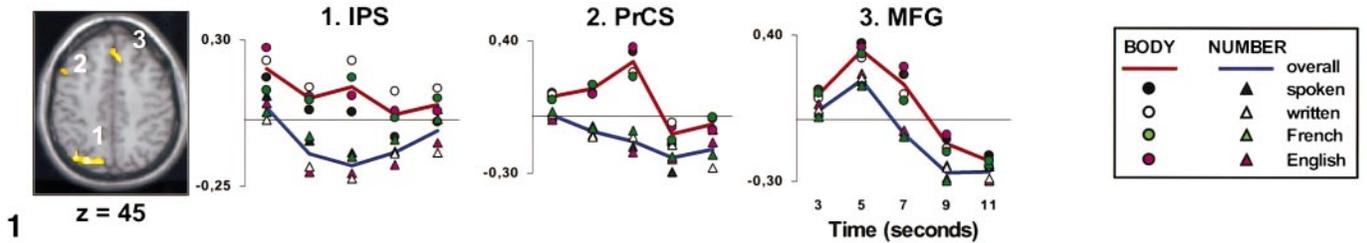ll conditions of modality and language. An extended network of common areas was found, among which three highly significant peaks were located in the left parietal lobe (PoCS, Talairach coordinates −42, −45, 51; IPS, −54, −30, 54; posterior superior parietal lobule, −24, −69, 57) and two in the right parietal lobe (PoCS, 39, −45, 48; IPS, 57, −30, 51). Although we cannot exclude that some of these shared regions were related to attentional or response components rather than to semantic processing, they indicate the existence of a large task-related network in the parietal lobes, within which only a few areas show a dependence on word category.

Behavior. The behavioral data were analyzed for possible confounds with categorical effects. In experiment 1, the average response time was 845 ms. An analysis of variance on median response times with category, modality, and language as within-subject factors revealed main effects of all three factors. Subjects were 29 ms faster with numerals than with body parts ($F(1,3) = 15.9$, $P = 0.028$), 147 ms faster with written words than with spoken words ($F(1,3) = 29.7$, $P = 0.012$), and 100 ms faster with their first language, French, than with the second language, English ($F(1,3) = 17.5$, $P = 0.025$). Two interactions were also significant. First, a language by modality interaction ($F(1,3) = 83.8$, $P = 0.003$) revealed that subjects were disproportionately slower with spoken English words than with any other combination of modality and language. Second, a category by modality interaction ($F(1,3) = 13.8$, $P = 0.034$) indicated that responses to numerals were faster than responses to body parts in the visual modality ($F(1,3) = 22.9$, $P = 0.017$), but not
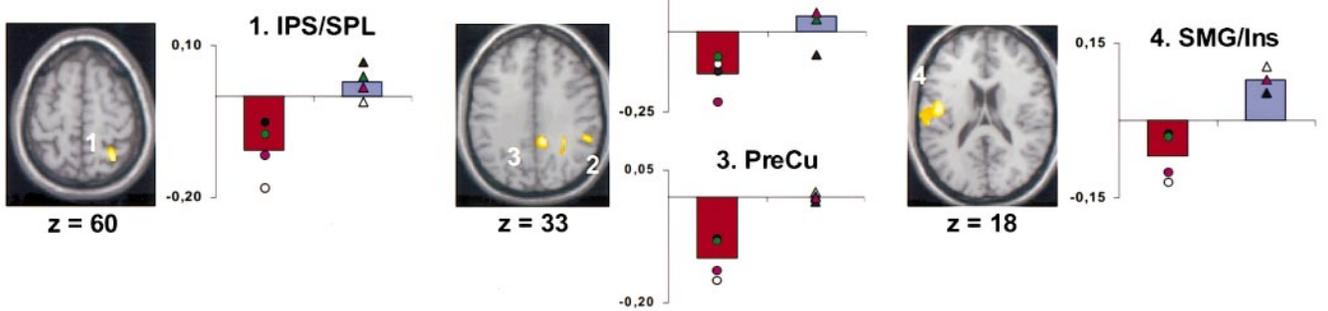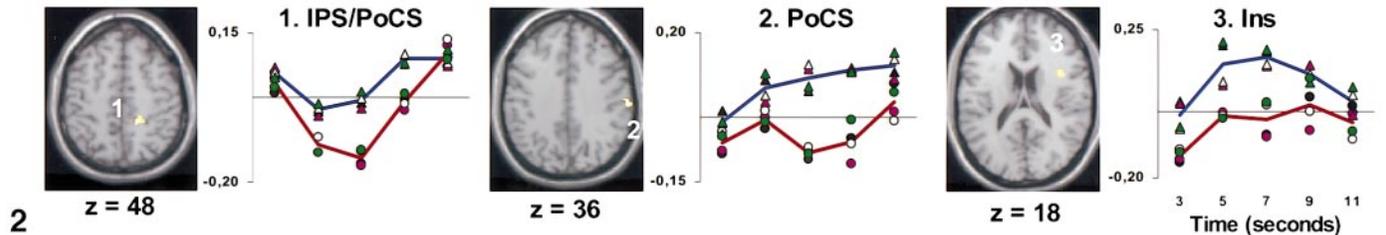
Experiment 1

Experiment 2

Experiment 1

Experiment 2

FIG. 1. Brain regions showing significantly greater activation for body parts than for numerals, irrespective of modality (spoken or written words) and language (French or English words). Abbreviations as in Table 1. For experiment 1, a block design was used; histograms indicate average percent signal change within each block of trials. For experiment 2, an event-related design was used; curves represent the average temporal profile of percentage signal change for a given type of trial. In both cases, percentages are relative to the average signal of the voxel across the entire experiment.

FIG. 2. Brain regions showing significantly greater activation for numerals than for body parts. For abbreviations and symbols, see Table 1 and Fig. 1.

in the auditory modality ($F < 1$). Errors were too infrequent (2.7%) to permit further analysis.

The behavioral results of experiment 2 were largely similar to those of experiment 1. The average response time was 869 ms. Subjects were 151 ms faster with numerals than with body parts ($F(1,4) = 25.2$, $P = 0.007$), 117 ms faster with written words than with spoken words ($F(1,4) = 21.4$, $P = 0.010$), 27 ms faster with French than with English ($F(1,4) = 27.0$, $P = 0.007$), and 60 ms faster when words were presented in their first language than in their second language ($F(1,4) = 15.3$, $P = 0.018$). An interaction of first versus second language with modality ($F(1,4) = 9.76$, $P = 0.035$) revealed that subjects were 116 ms faster with
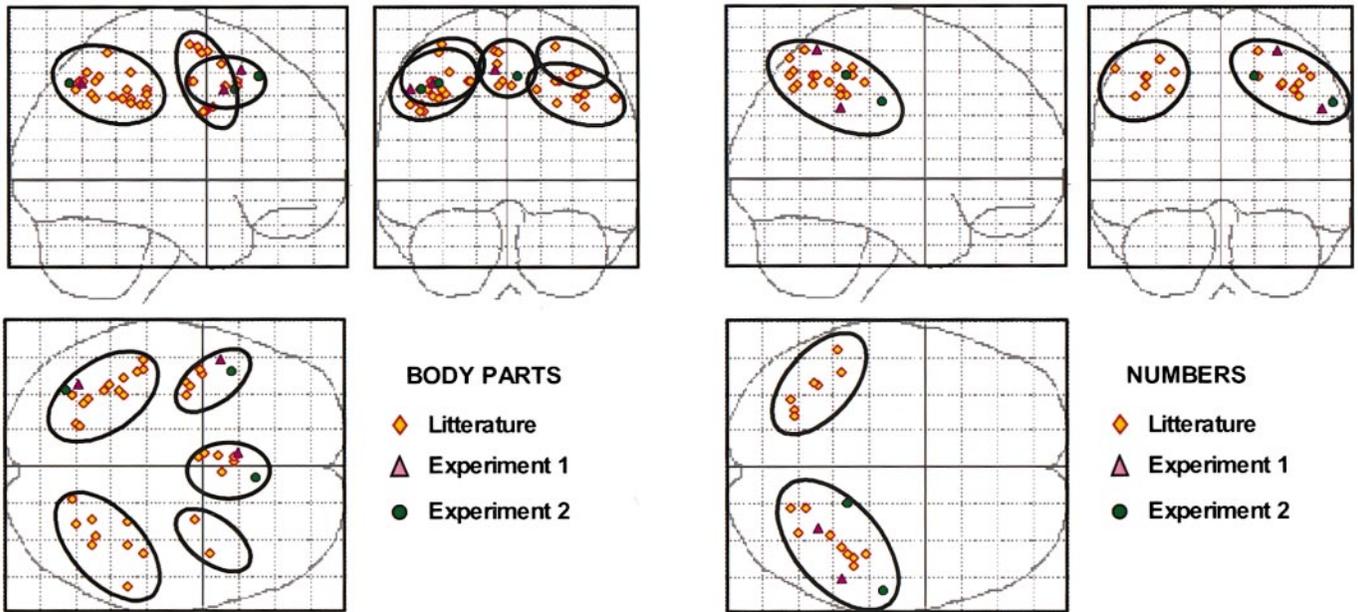
FIG. 3. Glass-brain views of peak activation sites observed in the present study and in previous publications. Left: Activations observed during body part processing in experiments 1 and 2, compared to a parieto-precentro-mesial network involved in transformations of the body in space (mental rotation of the hand) (Bonda *et al.,* 1995; Bonda *et al.,* 1996; Iacoboni *et al.,* 1999). The present activations, although tightly clustered across the two replications, appear more anterior in the frontal lobe and slightly more posterior in the parietal region. Note, however, that our stimuli covered a much greater range of body parts than just the hand. Right: Activations observed during number processing, compared to those observed in the parietal lobe during calculation versus letter processing (Chochon *et al.,* 1999; Dehaene *et al.,* 1999), approximate calculation relative to exact calculation (Dehaene *et al.,* 1999) and number comparison relative to the processing of meaningless symbols (Pesenti *et al.,* 2000). All previous studies identified a large bilateral intraparietal network, with considerable overlap with the one observed during body part processing. Our observed activation may represented a small subset of areas more specifically involved in number processing.

their first language than with their second language in the auditory modality ($F(1,4) = 21.2$, $P = 0.010$), while there was no such difference in the visual modality ($F < 1$). A small triple interaction of category, modality, and language ($F(1,4) = 8.00$, $P = 0.048$) also indicated that the response time difference between numbers and body parts varied across stimulus types. Posthoc tests indicated that it was insignificant for written French ($P = 0.16$), but significant in all other cases. Finally, errors were infrequent (4.7%).

DISCUSSION

The aim of our experiments was to identify brain regions associated with the manipulation of semantic knowledge about numbers and body parts. Using three criteria, greater activation to one category of words, amodal character, and independence from a specific language, areas were identified in high-level association cortices of the left and right parietal and frontal lobes, at localizations compatible with previous imaging studies using nonverbal stimuli. It is particularly noteworthy that each of these regions responded with a similar activation profile whether its preferred category was presented with spoken or with written words.

The visual and auditory modalities are initially processed in nonoverlapping modality-specific cortices.

Our results, however, reveal some of the cerebral areas where they converge. As predicted by some models of the lexicon, semantic-level word processing is associated with the activation of specific cortical regions that are amodal and whose activation depends in part on the semantic content that is being accessed (Caramazza and Shelton, 1998; Damasio *et al.,* 1996). Those regions are convergence areas in the minimal sense that they are lying at the convergence of auditory and visual word processing streams. It is possible that they constitute "convergence zones" in the sense of Damasio (Damasio *et al.,* 1996), i.e., putative regions that tie together the different fragments of a lexical concept. The present work, however, cannot distinguish this possibility from the alternative hypothesis that these regions are associated with fragments of semantic representations or with processes involved in semantic manipulation, which would differ across the two categories tested.

Interpretation of body-part-related activations. The left posterior parietal, left precentral, and mesial prefrontal activations for body parts are largely consistent with expectations based on previous imaging studies in which those regions were active when subjects imagined transformations of their body in space (mental rotation of the hand; Bonda *et al.,* 1995, 1996; Parsons *et al.,* 1995) (see Fig. 3). Studies in monkey indicate

TABLE 2
Response Times and Error Rates Recorded during fMRI Scanning in the Various Task Conditions

Modality	Language	Category	Experiment 1		Experiment 2	
			RT (ms)	Errors (%)	RT (ms)	Errors (%)
Spoken	French	Numbers	826	1.6	767	2.8
		Body parts	850	4.2	992	3.7
	English	Numbers	1011	1.9	906	2.8
		Body parts	985	5.1	1046	11.1
Written	French	Numbers	711	1.2	735	1.9
		Body parts	791	2.8	825	2.8
	English	Numbers	773	1.4	767	6.5
		Body parts	808	3.2	917	6.5

that these regions are interconnected and form a mosaic of segregated anatomical circuits, each containing neurons specialized for a certain sensorimotor transformation that allow for the perceptual guidance of body parts (Rizzolatti *et al.,* 1998). The body-part comparison task seems to rely on one such circuit.

Our body-part-related activations, although tightly replicated across the two experiments, appear more anterior in the frontal lobe and more posterior in the parietal region relative to previous studies (Fig. 3). This might be related to the fact that previous studies focused on the mental representation of hand and arm movements (Bonda *et al.,* 1995, 1996; Parsons *et al.,* 1995), which are know to be represented anteriorily in the intraparietal sulcus (Kawashima *et al.,* 1996), while our study used a greater range of body parts.

Another potential difference with previous work is that our observed body-part-related activations are exclusively found in the left hemisphere. In previous studies of mental rotation of hands, the active network was largely bilateral (Fig. 3), although activation was stronger in the left hemisphere (Bonda *et al.,* 1995; 1996; Parsons *et al.,* 1995). A left dominance for the internal representation of the body is compatible with neuropsychological studies. In particular, lesions to the left parietal region can result in the neuropsychological syndrome of autotopoagnosia, in which patients lose topographic body knowledge and become unable to locate body parts from their name (Ogden, 1985; Sirigu *et al.,* 1991). This syndrome, which is thought to result from a disruption of an internal "body schema," is almost exclusively found following left parietal damage (McCarthy and Warrington, 1990).

The left inferior precentral cortex, at a site slightly inferior to the activation reported here, is also active when subjects viewed pictures of tools as opposed to animals or nonsense objects (Martin *et al.,* 1996) and in some conditions when subjects observe actions performed by a third party (Decety *et al.,* 1997; Iacoboni *et al.,* 1999). Precentral cortex may thus have a general role in representing the linkage between body configurations and motor actions at an abstract level common to a variety of verbal and nonverbal perception, comprehension, and execution contexts. Consistent with this idea, the monkey ventral premotor field F5, a plausible homolog of the precentral activation in humans (Iacoboni *et al.,* 1999), contains mirror-neurons that encode actions irrespective of whether they are perceived or self-generated (Gallese *et al.,* 1996).

It is interesting to note that two of our body-part related sites, in precentral and mesial prefrontal cortices, are located just anterior to the somatotopically organized primary and supplementary motor areas (Grafton *et al.,* 1993; Picard and Strick, 1996). In this respect, our results are analogous to the previous finding that the retrieval of two other categories of knowledge (color and action knowledge) activates brain areas just anterior to those involved in the perception of the relevant attributes (color and movement) (Martin *et al.,* 1995). This suggests that semantic knowledge in high-level association cortices may ultimately be grounded in connections to relevant lower-level peripheral brain areas.

Interpretation of number-related activations. Turning to our second category of words, numbers, areas showing greater activation during number comparison were systematically located within the right parietal region. Because of the variable localization of activation maxima in the two populations we studied, and because at least one site appeared as a deactivation for body parts rather than a selective activation for numbers, interpretation should be cautious. Yet the results are consistent with previous brain-imaging studies of calculation, which all reported intense and extended parietal activation at similar loci during mental arithmetic tasks such as comparison, multiplication, subtraction, or approximation (Chochon *et al.,* 1999; Dehaene, 1996; Dehaene *et al.,* 1999, 1996; Pesenti *et al.,* 2000; Pinel *et al.,* 1999; Roland and Friberg, 1985; Rueckert *et al.,* 1996) (see Fig. 3).

In those earlier studies, parietal activity was always bilateral. However, a recent fMRI study, which contrasted number comparison with a non-semantic task

of number naming revealed a single focus of activation in the right postcentral sulcus, very close to the one reported here (Chochon *et al.,* 1999). Event-related potentials also indicate that the distance effect in number comparison originates mostly from the right parietal region (Dehaene, 1996). Finally, although acalculia is largely caused by lesions of the left parietal region, the simple task of number comparison is generally preserved in such cases (Dehaene and Cohen, 1995) and, contrarily, there is evidence that right parietal lesions can cause deficits in understanding relations between numbers (Langdon and Warrington, 1997; Rosselli and Ardila, 1989). Thus, the observed right lateralization of parietal activity in the present work may have been enhanced by our reliance on a simple number comparison task. Our current working hypothesis is that the right intraparietal region is associated with the encoding and manipulation of quantity relations between numbers (Dehaene *et al.,* 1998).

Possible sources of artifact. The consistency of the results with previous findings, and the systematicity of the observed differences in activation across different conditions make artifactual explanations of our results unlikely. The masking strategy that we used to analyze the data implies that the regions we report showed a significant advantage for a given semantic category, in both languages and in both modalities of presentation. This rules out any explanation of our findings that do not also apply across categories and languages. For instance, we were only partially successful in controlling for task difficulty, because response times were generally slower for body parts than for numerals. However, this task difficulty effect was not systematic, since in experiment 1 it was not found in the auditory modality. Because all brain areas reported here still showed a significant category effect ($P < 0.05$) with auditory stimuli, task difficulty cannot be the sole determinant of our results. Similarly, although there were some unavoidable frequency and length differences between the stimuli, none of them were systematically present across both languages and modalities, and thus none of them may explain our finding of systematically greater activation for one category of words.

One might suggest that the activation differences are due to a more general processing difference between abstract and concrete words, numbers being more abstract concepts than body parts. However, this seems unlikely, given that the concrete-abstract dimension is only known to affect right anterior temporal activation in regions quite distant from those observed here (Kiehl *et al.,* 1999). Similarly, it could be argued that subjects made use of visual imagery during the body part task, but not the number task. Thus, the activations would be related to the exploration of a concrete visual "body image" rather than a more abstract "body schema." Yet the fast response times and the absence of ventral visual activation typically observed during mental imagery of concrete words (D'Esposito *et al.,* 1997; Mellet *et al.,* 1998) go against the hypothesis of a strong contribution of generic visual imagery processes to the body-part task. It could still be argued that the parietal lobes contain a specific substrate for manipulating visual images of the body as opposed to other contents of visual imagery. While this cannot be excluded, it seems presently indistinguishable from the concept of an abstract semantic representation of the spatial relations between body parts. Both concepts of "body schema" and "body image" would have to be further elaborated theoretically before any sharp empirical distinction between them can be drawn (for discussion, see Bermudez *et al.,* 1995).

Finally, some of the activation for body parts could be related to a general process of part-whole segregation, an operation which would not be necessary for numbers. Yet, the existence of patients with selective deficits for body parts, but in whom the processing of part-whole relationships was demonstrably intact in other semantic domains, suggests that this interpretation, though it may apply to our data, cannot account for the full set of data on body-part knowledge (Goodglass and Budin, 1988; Suzuki *et al.,* 1997).

One limit of our study is that only a single task was used. The comparison task used here may have emphasized the metric properties of the mental representations of numbers and body parts. When subjects compare Arabic numerals, their performance improves when the numerical distance between the numbers increases, suggesting that the input numerals have been mentally converted into a notation-independent representation from which distance information can be recovered (Dehaene, 1989; Moyer and Landauer, 1967). We also have evidence that a similar distance effect holds when subjects judge the relative height of two named body parts (Le Clec'H and Dehaene, in preparation). Both effects suggest that, in the comparison task, given the name of a number or body part, subjects retrieve information about its metrical relations to other members of the category. Thus, the observed activations, particularly in the parietal lobe, might reflect more general metrical manipulation processes rather than category-specific regions. In future studies, it would therefore be desirable to examine whether the same regions still differentiate numbers from body parts when nonmetrical tasks are used.

We close this discussion by briefly considering the left insular/supramarginal region, an activation site that was found associated with number processing in experiment 1, but failed to be fully replicated in experiment 2 (although activations were seen in these regions at a lower threshold). In the left hemisphere, these regions have been related to verbal phonological

and/or articulation processes (Dronkers, 1996; Paulesu *et al.,* 1993; Price, 1998). A simple confound of the number comparison task may explain why there was greater phonological processing during the number than during the body part blocks. In both English and French, number words have regular word endings which correlate with number size. All French words ending with -ze or -ante, and all English words ending with -teen or -ty, can be readily classified as larger than 12. Thus, subjects might have partially performed the number task, not by using a semantic representation of quantity, but by relying on a phonological recoding strategy which would have caused left insular and supramarginal activation.

CONCLUSION

Our result demonstrate that names of numbers and body parts, even when presented in the context of similar comparison tasks, activate partially distinct cortical areas. In the parietal lobe, in particular, our findings concur with previous neuropsychological suggestions that the two categories, even though frequently affected simultaneously by brain lesions, can be dissociated and therefore rely on partly distinct areas. This dissociation, however, must be occurring in the context of a very large shared activation in both left and right parietal lobes (see Fig. 3). Our results therefore provide a partial reconciliation of both sides of the classical neuropsychological debate on Gerstmann's syndrome by suggesting that there is both a vast set of shared areas, whose exact function could not be established with the present experimental design, and a small subset of areas with a high degree of category-specificity for number versus body part processing.

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