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Naming actions and objects: cortical dynamics in healthy adults and in an anomic patient with a dissociation in action/object naming

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Abstract

Neuropsychological studies have demonstrated that the production of nouns and verbs can be dissociated in aphasia. These reports have been taken as evidence for separate representations of nouns and verbs in the human brain. We used whole-head magnetoencephalography to record cortical dynamics of action and object naming in 10 healthy adults and in 1 anomic patient with superior naming of verbs compared with nouns due to a left posterior parietal lesion. A single set of 100 line drawings was used for both action and object naming. In normal subjects, the activation sequences in action and object naming were essentially identical, advancing from the occipital to posterior temporoparietal and further to the left frontal cortex, without consistent involvement of the classical left inferior frontal (Broca) and temporal (Wernicke) language areas. In the anomic patient, pronounced differences between action and object naming emerged in the left hemisphere. The activation sequence was disrupted at the level of the damaged parietal cortex and did not reach the left frontal cortex even in the relatively easier action naming. The more severely impaired object naming was associated with exceptionally strong and early activation of the left inferior frontal cortex (Broca) and subsequent pronounced activation of the left middle temporal cortex, silent in action naming. Verb and noun retrieval thus utilized a spatiotemporally similar neuronal network in healthy individuals. A clear dissociation in cortical correlates of verb and noun retrieval only became evident in our anomic patient, in whom damage to the language network has resulted in disproportionately worse performance in object than action naming.

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Introduction

An impressive corpus of experimental data has been accumulated during the past decades concerning the retrieval and processing of lexical concepts and word forms within the brain. One of the most challenging findings was that in brain-damaged patients with aphasia the production of nouns and verbs could be impaired in a differential way. These results motivated a discussion about the internal organization of the lexical system: is the processing of nouns and verbs characterized by functional differences in similar neuroanatomical networks for both classes? Or does the

mental lexicon recruit anatomically distinct cortical representations for these word classes?

Although the first known report of an aphasic patient with a selective impairment of verbs compared to nouns is more than 250 years old (Denes and Dalla Barba, 1998), word-class-specific language deficits have only recently received broader attention. Several investigators have described patients with verb production impairments and a relative sparing of nouns (Miceli et al., 1984; McCarthy and Warrington, 1985; Williams and Canter, 1987; Caramazza and Hillis, 1991; Damasio and Tranel, 1993; Daniele et al., 1994; Manning and Warrington, 1996; Berndt et al., 1997; Breedin et al., 1998; Marshall et al., 1998). For normal speakers, verbs in general are frequently believed to be more difficult than nouns (Berndt et al., 1997). They have a greater range of meanings and a more complex syntactic structure. The hypothesis, however, that verbs are more prone to language deficits in aphasia simply due to their

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inherent complexity had to be abandoned when patients were presented who showed the opposite behavior, i.e., the superiority of verb to noun production (Miceli et al., 1984; Damasio and Tranel, 1993; Daniele et al., 1994; Miozzo et al., 1994; Berndt et al., 1997). Miceli et al. (1984) were the first to describe a correlation between the type of aphasia and word-class-specific language impairments. In their study on Italian-speaking patients, agrammatics demonstrated a worse production of verbs compared with nouns, while anomics had a worse production of nouns compared with verbs. Similar results were found in studies with Chinese- (Bates et al., 1991) and English-speaking aphasics (Berndt et al., 1997). Although most reports of selective verb deficits are on agrammatics, verb impairment is clearly not restricted to this type of aphasia, but can be observed in fluent aphasia as well (Caramazza and Hillis, 1991; Breedin et al., 1998).

Lesion studies have also suggested anatomical loci for category-specific deficits. Nearly all stroke patients with selective verb deficits which were investigated by computed tomography or magnetic resonance imaging (MRI) show frontal lesions, while those with selective noun impairment have temporal lesions (Damasio and Tranel, 1993; Daniele et al., 1994; Miozzo et al., 1994; Breedin et al., 1998).

In the present study we tested whether cortical dynamics, as measured by whole-head magnetoencephalography (MEG), are different during the production of verbs and nouns under normal conditions and in a case of word-class-specific anomia. We used the same set of simple line drawings for both action and object naming in 10 healthy subjects and 1 anomic patient with superior naming of verbs compared to nouns. Picture naming is a well-established paradigm in cognitive neuroscience and involves all levels of language production (Levelt et al., 1998). It has been employed successfully in behavioral and MEG studies (Glaser, 1992; Salmelin et al., 1994; Levelt et al., 1998). MEG is an excellent tool for investigating cortical activation during picture naming since it combines good spatial accuracy with excellent temporal resolution.

Methods

Participants

Ten healthy male university students or graduates (age 23–34 years, mean 27 years) and one 46-year-old aphasic male (JP) participated in this study. In November 1997 JP suffered from an embolic infarction in the posterior territory of the left middle cerebral artery. The MR images obtained 2 years after the stroke show a left-side cortical lesion in the posterior parietal and the superior temporal lobe (the lesion is displayed in Fig. 7). Based on the hospital records, he evidenced a conduction aphasia after the stroke. His aphasia improved moderately since then. At the time of this study (2 years poststroke), he had a residual aphasia with anomia and

tendency for producing phonological errors. Slight impairment of comprehension and severe impairments of naming and repetition of sentences characterized JP's language performance. His speech was relatively fluent, but included paraphasic expressions and empty words. His production of nouns was severely impaired, while his production of verbs was better spared. He had neither visual nor other cognitive impairments or other diseases.

All healthy subjects and the aphasic patient were strongly right-handed as indicated by a modified version of the Edinburgh Handedness inventory (handedness scores 90–100, mean 97) (Oldfield, 1971), were native speakers of Finnish, and had grown up in a monolingual family. All subjects gave their informed consent to participate in the study. The participation of JP was approved by the ethical committee of the Turku University Central Hospital.

Language tests

To characterize the type and severity of JP's aphasia and to assess the dissociation in action vs object naming, several behavioral tests were employed. The standardized Finnish version of the Boston Diagnostic Aphasia Examination (BDAE) (Laine et al., 1997b) and the Finnish version of the Boston Naming Test (BNT) (Laine et al., 1997a) were used to describe his general linguistic performance and the severity of anomia. The BDAE includes a short subtest to screen the performance level in action vs object naming. A specially designed picture naming task (the experimental pictures, see below) was employed to verify JP's superior performance on actions compared with objects.

In addition, JP's object naming impairment was assessed further by tasks taken from an experimental naming-related test battery (Laine et al., 1992, 1997c). The following tests were administered: (1) Odd-out test. Twenty sets of five drawings of objects were shown to the patient. Four of the pictures shared common semantic features in 15 of 20 sets. The remaining picture differed from the other alternatives at the within-category level (for example tiger, giraffe, camel, and lion are semantically closer to each other than any one of them to a pig). Five sets were made easier by introducing the semantic mismatch more clearly, that is, at the superordinate level (for example, knife, spoon, fork, and glass vs telephone). The name of each object was written underneath the picture to aid in the recognition process. In this test a strong semantic memory component is included, since the patient must judge which items form a semantic cluster and which item is an outlier. (2) Triad test. In this test the patient had to form a semantically matching pair from a selection of three pictures depicting various objects. This time written names of the objects were not given. The semantic categories used were the same as in the odd-out test. Items differed only at the within-category level. Eight picture sets of living objects and eight picture sets of nonliving objects were presented in this task. (3) Word-picture matching with objects. The target word was shown on top and five pictures

underneath it. The task was to associate the word with one of the pictures. In one matrix, two to three different semantic categories were used. The names of 24 living and 24 nonliving objects were presented in this task. (4) Naming test with simultaneous multiple-choice tasks. First, the subject had to name the picture depicting an object. Second, he had to choose the corresponding superordinate of eight alternatives (e.g., fruit for apple). Third, he had to judge which of the four meaning-related statements was most appropriate to describe the picture. Fourth, he had to judge how many letters the target word included. Finally, he had to choose the first syllable of the target word amongst five alternatives. All together 106 items were studied in this manner.

Laine et al. (1992) reported the performance of five neurologically intact 50 to 70 year-old individuals with only compulsory education on experimental naming tasks 1–4. Given the easiness of the tasks, their performances were close or at the maximum. These tasks were thus not administered to the healthy subjects studied here.

Stimuli and task for MEG measurements

One hundred simple and easily illustrable scenes were designed, each including simultaneously an object and an action. The actions were either performed on the object (e.g., a man smoking a pipe; 89 scenes) or by the object (e.g., a dog barking; 11 scenes). The object to be named was highlighted by thicker line type. The use of the same stimuli for action and object naming ensured identical visual input during both conditions. The depicted objects and actions were represented by Finnish words of mostly medium to high word frequency. The naming consistency for all objects and actions was evaluated by six graduate students. A scene was excluded when fewer than five subjects named the intended noun or verb.

The verbs and nouns illustrated in one scene always had different word stems, i.e., pairs like *vasara* (the hammer) and *vasaroida* (to hammer) were not used. The word frequency was checked using the WordMill lexical search programme (Laine and Virtanen, 1999) employing an unpublished computerized lexical database which includes 22.7 million word tokens from a major Finnish newspaper (Turun Sanomat). The cumulative stem frequency range was 0–624 per million words for the nouns (mean \pm standard deviation (SD); 63 ± 112) and 0–1510 per million words for the verbs (142 ± 274). The word length was 3–9 letters for the nouns (5.6 ± 1.3) and 4–11 letters for the verbs (6.8 ± 1.4). There was no significant difference in the word stem frequency or word length between verbs and nouns (Mann–Whitney *U* test, $P < 0.05$). For each scene a clear black and white line drawing was made by a skilled cartoonist (for examples see Fig. 1).

All subjects were instructed on the task and were shown three target pictures to familiarize them with the paradigm before the MEG measurement. During the measurement, a

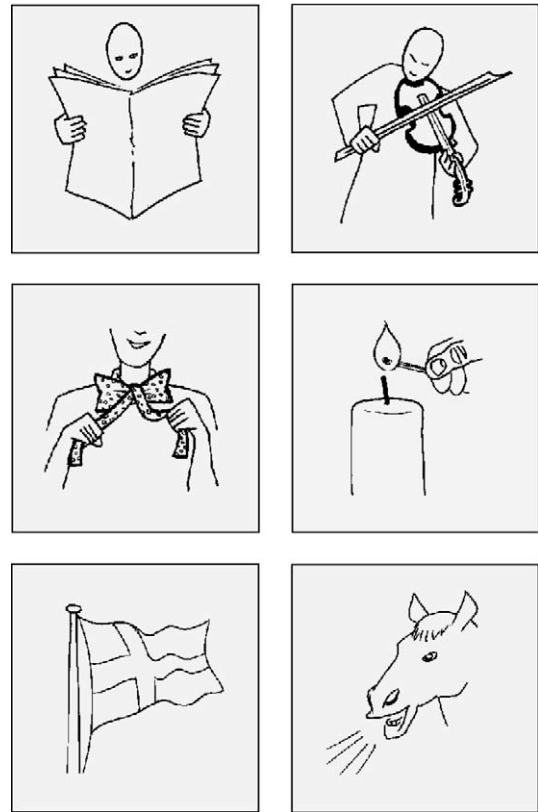


Fig. 1. Examples of the line drawings used as stimuli for action and object naming. The drawings illustrate a simple scene including an object and an action. A total of 100 different pictures were used.

short word prompt for the required answer was shown for 300 ms (either *tekee* = does or *esine* = object), instructing the subject to concentrate either on the action or on the object depicted in the following picture. Both words used for the instruction are familiar Finnish expressions and have an identical word length. After a blank interval of 300 ms, the picture was presented for 300 ms (sequence 1). This stimulation sequence was used for all 10 normal subjects. Fig. 2 gives a schematic illustration of this paradigm. Subjects were told to vocalize the required verb or noun as quickly as possible after picture onset.

The rapid changes of action and object naming, required in sequence 1, proved to be too complicated for patient JP. Thus, two different sequences without changes of the task were created. In sequence 2, all pictures were presented with the prompt “tekee” (=is doing). In sequence 3, all pictures were preceded by the prompt “esine” (=object). The timing of the prompt, picture presentation, blank intervals, and vocalization period were identical with sequence 1. In all sequences, a different pseudo-random order of pictures was employed. Prior to the start of sequences 2 and 3, patient JP was told that this measurement would require only object naming or action naming, respectively. In JP, the stimulus set was run twice in both sequence 2 and sequence 3 to increase the signal-to-noise ratio. To ensure that the brain responses during sequence 1 and sequences 2

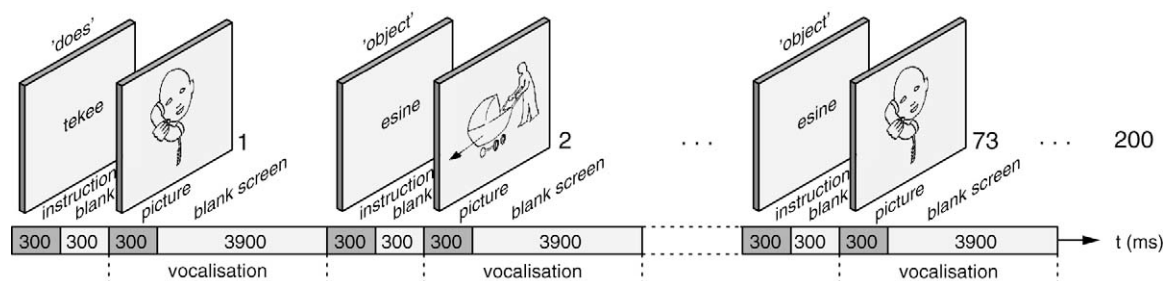


Fig. 2. Schematic illustration of the action and object naming experiment (sequence 1). After the onset of picture presentation, subjects were allowed 4200 ms to vocalize the required answer. The interval between epochs was 4800 ms.

and 3 were comparable, sequences 2 and 3 were also performed in five normal subjects. Two normal subjects completed sequence 2, two subjects completed sequence 3, and one subject completed sequences 2 and 3, always following sequence 1.

To verify JP's dissociation of action and object naming behaviorally and to investigate the stability of his naming performance, the action and object naming tasks were administered to him a few days before and after the MEG experiment in a silent room without MEG recording (Table 1). For these purely behavioral tests the same pictures were used in a different order than in the MEG sequences 2 and 3. The other parameters of picture presentation were identical during the behavioral tests and the MEG experiment.

MEG data acquisition

Neuromagnetic signals were recorded with the Vectorview whole-head MEG system (Neuromag, Helsinki, Finland). The system contains 102 triple sensor elements arranged on a helmet-shape detector array which covers the head. Each sensor element comprises two orthogonal planar gradiometers and one magnetometer. The sensor array is thus made of 204 gradiometers and 102 magnetometers, with 306 channels in total. Since MEG is most sensitive to currents of cortical neurons tangential to the surface of the brain, the recorded magnetic signals mainly reflect the activity of fissural cortex (Hämäläinen et al., 1993). In this study, the analysis was done on the data recorded by planar gradiometers which detect the maximum signal directly above the activated cortical area and which are less sensitive to external noise than the magnetometers.

Measurements were performed in a magnetically shielded room (Euroshield, Helsinki, Finland). Subjects were seated in a chair with their heads inside the sensor helmet of the MEG system. They were told not to move their heads during the measurement and to fixate their eyes on a back-projection screen placed 1 m in front of them. The pictures and the prompts were projected on the screen by a VistaPro data projector located outside the measurement room. MEG signals were recorded using a 0.03- to 100-Hz filter and sampled at 600 Hz. In addition to the continuous MEG signals, vertical and horizontal electro-oculogram

(EOG) and the signal of a small microphone near the subject's head were registered and stored on a magneto-optical disk for off-line analysis. Furthermore, the subject's oral responses were recorded on a digital audiotape.

Data analysis

The reaction times for verbs and nouns were determined separately as the latency between picture onset and onset of vocalization. The mean and SD of all response latencies were computed for each subject. Responses outside a time window of $\text{mean} \pm 2 \text{ SD}$ were excluded from further analysis. Reaction times are presented as geometric means $\pm \text{SD}$.

Since our picture sample contained 11 pictures with one object and 89 pictures with two or more objects, we performed a post hoc analysis to investigate the possible influence of object number on response latency. We compared the reaction times for verbs and nouns in those 11 pictures with only one object and in a randomly assigned subset of 11 pictures with multiple objects. In JP, correct answers were analyzed both for the purely behavioral action and object naming task and for the MEG sequences. As the naming latencies were not normally distributed, the non-parametric Wilcoxon signed-ranks test was performed to compare naming latencies for verbs and nouns. $P < 0.05$ was regarded as significant.

The magnetic brain responses were averaged off-line between -800 and 1500 ms with respect to picture onset, separately for action and object naming. A 200-ms period before the onset of the instruction (-800 to -600 ms of the analysis window) was used as the baseline. Epochs contaminated by eye or eyelid movements as indicated by EOG were rejected from averaging (EOG signal exceeded $150 \mu\text{V}$). Epochs containing no verbal response (in patient JP) or verbal responses outside the time window of mean reaction time $\pm 2 \text{ SD}$ were excluded as well. To reduce artifacts due to mouth movement, the characteristic artifact pattern was identified from MEG signals averaged with respect to the onset of vocalization. The onset of vocalization was determined by the onset of the acoustic signal as recorded by the microphone. We were able to identify a characteristic, bilateral artifact pattern during vocalization which was most

Table 1
Performance of patient JP in the background language tests and in the experimental picture naming task

Language test	Raw scores	% correct
1 Finnish version of the Boston Naming Test (BNT)	17/60	28
2 Finnish version of the Boston Diagnostic Aphasia Examination (BDAE)		
language comprehension	221/238	93
reading comprehension	60/72	83
reading aloud	60/80	75
speech repetition	22/52	42
visual confrontation naming	87/114	76
naming actions	18/18	100
naming objects	3/18	17
naming letters	18/18	100
naming digits	18/18	100
naming shapes	3/6	50
naming colours	15/18	83
naming body parts	12/18	67
responsive naming	20/30	67
naming actions	6/9	67
naming objects	6/12	50
naming digits	2/3	67
naming colours	6/6	100
3 Triad test		
living objects	6/8	75
non-living objects	6/8	75
4 Word-picture matching		
living objects	24/24	100
non-living objects	24/24	100
5 Naming test with simultaneous multiple-choice tasks		
naming the picture	32/106	30
identification of the superordinate	99/106	93
identification of a semantic feature relevant to the picture	84/106	79
identification of the length of the word	65/106	61
identification of the first syllable	82/106	77
identification of the written word	97/106	92
6.1 Picture naming before MEG measurements		
naming actions	46/82	56
naming objects	30/82	37
6.2 Picture naming during MEG measurements		
naming actions	71/164	43
naming objects	54/164	33
6.3 Picture naming after MEG measurements		
naming actions	40/82	49
naming objects	24/82	29

pronounced in the inferior sensors, near the rim of the MEG helmet. The field pattern of this artifact was modeled for each subject separately at the time point of least simultaneous brain activity and removed from the MEG averages using the signal space projection method (SSP) (Uusitalo and Ilmoniemi, 1997). After the individual artifact pattern was removed, the original and the processed waveforms were superimposed. Visual inspection of these curves revealed that only the artifact field pattern had been removed and no other aspects of the MEG waveforms had been affected. In four control subjects, frequent eye blinks oc-

curred. In those four subjects, epochs contaminated by eye blinks were not rejected. Instead, the eye-blink-related artifact field, as determined from MEG signals averaged with respect to blink onsets, was removed by SSP. A low-pass filter of 40 Hz was applied off-line before further analysis.

The sources of cortical activity were modelled as equivalent current dipoles (ECD) in a spherical volume conductor. The location, orientation, and amplitude of the dipole represent the center of gravity of the activated cortical area and the direction and strength of the measured current flow. The sphere model for the volume conductor was constructed for each subject using his individual MRI, with the highest accuracy at the lateral curvatures of the brain. In each subject, 8–11 single dipoles were modeled at the time points of the clearest dipolar field patterns using subsets of MEG sensors (10 to 20 sensors). The single dipoles were then introduced into a multidipole model, keeping their locations and directions fixed while their strengths were allowed to vary to achieve optimal explanation of the magnetic signals measured by all 204 gradiometers. The MEG responses to action and object naming were modeled separately. Since visual inspection of the original magnetic waveforms and of the derived source models revealed very similar activation patterns under both experimental conditions, a single set of ECDs was selected for each subject from both source models which best explained the magnetic responses in both conditions. The individual source models developed for sequence 1 were also adequate for data collected with sequences 2 and 3 in the same subjects; after source modeling no unexplained brain activity of dipolar distribution was found.

Regarding significant amplitude and latency differences between action and object naming, we accepted only sources which had their maximum amplitude after picture onset. For all those sources, we first determined the standard deviation during the baseline period and the peak amplitude and latency. After that, we also determined the half-value latency, i.e., the latency at which the source strength (amplitude) was at 50% of its maximum on the ascending side, and the onset latency, i.e., the latency at which the source strength exceeded the level of 2 SD.

For group analysis, five regions of interest (ROIs) were defined (for details of the anatomical borders, see Results). Previous studies demonstrated that brain activity during picture naming advances from occipital to frontal areas (Salmelin et al., 1994, Levelt et al., 1999). Based on the anatomical and temporal results of these studies and on the source clusters found here, we defined the (posterior) temporoparietal ROIs L1 and R1 by grouping the sources which were found in the bilateral temporoparietal cortices and which were active 200–400 ms after picture onset. Similarly, we defined the (anterior) ROIs L2 and R2 and the left occipital ROI OCC by grouping the sources which were active in frontoparietal and occipital areas 400–800 ms after picture onset.

If one subject contributed more than one source to a single ROI, only the source which first reached its maximum was included in the analysis. This was done in order to minimize problems inherent in selecting an unequal number of sources per subject. As the latencies of cortical sources were not normally distributed, statistically significant differences between action and object naming were assessed using the nonparametric Wilcoxon signed-ranks test with $P < 0.05$. Correlations between the individual source latencies in the ROIs and the vocal reaction times were assessed by calculating Spearman's correlation coefficient ρ because the two variables were not normally distributed.

We also evaluated significant differences between action and object naming in these ROIs at the individual level. For peak amplitudes to differ significantly, a difference of at least 2 SD of the baseline variation was required. Only source latencies with a minimum difference of six sampling points were considered significant. Based on the sampling rate of 600 Hz, this corresponds to differences of at least 10 ms. The half-value latencies can be assessed with the highest accuracy and therefore were tested first. Peak latencies tend to be less well defined especially for sustained activity and they were tested only if no significant differences emerged in the half-value latencies.

Since patient JP was only able to name correctly 71 of 164 actions and 54 of 164 objects presented during the MEG experiment, six different MEG data sets were processed in his case. The first two data sets included all collected responses for action and object naming, data sets 3 and 4 contained only correct action and object responses, and data sets 5 and 6 included only responses with reaction times within a time window of the mean reaction time for actions and objects 2 SD. All data sets were analyzed separately. For the analysis of evoked fields, the average of all correct responses was used. However, the same set of ECDs accounted for signal variation in all data sets.

MEG–MRI integration

For anatomical localization of the activated cortical areas, MEG sources were projected onto the individual T1-weighted MRIs which were available for all subjects. Before the MEG measurement, four small coils were fixed on the subject's head. The relative position of these coils with respect to three anatomical landmarks on the head (nasion as well as left and right preauricular points) were determined using a three-dimensional digitizer (Isotrak, Polhemus, Colchester, VT, USA). At the beginning of the MEG measurement, the position of the coils with respect to the sensor array was determined by energizing the coils briefly. After identification of the anatomical landmarks in the MRI data set, the locations of the individual ECDs were superimposed on axial, coronal, and sagittal slices. To compare the sources across subjects and experimental condi-

tions, the ECD locations of all subjects were projected onto one surface-rendered brain image.

Results

Language tests in JP

The results of the language tests administered to the aphasic patient JP and his performance level on action vs object naming during the MEG measurements are presented in Table 1. JP's naming disturbance was of moderate severity (Table 1, Tests 1 and 2) and with a primarily phonological component, indicated by difficulties in determining word length and first syllable of items (Test 5). He had also some semantic impairment, as indicated by difficulties in detecting properties related to objects (Test 5). Naming disturbance was not limited to a specific semantic category, and there was no dissociation between naming animate vs inanimate objects (Tests 2, 3, and 4). In naming tasks, JP produced several semantic errors of which he was mostly unaware. He also produced phonological errors, which he was unable to correct. Visual confrontation naming in the BDAE and naming performance tested with the pictures made for this study revealed superior action naming compared to object naming. On this basis, the diagnosis of a dissociation of action vs object naming was made, which has been supported by naming tests using the stimuli made for this study.

In the purely behavioral experiment before the MEG measurement, 56% of actions and 37% of objects were named correctly ($\chi^2 = 4.384$; $P = 0.036$). In the purely behavioral measurement shortly after the MEG measurement, 49% of actions and 29% of objects were named correctly ($\chi^2 = 4.970$; $P = 0.026$). During the MEG measurement, the difference in action vs object naming was less marked, since 43% of actions and 33% of objects were named correctly ($\chi^2 = 3.736$; $P = 0.053$).

Reaction times

The vocal reaction times for action and object naming in normals and in patient JP are displayed in Table 2. All healthy subjects named at least 92% of the pictures correctly. Action naming was faster in 9 of 10 normal subjects during sequence 1 (mean \pm SEM, 30 ± 10 ms; $P < 0.001$). When only actions (sequence 2) or objects (sequence 3) were named, all normals were faster than during the mixed sequence 1 (range of difference between sequence 1 and sequence 2 or 3 was 20–310 ms). In a post hoc analysis of healthy participants comparing pictures showing only one object with pictures depicting multiple objects, no significant difference in reaction times was found either for verbs or for nouns.

When all vocal responses were counted, patient JP was considerably slower than the normal subjects in action and

Table 2
Reaction times (ms) for action and object naming in normal subjects (n = 10) and in patient JP

Subject	Action naming (sequence 1)	Object naming (sequence 1)	Action naming (sequence 2)	Object naming (sequence 3)
<i>Normal subjects</i>				
s1	1050 ± 350	1060 ± 310		
s2	1130 ± 540	1100 ± 370	910 ± 310	
s3	830 ± 170	870 ± 190	710 ± 110	
s4	960 ± 300	1010 ± 340	940 ± 220	940 ± 320
s5	1050 ± 300	1130 ± 310		910 ± 190
s6	1310 ± 480	1360 ± 380		1050 ± 220
s7	1260 ± 310	1300 ± 430		
s8	940 ± 300	970 ± 310		
s9	970 ± 340	1020 ± 430		
s10	1160 ± 320	1200 ± 380		
Mean ± SD	1070 ± 150	1100 ± 150	850 ± 130	970 ± 70
<i>Patient JP</i>				
All responses			2140 ± 820	2300 ± 870
Correct responses run 1			1390 ± 1080	1660 ± 1070
Correct responses run 2			1430 ± 1130	1760 ± 1340

Note. Individual data is presented as geometrical mean ± standard deviation (SD), group average is presented as arithmetic mean ± SD.

object naming (sequence 1), action naming (sequence 2), and object naming (sequence 3). When only correct responses were included in the analysis, the difference in reaction times between normals and the patient decreased, but JP remained clearly slower than the controls. For the two presentations of the same stimuli in the MEG session, JP was consistently faster in naming actions than in naming objects (difference in the first measurement 270 ms, in the second measurement 330 ms; Table 2) which is in line with his dissociation of action vs object naming.

Evoked responses

The results of MEG source analysis demonstrated that within each individual, the same cortical areas were activated during action and object naming. Thus, a single source model in each individual sufficed to describe the measured brain activity during both conditions. Evoked magnetic fields, as detected by the planar gradiometers, and the source model of one normal control are shown in Fig. 3. The spread of cortical activation from occipital to temporal and frontal areas was overall similar in all normal subjects, but the exact anatomical locations, timings, and activation strengths of the source areas varied among individual subjects.

The source model developed for sequence 1 (action and object naming in a pseudo-random order) was also adequate to describe the brain responses in sequences 2 and 3 (exclusive action or object naming). The right frontoparietal sources tended to be activated earlier during exclusive action or object naming than during the mixed sequence. Fig. 4 illustrates the similarity of the responses to action vs object naming during randomized presentation and during categorical presentation in the subject who performed all these sequences.

Fig. 5 displays all source areas of the normal subjects with peak latencies within the time windows of 0–200, 200–400, and 400–800 ms on the surface of a 3D reconstructed MRI. Within the first 200 ms after picture onset, mainly early visual sources were active. During the next 200 ms (200–400 ms postpicture onset), activation spread to areas around the posterior part of the sylvian fissure of both hemispheres. Isolated sources in the left frontal and the bilateral occipital cortices were active at this time, too. At 400–800 ms after picture onset, source clusters were found in the left and right frontoparietal cortex as well as in the left occipital cortex.

Based on the spatiotemporal clustering of individual sources (see Fig. 5) and on anatomical borders, five ROIs were defined for the analysis of systematic amplitude and latency differences: left posterior region (L1), including the posterior part of the superior temporal gyrus, the angular gyrus, the supramarginal gyrus, and anterior parts of the inferior parietal lobule; left anterior region (L2), including the postcentral gyrus, the precentral gyrus, and the posterior part of the middle frontal gyrus; right posterior region (R1), and right anterior region (R2), including the corresponding areas in the right hemisphere, as well as occipital region (OCC), including the medial part of the left occipital cortex (Fig. 5). Only sources which reached their maximum after 300 ms were included in L2. To exclude early visual responses from OCC, this ROI comprised sources which reached their maximum after 400 ms. For further analysis, only one source per subject, the one which showed the earliest maximum, was accepted in each ROI (see Methods).

The mean peak latencies for action and object naming during stimulus sequence 1 in the five different ROIs are presented in Fig. 6. In the group analysis, no statistically significant latency differences between the two conditions

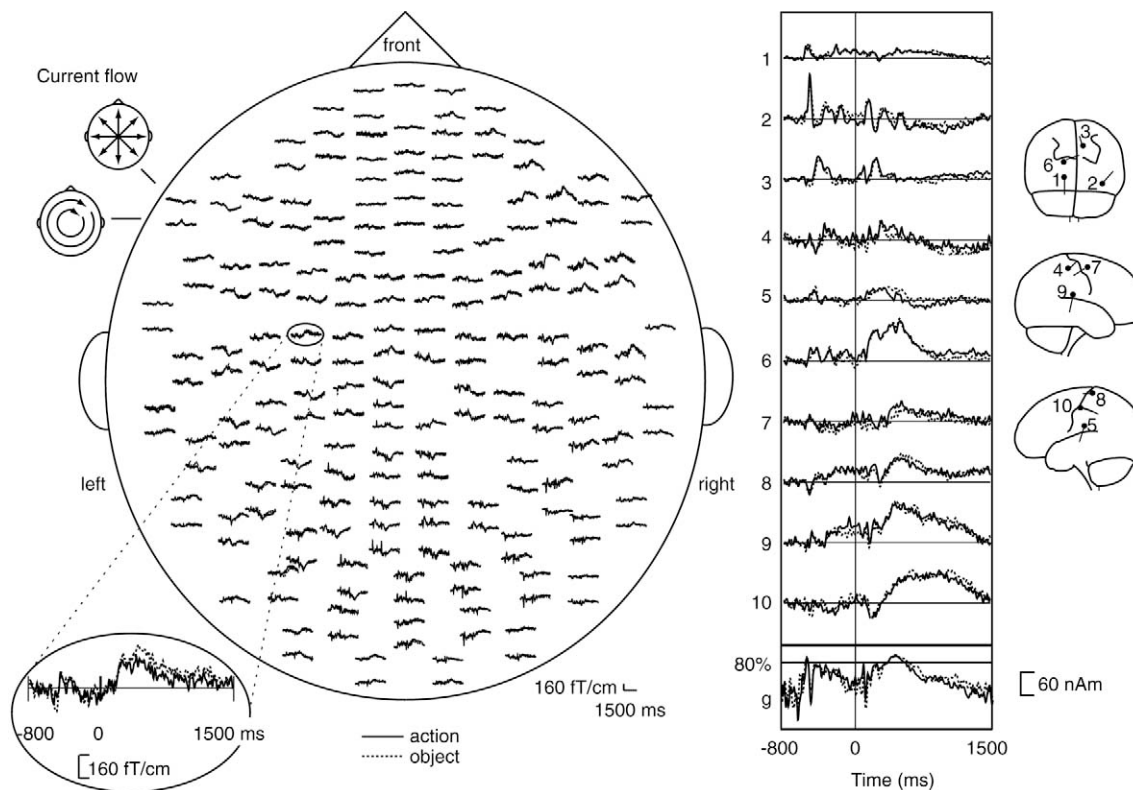


Fig. 3. MEG responses and the source analysis of one healthy subject (s3). Left: MEG signals were averaged in the time window -800 to 1500 ms with respect to picture onset. The helmet-shape sensor array of the Vectorview is flattened to a plane and is viewed from above with the nose pointing upward. Variation of the magnetic field (in femtotesla per centimeter, fT/cm) is shown on the vertical axis. At each measurement location, signals of two overlaid planar gradiometers are shown. The upper sensor is most sensitive to longitudinal currents and the lower sensor to latitudinal currents, as illustrated on the schematic heads in the upper left corner. Brain responses during action naming (solid lines) and object naming (dashed lines) are superimposed. The signals of one sensor are enlarged in the lower left corner. Right: Source analysis with altogether 10 ECDs. The vertical axis displays the source strength (in nanoamperemeter, nAm). The goodness-of-fit value (g) is shown below. The location and orientation of each source are depicted on a schematic brain surface.

were found nor were there any significant correlations between the source latencies in the five ROIs and the vocal reaction times. At the individual level, occasional spatially and temporally scattered differences between action and object naming were seen in source strength and latency. A fairly systematic difference was detected in L2, where seven of nine subjects showed a faster response to action than object naming (difference 15 – 430 ms, median 85 ms). At the group level, the difference did not reach significance.

The results of the source analysis for patient JP are illustrated in Fig. 7, representing the average of all correct responses. As in normals, brain activation during action naming spread from posterior to anterior areas in both hemispheres. Sources were found in the left occipital cortex, in the right parietotemporal cortex, and in the language-related areas of the left hemisphere. The same set of 10 dipoles was adequate to describe activity in both action and object naming. The timing and location of the left occipital sources was very similar to those in the normal subjects, with no differences between action and object naming.

Significant differences in activation strength between action and object naming emerged in four source areas: action naming was accompanied by a 39% stronger re-

sponse in the left angular gyrus (source 2; activation in the L1 area was found in 6/10 controls, significant action–object difference in 3 sources, 12–27%). During object naming, a stronger and earlier response was seen in the left inferior frontal cortex, approximately Broca's area (source 7, difference 45%; same area in 3/10 controls, significant action–object difference in 3 sources, 14–22%), and in the left superior parietal cortex (source 6, difference 27%; L1 area in 6/10 controls, action–object difference 12–27%). The late activation of the left middle temporal cortex was evident for object naming but not for action naming (source 10, difference 100%; same area in 3/10 controls, significant action–object difference in 2 sources, 16–25%). Action vs object differentiation in source areas 2, 7, and 10 thus clearly exceeded the normal range.

During action naming, Broca's area became active only after the signal in the angular gyrus had reached its maximum, whereas during object naming, these two source areas were active simultaneously. The three source areas in JP's right hemisphere, including the strongly activated right superior temporal gyrus, showed no differences between action and object naming. In contrast to the majority of the normal subjects, JP did not activate the left anterior ROI L2.

Discussion

We conducted a picture naming experiment on 10 normal subjects and 1 aphasic patient and recorded magnetic brain activity during the naming of actions and objects. Our results suggest that the cortical dynamics related to action and object naming are very similar in space and time under normal conditions. A single complex network covering wide areas of both hemispheres is active during retrieval of

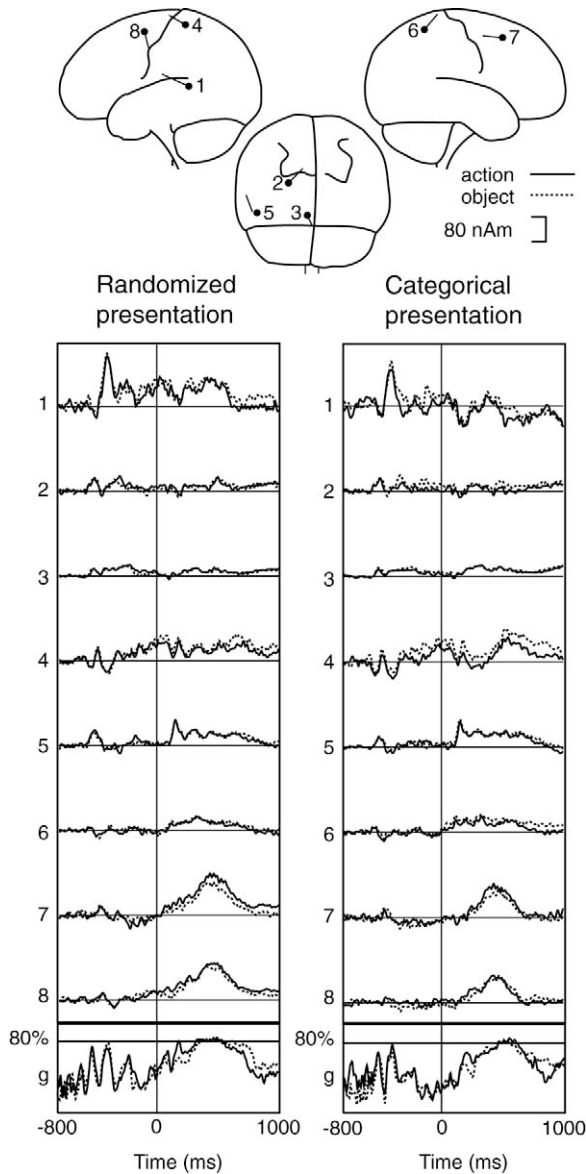


Fig. 4. MEG source waveforms of a healthy subject (s4) for sequences 1, 2, and 3. Top: Source locations on schematic illustrations of brain surface. Left: Source waveforms during action vs object naming in sequence 1, i.e., when the action and object naming requests were presented in a pseudo-randomized order. Source strength (in nanoampere, nAm) is displayed on the vertical axis. The goodness-of-fit value (*g*) is shown below. Right: Source waveforms during action vs object naming in sequences 2 and 3, i.e., when the action and object naming conditions were presented in blocked sequences.

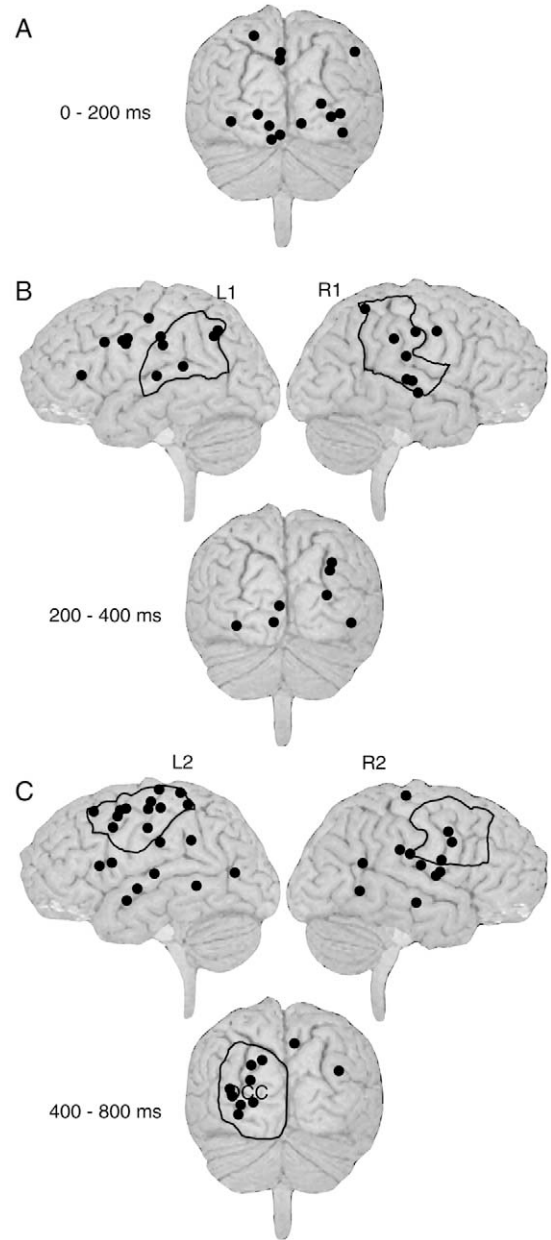


Fig. 5. Locations of cortical sources in the 10 normal subjects, displayed on a 3D-reconstructed MRI in the time windows 0 to 200 ms (top), 200 to 400 ms (middle), and 400 to 800 ms (bottom) after picture onset. The borders of five regions of interest (ROIs) are shown: L1 and R1, including parts of the superior temporal gyrus, the angular and the supramarginal gyrus of the left and the right hemisphere, respectively, L2 and R2, including parts of the postcentral and the precentral gyrus and of the premotor cortex, and OCC, comprising the left occipital lobe.

verbs and nouns. In aphasia, this network can be disrupted, leading to different activation patterns for the production of verbs and nouns, as evidenced by our patient who exhibited a noun–verb dissociation in picture naming.

This investigation was motivated by neuropsychological lesion studies demonstrating a double dissociation between the processing of verbs and nouns. Sophisticated language testing has revealed aphasic patients whose understanding

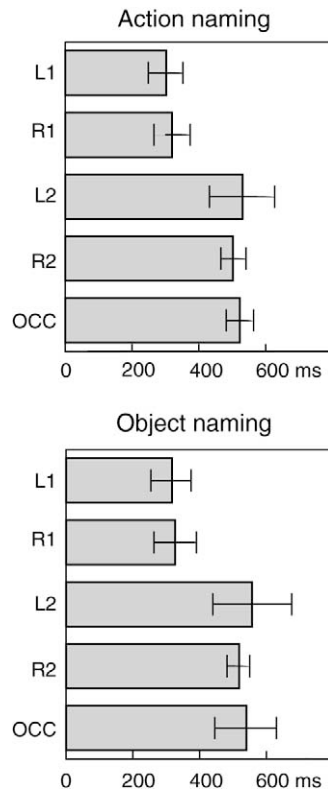


Fig. 6. Peak latency (mean \pm standard deviation) of the sources found in one of the five ROIs (see Fig.5). The graph represents group data from 10 healthy subjects for action naming (top) and object naming (bottom).

and production of nouns is less impaired than the understanding and production of verbs (Marshall et al., 1998). On the other hand, patients with the opposite behavior, i.e., the relative sparing of verbs compared with nouns, have been reported as well (Berndt et al., 1997).

Verb generation (i.e., the retrieval of a verb related to a given object) has been extensively studied in functional neuroimaging (for review see Grabowski and Damasio, (2000)). Studies using a verb generation task found predominant activation of the left inferior frontal gyrus and the left middle temporal gyrus (Martin et al., 1995; Fiez et al., 1996; Poline et al., 1996). Activation of the left frontal cortex seems to be a constant finding in verb generation studies (Herholz et al., 1996). These experiments used positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) to assess brain activation during verb generation; however, both techniques revealed very similar results in a direct comparison (Votaw et al., 1999). Confrontation naming of objects is also a widely studied task in brain mapping experiments (for reviews see Humphreys et al. (1999); Grabowski and Damasio (2000)). The activation pattern here differs from verb generation and involves the bilateral ventral temporal cortex (Damasio et al., 1996; Martin et al., 1996; Price et al., 1996). The bilateral fusiform cortex is also consistently activated in object naming (Henry et al., 1998; Chao et al., 1999; Murtha et al., 1999) and

seems to play an important role in the encoding of an object's structure (Whatmough et al., 2002).

Several brain imaging studies have attempted to directly compare the neural generators of verb and noun processing in healthy adults. Neurophysiological studies on normal volunteers have found subtle changes in the pattern of brain activation between verbs and nouns in a lexical decision task (Preissl et al., 1995) and in silent reading of verbs and nouns (Koenig and Lehmann, 1996) but a double dissociation of verb and noun processing has not been demonstrated. As for PET and fMRI, direct comparison of verb and noun processing has revealed greater activation in the left prefrontal cortex during verb generation (Petersen et al., 1988; Martin et al., 1995) or during visual lexical decision on verbs (Perani et al., 1999), consistent with the results of lesion studies showing selective verb processing difficulties

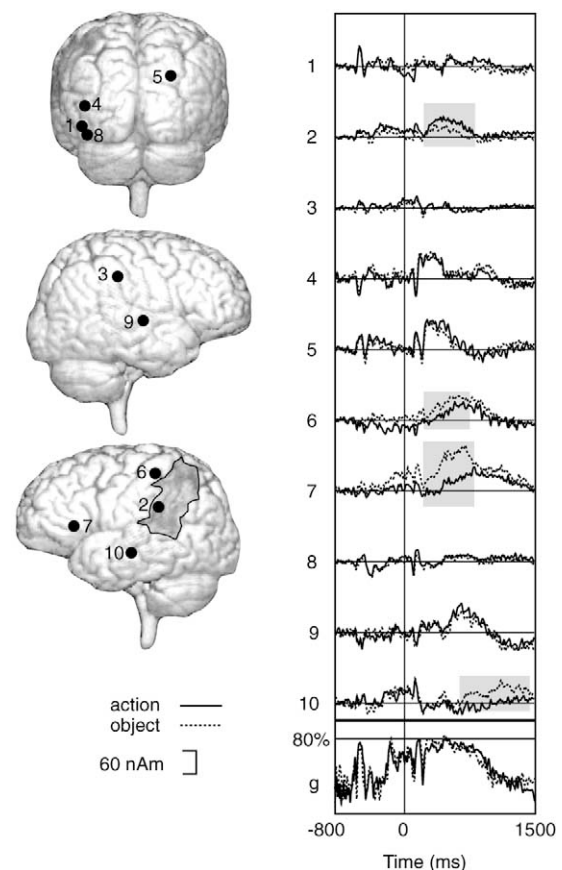


Fig. 7. Location of active cortical areas and their time-course during action and object naming in the aphasic patient JP. The time courses of activation represent the average of all correct responses. Left: Source locations are shown on the surface of JP's MRI. The infarction in the posterior territory of the left middle cerebral artery can be seen as a dark area on the cortex. Right: Source analysis resulted in 10 dipolar sources explaining the measured magnetic field during the two conditions. Source strength (vertical axis; nAm) is displayed as a function of time for -800 to 1500 ms with respect to picture onset (vertical line) during action naming (solid lines) and object naming (dashed lines). The goodness-of-fit value (g) is shown below. The gray boxes indicate intervals of significant differences between action and object naming.

after left frontal damage. Other studies, in contrast, have not found differences along the anterior–posterior axis of the left hemisphere in silent generation of verbs and nouns (Warburton et al., 1996; Damasio et al., 2001; Tyler et al., 2001), in lexical decision and semantic categorization (Tyler et al., 2001), in naming pictures of actions and pictures of single static objects (Damasio et al., 2001), or in silently naming actions and objects from the same pictures (Hernandez et al., 2001).

The studies on verb and noun processing published so far used varying paradigms including picture naming, word generation, lexical decision, and semantic decision activating different subcomponents of the language system (Indefrey and Levelt, 2000). All but one (Hernandez et al., 2001) of those studies used different tasks or stimuli for the investigation of verb vs noun processing. We chose overt picture naming as the paradigm since this is a well-defined natural language task which involves all levels of language production (Glaser, 1992; Johnson et al., 1996; Levelt et al., 1998). As differences in stimulus properties may well affect brain activity in the later, more cognitive stages, we investigated action and object naming using identical stimuli for both tasks. A time-sensitive method like MEG readily detects any differences in perceptual analysis of stimulus images. A major challenge in this study was to define a sufficient number of scenes with the action and object names fulfilling a large number of strict criteria (familiar words, different stems for verbs and nouns, no compound words, etc.). Moreover, the scenes had to be easily depicted and unanimously named with a high intersubject naming agreement.

Reaction times in healthy adults

Verbs play a crucial role in the production and comprehension of sentences. In general, verbs represent the lexicalization of relational concepts. Their semantic content defines the argument structure of the predicate of a sentence (Levelt, 1989). Because of their central syntactic role, verbs have a greater morphological complexity than nouns. Verbs are learned later in normal language acquisition, are harder to remember, and have a broader range of meanings relative to nouns (Gentner, 1981).

In this study, normal subjects were on the average 30 ms faster in naming actions than objects (Table 2). This result was unexpected in the light of the greater semantic and syntactic complexity of verbs and their slower processing in lexical decision and categorization tasks (Sereno, 1999). In the design of our experiment every care was taken to match verbs and nouns regarding their average frequency, level of concreteness, and length. Thus, it is unlikely that the observed differences in reaction times are influenced by these variables.

In some pictures a single object was sufficient to illustrate an ongoing action (“dog,” “to bark”). In the majority of illustrations, though, two or more objects were needed to

ensure reliable naming of the related action (“candle,” “match,” “hand,” “to light”). Although our subjects named, as intended, the central objects of those pictures in practically all object naming trials (92% correct), the choice among multiple objects might have increased their naming latencies compared to pictures with only one object (and hence prolonged the latencies for object naming relative to action naming as there is often a choice of objects but only a single depicted action). Increasing complexity of a picture per se does not make an independent contribution to response latency (Kremin et al., 2000) and should influence both action and object naming in a similar way. A comparison of response latencies to single- vs multiple-object illustrations gave additional evidence that the number of depicted objects did not influence the naming latencies in the present study. We did not find a significant difference in object naming latencies when comparing responses to pictures with one or more objects.

We suppose, in contrast, that differences in naming latencies reflect differences in cognitive processing during action and object naming. Longer reaction times in one of two similar tasks are believed to result from an additional cognitive step or demand needed for the slower task (Glaser, 1992). The pictures used in our study do not represent single entities but scenes. The delay of object relative to action naming suggests that object naming in propositional context requires not only the complete retrieval of the noun and its properties but also an understanding of the argument structure of the verb which would require an additional cognitive step and hence additional time of processing (Levelt et al., 1999).

Evoked responses in healthy adults

The most remarkable result of our action and object naming experiments in healthy subjects is that the spatio-temporal patterns of cortical activation were essentially identical under both conditions. Using directly comparable paradigms, i.e., naming of actions and objects from a single set of images, both hemodynamic measures (Hernandez et al., 2001) and the present neurophysiological data converge on the conclusion that retrieval of nouns and verbs is not dissociated in the healthy human brain.

The propagation of activation from occipital to temporo-parietal and frontal areas of both hemispheres, first described by Salmelin et al. (1994), represents the activity of a complex neuronal network which shows consistency within all healthy subjects investigated here. This network covers all stages of the naming process: object recognition, retrieval of the lexical concept, lemma selection, phonological encoding, and articulation (Levelt et al., 1998).

Although there was interindividual variability regarding the exact location and timing of naming-related brain activation, a common chain of activation was evident in most healthy subjects. Activation of the left and right secondary visual cortices within 200 ms after picture onset is likely to

represent object recognition (Vanni et al., 1996; Tarkiainen et al., 1999).

In the time window of 200 to 400 ms, sources were found in posterior temporoparietal areas (corresponding to the ROIs L1 and R1; see Fig. 5). Activation of the posterior end of the superior temporal gyrus and of the temporoparietal junction has been related to lemma selection during picture naming (Levelt et al., 1998). In contrast to the study of Levelt et al. (1998), which found a clustering of sources in the right temporoparietal cortex, our results show a bilateral activation of this area. The activation of the temporoparietal junction occurred later in our study (time window 200 to 400 ms) than in the experiment by Levelt et al. (1998) (time window 150 to 275 ms), apparently corresponding to the longer verbal reaction times in our more complicated naming task. We found a cluster of sources around the left sensorimotor cortex in the time frame of 400 to 800 ms after picture onset (9 of 10 subjects), possibly reflecting preparation for articulatory movements (Salmelin et al., 1994). Lateralized activation of the left frontal cortex has been reported both in verb generation (Herholz et al., 1996) and in naming of familiar tools (Grafton et al., 1997). Since the activation of this area was strongly lateralized to the left hemisphere, it is possible that genuine linguistic processes, such as phonetic encoding (Levelt et al., 1998), are also reflected in these responses. In the time window of 400 to 800 ms, activation of the left occipital cortex was found in 8 of 10 subjects, suggesting reactivation of visual association areas after the retrieval of the word form (Damasio, 1989).

Activation of Broca's and Wernicke's area, in contrast, was only inconsistently found in our picture naming task. In the time window of 400–800 ms, two subjects showed activation in the inferior frontal gyrus (Broca's area) and three subjects in the superior temporal gyrus (Wernicke's area). As these small numbers of sources are unlikely to yield representative data, we did not define separate ROIs for these areas. This result is in close agreement with previous PET studies of picture naming (Murtha et al., 1999). Confrontation naming of everyday objects is believed to involve a specific neural network of object recognition and labeling, different from the classical Broca–Wernicke language network (Etard et al., 2000). Our results demonstrate that, at least in healthy subjects, neither naming of common objects nor naming of common actions relies on the classical language areas of Broca and Wernicke but instead is subserved by a complex occipitoparietofrontal network.

Although action and object naming activated the same cortical areas in healthy subjects, individual timing differences were found between the two conditions. The most consistent difference was seen in the left sensorimotor cortex (area L2 in Fig. 5), where 7 of 9 subjects showed faster responses during action than object naming. Earlier brain activation in the action naming condition, especially in the left sensorimotor cortex, corresponds well with the shorter vocal reaction times for action naming found in 9 of 10

normal subjects. However, when compared at a group level, these timing differences did not reach statistical significance, nor was there a direct correlation between the cortical and behavioral measures. It is possible that significant differences in timing in L2 could be detected in a larger group of subjects. However, this would only suggest a functional difference in noun vs verb production. This result would not corroborate the anatomical differences reported in the lesion literature.

An important aim of this study was to simulate the natural production of nouns and verbs. To achieve this goal we created stimuli which illustrated one or more objects and one action. Although the subject's attention was directed to an object or an action, viewing these stimuli certainly resulted in the recognition of the depicted action and object(s) and produced prelexical knowledge of those actions and objects. The task of our experiment (to name the object or the action as quickly as possible), however, ensured that participants only selected the word form of and performed the phonological encoding for (Levelt et al., 1999) the required noun or verb. It is therefore unlikely that our stimuli simultaneously evoked language-related brain activity related to phonological encoding of both the relevant noun and the verb. In sequence 1, participants had to switch between action and object naming. The interval between the onset of the instruction and the onset of the picture was 600 ms, and the interval between two subsequent instructions was 4800 ms. The high naming accuracy in controls (92% or more responses were correct) suggested that the requested switch between different tasks was successful in almost all presented items. In sequences 2 and 3, subjects did not switch between tasks. In all six data sets obtained with sequences 2 and 3, the source locations between categorical and mixed presentation were nearly identical. This result supports our notion that essentially the same cortical areas are activated by the categorical and mixed presentation of our stimuli.

Naming performance in JP

JP displayed severe anomia in behavioral language tests. His left posterior parietal and his left superior temporal cortex were affected by the cerebrovascular accident. Lesions of the parietotemporal junction are frequently found in patients with anomic aphasia (Goodglass and Wingfield, 1997). Language comprehension, in contrast, was well preserved, suggesting an intact function of Wernicke's area. His naming abilities were impaired, as indicated by the BNT (28% correct; Table 1). Visual confrontation naming in the BDAE suggested differences in naming performance according to the grammatical class of the items. The possible dissociation of verb and noun production was confirmed by testing him with the line drawings of this study. JP's naming performance with these pictures was only slightly better in the pure behavioral testing before the MEG recordings than during the actual MEG measurement. Obviously, the MEG

measurement situation, previously unknown to him, and the short 300-ms exposure time for picture presentation had no marked effect on his naming abilities. However, JP did not display a practice effect along the three sessions he had to name the pictures (Table 2). Since the paradigm involved a cerebral process damaged in JP, we suppose that he had to use a maximum of his cognitive resources. This high workload made him tired easily and prevented a benefit from repetition priming seen in normal subjects.

JP was consistently slower than the healthy subjects in both action and object naming (Table 2). This is presumably a general effect of his left hemispheric damage. The advantage of action naming was also seen in the analysis of JP's vocal reaction times during the MEG session, where action naming was 300 ms faster than object naming. The results of these behavioral tests demonstrated that even a small left temporal lesion together with a more extended left posterior parietal lesion is sufficient to produce word-class-specific anomia with superior production of verbs compared to nouns.

In summary, JP was impaired in the production of both nouns and verbs. His impairment was consistently stronger when he produced nouns compared to verbs. These results demonstrated a clear dissociation of action and object naming in JP.

Evoked responses in JP

The early occipitoparietal responses, apparently related to picture recognition, were similar to those in normal subjects, i.e., intact. In contrast to the healthy subjects, JP's action and object naming segregated in the later activations.

Action naming was easier for JP. This was reflected by a relatively unimpaired chain of activation, advancing from the occipital to the left inferior parietal cortex, similar to that in normals. The only area showing a stronger or earlier response during action than object naming in JP was the left angular gyrus. The left inferior parietal cortex has been suggested to play a relevant role in phonological storage and encoding (Paulesu et al., 1993).

The malfunction of the normal naming-related network had a particularly severe effect on object naming, apparently forcing JP to recruit areas unaffected by the infarction. Our measurements revealed a specific activation pattern for JP's naming of objects, distinct from his naming of actions and from the naming-related responses in normals. The left inferior frontal cortex, approximately Broca's area, was involved both in action and in object naming, but showed significantly earlier and stronger activation when naming objects. In connection with the increased naming latencies for nouns compared with verbs and other behavioral data this result suggests a temporally deviant and impaired activation of Broca's area in JP.

A response in the left middle temporal lobe was evident during object naming but not during action naming in JP. This area is supposed to be critical for conceptual and/or

lexical selection in word production (Damasio et al., 1996; Indefrey and Levelt, 2000), and its late activation for objects is likely to reflect the particular difficulty in accessing object names. No sources in area L2 were found in JP. In healthy subjects, the cortical activation advances from the posterior area L1 to the anterior area L2. We assume that the loss of activation in L2 is related to the impaired processing in L1 which has been affected by the infarction.

Here, we thus demonstrate a dissociation of activation patterns in action vs object naming. In three cortical areas (Broca's area, left middle temporal cortex, and left superior parietal cortex), object naming elicited stronger responses than action naming. However, activation of the left inferior parietal lobe was stronger for action than object naming.

It must be noted that the picture naming paradigm used for JP's measurements differed from that primarily used in the healthy subjects. Since a rapid change between action and object naming (sequence 1) was too difficult for JP, he received sequences requiring only action (sequence 2) or object naming (sequence 3). To investigate whether these differences in the experimental setting could influence the recorded brain activations, sequences 2 and 3 were run in five normal subjects after administration of sequence 1. Since data analysis demonstrated that the same source areas were active in a similar fashion during sequences 1, 2, and 3 in healthy subjects (Fig. 4), we assume that the differences in cortical activation between JP and the normal subjects are not due to differences in the experimental task. Moreover, it is unlikely that the age difference between the normal control group (mean age 27 years) and JP (46 years) was responsible for the differences in brain activation seen in our study. In a recent study, the reaction time and correctness of naming common nouns were not significantly different between healthy volunteers of younger and older age (Evrard, 2002).

There is an ongoing discussion about the changes in brain organization associated with the recovery from aphasia (for review see Rijntjes and Weiller, 2002). Since JP's infarction took place more than 2 years before the MEG measurements reported here, it can be assumed that any major reorganizational changes have already taken place. We found no definite evidence for the additional recruitment of right-hemisphere homologues of the language areas. The strong activation of the right superior temporal gyrus (source 9, Fig. 7) was similar to that found in three healthy subjects and thus cannot be interpreted as compensatory recruitment of the right-hemisphere homologue of Wernicke's area. The differences in brain activation seen between JP and normal controls suggest that his infarction led to functional changes of complex networks only in the left hemisphere. This result is in the line with the observations of recent PET studies demonstrating the important role of the left hemisphere in recovery from aphasia (Warburton et al., 1996; Heiss et al., 1999).

In summary, we demonstrate, for the first time, a neuro-functional basis for a dissociation of verb and noun produc-

tion in an aphasic patient. Our results suggest that differences in brain activation related to noun and verb retrieval are not evident in healthy individuals but only emerge after the disruption of normal language network.

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References

- Bates, E., Chen, S., Tzeng, O., Li, P., Opie, M., 1991. The noun-verb problem in Chinese aphasia. *Brain Lang.* 41, 203–233.
- Berndt, R.S., Mitchum, C.C., Haendiges, A.N., Sandson, J., 1997. Verb retrieval in aphasia. 1. Characterizing single word impairments. *Brain Lang.* 56, 68–106.
- Breedin, S.D., Saffran, E.M., Schwartz, M.F., 1998. Semantic factors in verb retrieval: an effect of complexity. *Brain Lang.* 63, 1–31.
- Caramazza, A., Hillis, A.E., 1991. Lexical organization of nouns and verbs in the brain. *Nature* 349, 788–790.
- Chao, L.L., Haxby, J.V., Martin, A., 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat. Neurosci.* 2, 913–919.
- Damasio, A.R., 1989. Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition* 33, 25–62.
- Damasio, A.R., Tranel, D., 1993. Nouns and verbs are retrieved with differently distributed neural systems. *Proc. Natl. Acad. Sci. USA* 90, 4957–4960.
- Damasio, H., Grabowski, T.J., Tranel, D., Hichwa, R.D., Damasio, A.R., 1996. A neural basis for lexical retrieval. *Nature* 380, 499–505.
- Damasio, H., Grabowski, T.J., Tranel, D., Ponto, L.L., Hichwa, R.D., Damasio, A.R., 2001. Neural correlates of naming actions and of naming spatial relations. *NeuroImage* 13, 1053–1064.
- Daniele, A., Giustolisi, L., Silveri, M.C., Colosimo, C., Gainotti, G., 1994. Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia* 32, 1325–1341.
- Denes, G., Dalla Barba, G., 1998. G.B. Vico, precursor of cognitive neuropsychology? The first reported case of noun-verb dissociation following brain damage. *Brain Lang.* 62, 29–33.
- Etard, O., Mellet, E., Papathanassiou, D., Benali, K., Houde, O., Mazoyer, B., Tzourio-Mazoyer, N., 2000. Picture naming without Broca's and Wernicke's area. *NeuroReport* 11, 617–622.
- Evrard, M., 2002. Ageing and lexical access to common and proper names in picture naming. *Brain Lang.* 81, 174–179.
- Fiez, J.A., Raichle, M.E., Balota, D.A., Tallal, P., Petersen, S.E., 1996. PET activation of posterior temporal regions during auditory word presentation and verb generation. *Cereb. Cortex* 6, 1–10.
- Gentner, D., 1981. Verb semantic structures in memory for sentences: evidence for componential representation. *Cogn. Psychol.* 13, 56–83.
- Glaser, W.R., 1992. Picture naming. *Cognition* 42, 61–105.
- Goodglass, H., Wingfield, A., 1997. *Anomia: Neuroanatomical and Cognitive Correlates*. Academic Press, San Diego.
- Grabowski, T.J., Damasio, A.R., 2000. Investigating language with functional neuroimaging, in: Toga, A.W., Mazziotta, J.C. (Eds.), *Brain Mapping. The Systems*. Academic Press, San Diego, pp. 425–461.
- Grafton, S.T., Fadiga, L., Arbib, M.A., Rizzolatti, G., 1997. Premotor cortex activation during observation and naming of familiar tools. *NeuroImage* 6, 231–236.
- Hämäläinen, M., Hari, R., Ilmoniemi, R.J., Knuutila, J., Lounasmaa, O.V., 1993. Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Rev. Mod. Phys.* 65, 413–497.
- Heiss, W.D., Kessler, J., Thiel, A., Ghaemi, M., Karbe, H., 1999. Differential capacity of left and right hemispheric areas for compensation of poststroke aphasia. *Ann. Neurol.* 45, 430–438.
- Henry, T.R., Buchtel, H.A., Koeppel, R.A., Pennell, P.B., Kluin, K.J., Minoshima, S., 1998. Absence of normal activation of the left anterior fusiform gyrus during naming in left temporal lobe epilepsy. *Neurology* 50, 787–790.
- Herholz, K., Thiel, A., Wienhard, K., Pietrzyk, U., von Stockhausen, H.M., Karbe, H., Kessler, J., Bruckbauer, T., Halber, M., Heiss, W.D., 1996. Individual functional anatomy of verb generation. *NeuroImage* 3, 185–194.
- Hernandez, A.E., Dapretto, M., Mazziotta, J., Bookheimer, S., 2001. Language switching and language representation in Spanish-English bilinguals: an fMRI study. *NeuroImage* 14, 510–520.
- Humphreys, G.W., Price, C.J., Riddoch, M.J., 1999. From objects to names: a cognitive neuroscience approach. *Psychol. Res.* 62, 118–130.
- Indefrey, P., Levelt, W.J., 2000. The neural correlates of language production, in: Gazzaniga, M.S. (Ed.), *The New Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 845–865.
- Johnson, C.J., Paivio, A., Clark, J.M., 1996. Cognitive components of picture naming. *Psychol. Bull.* 120, 113–139.
- Koenig, T., Lehmann, D., 1996. Microstates in language-related brain potential maps show noun-verb differences. *Brain Lang.* 53, 169–182.
- Kremin, H., Hamerel, M., Dordain, M., De Wilde, M., Perrier, D., 2000. Age of acquisition and name agreement as predictors of mean response latencies in picture naming of French adults. *Brain Cogn.* 43, 286–291.
- Laine, M., Koivuselkä-Sallinen, P., Hänninen, R., Niemi, J., 1997a. Bostonin Nimentätesti. *Psykologien Kustannus Oy, Helsinki*.
- Laine, M., Kujala, P., Niemi, J., Uusipaikka, E., 1992. On the nature of naming difficulties in aphasia. *Cortex* 28, 537–554.
- Laine, M., Niemi, J., Koivuselkä-Sallinen, P., Tuomainen, J., 1997b. Bostonin Diagnostinen Afasiatutkimus. *Psykologien Kustannus Oy, Helsinki*.
- Laine, M., Virtanen, P., 1999. *WordMill Lexical Search Program*. Center for Cognitive Neuroscience, University of Turku, Turku, Finland.
- Laine, M., Vuorinen, E., Rinne, J., 1997c. Picture naming deficits in vascular dementia and Alzheimer's disease. *J. Clin. Exp. Neuropsychol.* 19, 126–140.
- Levelt, W.J., 1989. *Speaking: From Intention to Articulation*. MIT Press, Cambridge, MA.
- Levelt, W.J., Praamstra, P., Meyer, A.S., Helenius, P., Salmelin, R., 1998. An MEG study of picture naming. *J. Cogn. Neurosci.* 10, 553–567.
- Levelt, W.J., Roelofs, A., Meyer, A.S., 1999. A theory of lexical access in speech production. *Behav. Brain Sci.* 22, 1–75.
- Manning, L., Warrington, E.K., 1996. Two routes to naming: a case study. *Neuropsychologia* 34, 809–817.
- Marshall, J., Pring, T., Chiat, S., 1998. Verb retrieval and sentence production in aphasia. *Brain Lang.* 63, 159–183.
- Martin, A., Haxby, J.V., Lalonde, F.M., Wiggs, C.L., Ungerleider, L.G., 1995. Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270, 102–105.
- Martin, A., Wiggs, C.L., Ungerleider, L.G., Haxby, J.V., 1996. Neural correlates of category-specific knowledge. *Nature* 379, 649–652.
- McCarthy, R., Warrington, E.K., 1985. Category specificity in an agrammatic patient: the relative impairment of verb retrieval and comprehension. *Neuropsychologia* 23, 709–727.
- Miceli, G., Silveri, M.C., Villa, G., Caramazza, A., 1984. On the basis for the agrammatic's difficulty in producing main verbs. *Cortex* 20, 207–220.

- Miozzo, A., Soardi, M., Cappa, S.F., 1994. Pure anomia with spared action naming due to a left temporal lesion. *Neuropsychologia* 32, 1101–1109.
- Murtha, S., Chertkow, H., Beaugregard, M., Evans, A., 1999. The neural substrate of picture naming. *J. Cogn. Neurosci.* 11, 399–423.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Paulesu, E., Frith, C.D., Frackowiak, R.S., 1993. The neural correlates of the verbal component of working memory. *Nature* 362, 342–345.
- Perani, D., Cappa, S.F., Schnur, T., Tettamanti, M., Collina, S., Rosa, M.M., Fazio, F., 1999. The neural correlates of verb and noun processing. A PET study. *Brain* 122, 2337–2344.
- Petersen, S.E., Fox, P.T., Posner, M.I., Mintun, M., Raichle, M.E., 1988. Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331, 585–589.
- Poline, J.B., Vandenberghe, R., Holmes, A.P., Friston, K.J., Frackowiak, R.S., 1996. Reproducibility of PET activation studies: lessons from a multi-center European experiment. EU concerted action on functional imaging. *NeuroImage* 4, 34–54.
- Preissl, H., Pulvermüller, F., Lutzenberger, W., Birbaumer, N., 1995. Evoked potentials distinguish between nouns and verbs. *Neurosci. Lett.* 197, 81–83.
- Price, C.J., Moore, C.J., Humphreys, G.W., Frackowiak, R.S., Friston, K.J., 1996. The neural regions sustaining object recognition and naming. *Proc. R. Soc. Lond. B Biol. Sci.* 263, 1501–1507.
- Rijntjes, M., Weiller, C., 2002. Recovery of motor and language abilities after stroke: the contribution of functional imaging. *Prog. Neurobiol.* 66, 109–122.
- Salmelin, R., Hari, R., Lounasmaa, O.V., Sams, M., 1994. Dynamics of brain activation during picture naming. *Nature* 368, 463–465.
- Sereno, J.A., 1999. Hemispheric differences in grammatical class. *Brain Lang.* 70, 13–28.
- Tarkiainen, A., Helenius, P., Hansen, P.C., Cornelissen, P.L., Salmelin, R., 1999. Dynamics of letter string perception in the human occipitotemporal cortex. *Brain* 122, 2119–2132.
- Tyler, L.K., Russell, R., Fadili, J., Moss, H.E., 2001. The neural representation of nouns and verbs: PET studies. *Brain* 124, 1619–1634.
- Uusitalo, M.A., Ilmoniemi, R.J., 1997. Signal-space projection method for separating MEG or EEG into components. *Med. Biol. Eng. Comput.* 35, 135–140.
- Vanni, S., Revonsuo, A., Saarinen, J., Hari, R., 1996. Visual awareness of objects correlates with activity of right occipital cortex. *NeuroReport* 8, 183–186.
- Votaw, J.R., Faber, T.L., Popp, C.A., Henry, T.R., Trudeau, J.D., Woodward, J.L., Mao, H., Hoffman, J.M., Song, A.W., 1999. A confrontational naming task produces congruent increases and decreases in PET and fMRI. *NeuroImage* 10, 347–356.
- Warburton, E., Wise, R.J.S., Price, C.J., Weiller, C., Hadar, U., Ramsay, S., Frackowiak, R.S.J., 1996. Noun and verb retrieval by normal subjects. Studies with PET. *Brain* 119, 159–179.
- Whatmough, C., Chertkow, H., Murtha, S., Hanratty, K., 2002. Dissociable brain regions process object meaning and object structure during picture naming. *Neuropsychologia* 40, 174–186.
- Williams, S.E., Canter, G.J., 1987. Action-naming performance in four syndromes of aphasia. *Brain Lang.* 32, 124–136.