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Word-category specific deficits after lesions in the right hemisphere

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Abstract

A speeded lexical decision task was used to investigate word-category deficits in patients suffering from lesions in the right hemisphere and in neurological controls without cortical lesion. In all patients from one group ($n = 12$), the right frontal lobe was affected causing a left-sided hemiparesis. In the second group ($n = 6$), lesions primarily affected areas in the right inferior temporo-occipital lobes. Patients with motor deficits due to lesions in the spinal cord or in the periphery served as neurological controls ($n = 9$). Processing of three categories of words was investigated: verbs referring to actions (action verbs (acVs)); nouns with strong visual associations (visually-related nouns (viNs)); and nouns with both strong action and visual associations (bimodal nouns (biNs)). Stimulus categories were matched for word length and normalized lexical frequency. Error scores revealed a significant word category by patient group interaction. Patients with lesions in the right frontal lobe showed most severe deficits in processing action verbs, whereas those with lesions in their right temporo-occipital areas showed most severe deficits in processing visually-related nouns. Neurological controls did not show any differences between word categories. The double dissociation of the processing impairments seen in frontal versus temporo-occipital patients demonstrates that specific word-category deficits can arise from lesions in the right non-dominant hemisphere. An account for these results in terms of distributed neuronal systems representing words is offered.

Keywords: Category-specific deficit; Language; Right hemisphere; Word category

1. Introduction

It was Freud's [16] original proposal that the brain correlates of words are not housed in, and restricted to, two left-hemispheric language centers, as most researchers believed at his time. Instead, he believed that words are stored together with their semantic features in associative word-related networks widely scattered over various cortical areas of both hemispheres. He even thought about ways to prove this experimentally, but did not come up with an experimental design that meets modern standards. In this paper, we report on a study of patients with lesions in their right hemispheres not dominant for language. These patients showed word-category specific deficits. There was a relationship between the right-hemispheric areas affected and the meaning of the words whose processing was impaired. We interpret the category-specific processing limitations for words arising from right-hemispheric lesions as evidence for the Freudian view of distributed word-related neuronal systems and offer a neurobiological model accounting for the results obtained.

Word-category specific cortical processes have gained some attention in recent neurophysiological and neuropsychological research. There are data indicating that areas outside the traditional *core language areas* of Wernicke [56] make additional contributions to the processing of words. The "additional areas", or, as we will say, the *complementary language areas*, are of particular interest for category-specific processes. There is increasing evidence from both neurophysiological and neuropsychological studies that complementary language areas are not only housed in the language-dominant hemisphere but that the non-dominant hemisphere, usually the right, is also relevant for processing particular word types (for review, see [40,41]). In Section 1.1, we give a brief overview of this evidence.

1.1. Evidence for complementary language areas in both hemispheres

Within the dominant left hemisphere, various areas have an established role in word processing. Neuropsychological

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data suggest that left-frontal and -temporal areas differentially contribute to the processing of verbs and nouns, respectively, although there are exceptional cases that do not neatly fit in this rough scheme [14]. Metabolic neuroimaging studies showed that naming of animals and tools activates specific areas in left frontal, temporal and occipital lobes (for example, [11,24,38]). Neurophysiological studies, EEG and MEG, indicate that the differential involvement of frontal and occipital lobes in the processing of action- and visually-related words already begins 100–200 ms after word presentation (for example, [39,44,46–48]). All of these data are evidence of differential contributions of the complementary language areas in the left dominant hemisphere to the processing of specific word categories [17].

The classical investigations of split brain and hemispherectomy patients have demonstrated that the dominant left hemisphere is not the only one capable of word processing and lexical access. The non-dominant right hemisphere alone achieves to process stimulus words, particularly if they are common and concrete in meaning [57–59]. Neurophysiological data recorded from healthy individuals further support this result: whereas highly abstract function words elicited strongly left-lateralized brain responses, content words (including nouns and verbs) elicited more symmetrical evoked potentials over the hemispheres (see, e.g. [33,43]). Finally, there is also evidence suggesting that word processing is more effective if both hemispheres have access the stimulus information compared with stimulation of the left-dominant hemisphere alone, implying a facilitatory effect of the right hemisphere's word processor on that in the left [29,30]. These results further confirm the existence of complementary language areas outside the left-hemispheric core areas, and suggest category-specific processes even on the non-dominant side of the brain.

The results obtained so far demonstrate that the right-hemispheric areas are *activated* when certain words are being processed, that they can be *sufficient* for processing of certain words and that they can *facilitate* the left hemisphere in processing words. What has not been provided until now is a proof that the right hemisphere is *necessary for processing specific word categories*. While there is strong evidence for a differential contribution of defined areas in the dominant left hemisphere to word-category specific processes, such evidence is sparse for the right cortex. Here, we present two groups of patients with right-hemispheric lesions and ask whether word-category specific deficits can be detected with sensitive neuropsychological experimental paradigms. If present, such deficits may have implications for the role of right-hemispheric areas in the processing of defined word categories. Word-category specific deficits following right-hemispheric damage would prove that right-hemispheric neuronal circuits in the right hemisphere are necessary for unimpaired processing of certain kinds of words.

1.2. Hypotheses and experimental approach

For generating hypotheses about the degradation of the processing of specific word categories following right-hemispheric lesions, we used a neurobiological model postulating that words are processed by cortical cell assemblies [18], that is, functionally inter-dependent sets of neurons distributed over left-perisylvian language regions and complementary language areas [40,41]. According to one view, the complementary areas involved depend on semantic word properties. Hebbian correlation learning implies that a word frequently co-occurring with a visual stimulus will be stored in the cortex by means of strong connections between neurons in visual and language areas. On the other hand, if a word is frequently perceived while performing an action, the word-action contingency will be stored by strong links within an ensemble of neurons in core language areas and complementary language areas necessary for controlling actions. Importantly, neurons in both hemispheres are related to the execution of body movements and to the perception of objects. This suggests that action- and visually-related areas in both hemispheres serve as complementary language areas involved in category-specific processes. Sketches of cell assemblies presumably underlying the cortical processing of action words, visually-related words, and words related to both visual perceptions and actions are illustrated in Fig. 1. On the basis of this model, we intended to test the following hypotheses.

(i) Right-hemispheric lesions in the motor cortex and adjacent fronto-parietal sites will primarily impair the processing of action-related words most severely.
(ii) Right-hemispheric lesions in the visual areas of the inferior temporo-occipital lobes will primarily impair the processing of visually-related nouns most severely.

Because of their wide distribution and large number of neuronal elements, the word webs of nouns intimately related to both visual perceptions and actions may be less vulnerable and therefore persist following focal lesions. Therefore, these "bimodal nouns" were chosen as control word stimuli for which no specific processing deficit was expected.

While there is some indication that temporal lesions in the right hemisphere may lead to fine-grained word processing deficits (e.g. for proper names [51]) earlier neuropsychological investigations did not report word processing impairments after lesions in the right frontal lobe (e.g. [52]). However, it is possible that the tasks used in such earlier clinical studies were not sensitive enough to reveal a fine-grained language processing deficit such as it might appear after lesion of the non-dominant hemisphere. We applied a lexical decision task, a standard procedure in many psycholinguistic experiments where the subject has to decide for individual stimuli whether they are words or meaningless pseudowords. Accuracy on this task can be high in patients with neurological language deficits, so that it can become feasible to

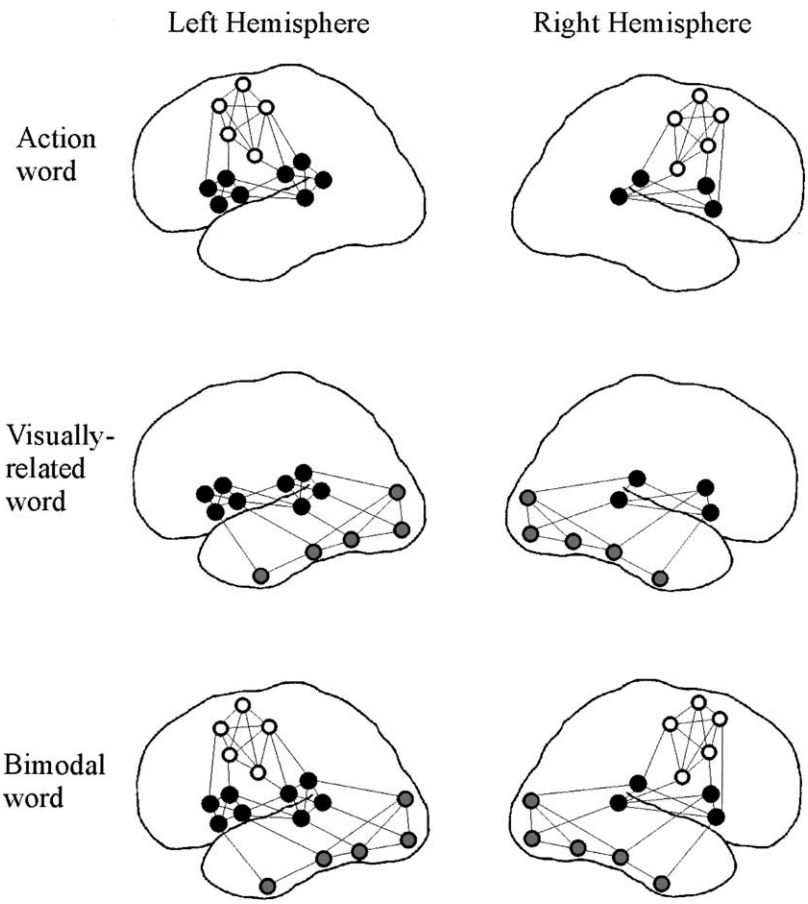

Fig. 1. Visually-related nouns may be represented by cortical cell assemblies distributed over perisylvian and additional visual cortices, whereas action verbs may be organized as assemblies distributed over perisylvian and additional motor cortices. Cell assemblies representing noun related to both visual perceptions and actions may be spread out over perisylvian, visual and motor cortices. Circles represent local neuron clusters and lines long-distance connections. The left- and right-hemispheric parts of the networks are shown on the left and right, respectively.

obtain both response times and accuracy measures in aphasics with substantial cortical damage [42]. If subjects respond as fast and as accurately as possible, the lexical decision task is sufficiently challenging so that language processing deficits that are masked by a ceiling otherwise may become apparent on either measure. We hoped that the speeded lexical decision task might be sufficiently sensitive to uncover putative category-specific word processing deficits in patients with lesions in different areas of their right hemisphere.

2. Materials and methods

2.1. Subjects

One group of patients, the frontal group, included 12 monolingual German native-speakers. All patients had suffered a single ischemic insult causing left hemiparesis. Table 1 shows the patients' age, sex, education level, etiology, lesion site, months post-onset of the disease, motor and somatosensory deficit and visual deficit.

There was no sign of any left-hemispheric lesion in any of these patients. In all patients, lesions affected motor and premotor areas in the right hemisphere. Additional involvement of the parietal lobes was present in 11 patients, and perisylvian lesions including inferior parietal and superior temporal areas was seen in 8 patients. In an earlier study [32], we found that small lesions restricted to the right motor and premotor cortex and larger right-perisylvian lesions including motor, premotor and inferior prefrontal areas caused the same category-specific deficits in word processing. Therefore, we grouped these patients together here. All patients suffered from left hemiparesis and somatosensory deficits.

Examples of MRI and CT scans of patients in the frontal group are presented in Figs. 2 and 3. In patient no. 2 (Fig. 2a), there was a focal lesion in the fronto-central areas involving a small portion of the motor, pre-motor and adjacent pre-frontal areas in the right hemisphere. Another example of a patient with very focal lesion was patient no. 8 (Fig. 2b). In this case, there was right superior fronto-central involvement. Larger perisylvian lesions were also seen, as in patient no. 12 (Fig. 3). Here, the right inferior frontal and parietal

Table 1
Sociodemographic and medical information about the group of patients with right frontal lesions

No.	Age (years)	Sex	Education (years)	Etiology	Lesion site	Months post-onset	Motor deficit	Somatosensory deficit	Visual deficit
1	48	Female	10	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	18	Hemiparesis left	Left body side	–
2	48	Male	10	Ischemic CVA	Middle fronto-central areas, basal ganglia	6	–	–	–
3	56	Male	9	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	19	Hemiparesis left	Left body side	–
4	30	Female	13	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	42	Hemiparesis left	Left body side	–
5	53	Male	10	Ischemic CVA	Superior fronto-central areas, basal ganglia	2	Hemiparesis left	Left arm	–
6	45	Male	9	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	32	Hemiparesis left	Left body side	–
7	34	Female	10	Ischemic CVA	Right frontal and temporal lobe, n. lentiformis, capsula interna	9	Hemiparesis left	Left body side	–
8	33	Male	10	Ischemic CVA	Superior fronto-central areas, basal ganglia	2	Hemiparesis left	Left body side	–
9	38	Female	9	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	2	Hemiparesis left	Left body side	–
10	34	Female	13	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	12	Hemiparesis left	Left body side	–
11	49	Male	13	Ischemic CVA	Superior fronto-central areas, basal ganglia	48	Hemiparesis left	Left body side	–
12	41	Male	10	Ischemic CVA	Right inferior frontal and parietal lobes and superior temporal lobe, basal ganglia	10	Hemiparesis left	Left body side	–

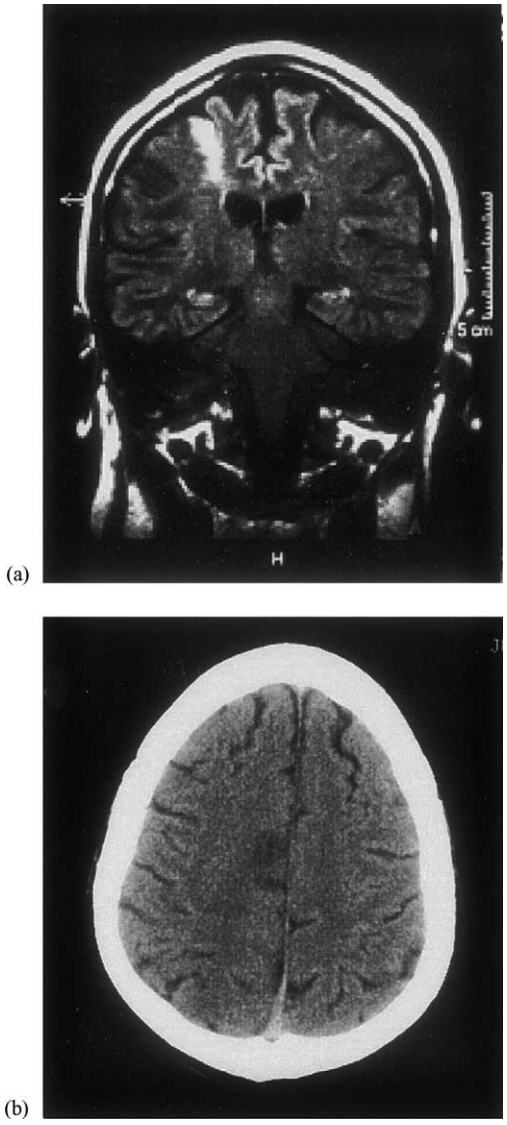

Fig. 2. MRI scans of patients with small focal lesions affecting the frontal cortex. (a) In patient no. 2, the fronto-central lesion involved a small portion of the motor, pre-motor and adjacent pre-frontal areas in the right hemisphere. (b) In patient no. 8, the right superior fronto-central areas were affected.

lobes, the right superior temporal lobe and the basal ganglia were affected.

In the temporo-occipital group, there were six patients. All were monolingual native speakers of German. Four of them had suffered from a single ischemic insult. In one patient, there was a cortical lesion caused by encephalitis affecting primarily the right hemisphere, with minor left-hemispheric involvement. Therefore, we included this patient in the right-hemispheric group. Another patient had received the diagnosis progressive stroke, although MRI scans document only one single temporal lesion on the right. In all patients, visual right inferior temporo-occipital areas were affected. Table 2 shows the patients' age, sex, education level, etiology, lesion site, months post-onset of the disease, motor and somatosensory deficit and visual deficit.

Fig. 3. Example of a larger perisylvian lesion as exhibited by some of the patients included in the frontal group. In this patient (no. 12), the right inferior frontal and parietal lobes, the right superior temporal lobe and the basal ganglia were lesioned.

In Fig. 4, lesions of patients in the temporo-occipital group are illustrated. In patient no. 15 (Fig. 4a), there was involvement of right inferior and middle temporal lobes and basal ganglia. In patient no. 16 (Fig. 4b), primarily the right inferior temporal lobe and in addition the right occipital lobe were affected.

In the control group, there were nine neurological patients without cortical lesion. As the patients in the two other groups, all of them were monolingual native-speakers of German. Their neurological deficits were either at the spinal level or at the level of peripheral efferent nerves. Table 3 shows the patients' age, sex, education level, etiology, lesion site, months post-onset of the disease, motor and somatosensory deficit and visual deficit.

The three groups were matched for time post-onset of the disease. Age and education level did not differ between the groups with right frontal lesions and the neurological controls. The temporo-occipital group was slightly older and had a slightly higher education level (cf. Tables 1–3).

2.2. Neuropsychological assessment

The Benton Visual Retention Test [4] was used to examine visual short-term memory. This test is sensitive to cortical lesions. Subjects have to remember and to re-draw line drawings of increasing complexity. Visual short-term memory deficits are reflected in the number and type of errors made.

The d2 Test [6] was administered to examine selective attention. Subjects have to carry out a visual pattern detection task for about 5 min, as fast and accurately as possible. The quantity and quality of the performance allows for assessing deficits in selective attention.

The Corsi Block-Tapping Test [50] was used to test spatial short-term memory. This test is performed using an array of

Table 2
Sociodemographic and medical information about the group of patients with lesions in right inferior temporal and/or occipital areas

No.	Age (years)	Sex	Education (years)	Etiology	Lesion site	Months post-onset	Motor deficit	Somatosensory deficit	Visual deficit
13	41	Female	10	Encephalitis	Right inferior temporal involvement	155	–	–	–
14	72	Male	13	Ischemic CVA	Right occipital lobe	3	–	–	Hemianopia, left visual field
15	57	Male	10	Ischemic CVA	Right inferior and medial temporal lobe, basal ganglia	114	Left arm and leg	–	–
16	73	Male	13	Ischemic CVA	Primarily right posterior inferior temporal and occipital involvement	2	–	–	Hemianopia, left visual field
17	51	Male	13	Progressive stroke	Right inferior temporal involvement	35	Left arm and leg	Left arm and leg	–
18	60	Male	13	Ischemic CVA	Right occipital lobe, basal ganglia	2	–	–	Hemianopia, left visual field

(a)
(b)

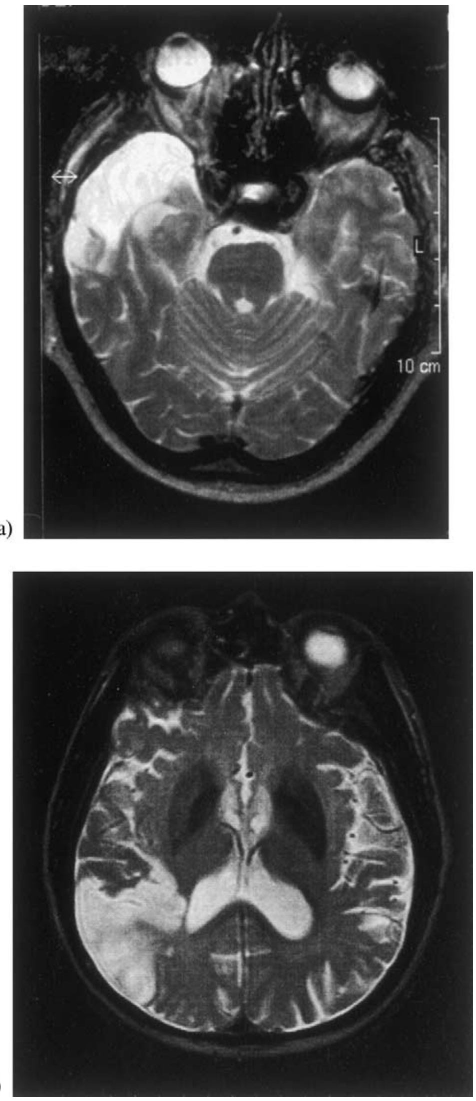

Fig. 4. MRI scans of patients included in the temporo-occipital group. (a) In patient no. 15, there was involvement of the right temporal pole, the inferior and middle temporal gyri, and the basal ganglia. (b) In patient no. 16, primarily the right posterior inferior temporal lobe and the right occipital lobe were affected.

small square blocks arranged within a rectangular perimeter. The examiner sequentially points to a number of blocks, and the patient has to repeat the sequence. The complexity of the task (number of blocks to be sequentially pointed to) is increased until mistakes occur. The errors in reproducing the spatio-temporal patterns allow for assessing spatial short-term memory deficits.

The Token Test [15], a test for separating aphasics from other brain-damaged patients, was used to assess the presence of an aphasia. The German version of this test [35] was administered. The Token Test consists of a series of instructions of increasing complexity. The patient has to follow them by pointing at, or manipulating colored tokens of different size and form. There is an age-corrected cut-off number of errors below which the presence of an aphasia

Table 3
Sociodemographic and medical information about the neurological control patients exhibiting motor and/or somatosensory deficits not caused by a cortical lesion

No.	Age (years)	Sex	Education (years)	Etiology	Lesion site	Months post-onset	Motor deficit	Somatosensory deficit	Visual deficit
19	35	Male	10	Slipped disc	No cortical lesion	1	Incomplete paraplegia	Legs	–
20	46	Female	10	Slipped disc	No cortical lesion	1	–	Right body side	–
21	41	Female	9	Cervico brachialgia	No cortical lesion	25	–	Arms	–
22	45	Female	10	Poliomyelitis	No cortical lesion	480	Incomplete paraplegia	–	–
23	46	Female	10	Lumboischialgia	No cortical lesion	38	–	Legs	–
24	72	Female	10	Lumboischialgia	No cortical lesion	1	Incomplete paraplegia	Legs	–
25	57	Male	9	Guillain–Barré syndrome	No cortical lesion	4	Incomplete paraplegia	–	–
26	37	Female	10	Syringomyelia	No cortical lesion	440	–	Arms	–
27	52	Male	9	Spinal fistula	No cortical lesion	65	Incomplete paraplegia	Legs	–

can be excluded with some certainty in a neurological patient.

To further screen for aphasic language deficits, parts of the Aachen Aphasia Battery [20] were used. The comprehension test and items from the naming test were administered with all patients suffering from cortical lesion. The comprehension test includes quadruplets of pictures one of which the patient has to point to on instruction. Single words, longer phrases and sentences of increasing complexity are used to describe the pictures. Half of the test consists of spoken instructions, in the other half the instructions are given in written form. Therefore, good performance on this test implies a certain level of reading abilities. From the naming test, object pictures were chosen and the patient had to articulate the name.

A neglect screening was carried out. Patients were asked to mark the middle of lines on a sheet of paper placed in front of them. The lines were in the middle, or to the left or right of the center of the paper. Further, objects were placed in front of the patient and to his or her left and right and instructions to point to individual objects were given. It was assessed whether the patients had any difficulty carrying out these tasks when stimuli appeared at fixation or in either hemifield. Each of the tasks administered is known to be sensitive to neglect, and is widely used in clinical testing.

An apraxia screening was used to assess actions typically affected in apraxics. This screening instrument consisted of 20 questions about activities typically affected in facial apraxia, ideomotoric apraxia (symbolic and asymbolic tasks) and ideatoric apraxia. Also, patients were asked to carry out example tasks of all of these types. It was assessed whether errors were made on these tasks, and whether deficits were reported.

Finally, a short version of Oldfield's [34] handedness inventory (six items) was administered. For different manual activities (e.g. throwing a ball or cutting with scissors) subjects have to indicate whether they usually carry them out with the left or right hand. Patients were instructed to indicate the hand they had used *before* the occurrence of their cortical lesion. This was done to assess the pre-morbid handedness of the patients.

2.3. Lexical decision experiment

2.3.1. Stimuli and stimulus ratings

One hundred fifty concrete German nouns and action verbs and 150 pseudowords were chosen as stimuli. The words included 50 concrete nouns with strong visual associations (visually-related nouns (viNs), sometimes abbreviated further), 50 concrete nouns with both strong visual and motor associations (bimodal nouns (biNs)) and 50 action verbs which caused strong motor associations (action verbs (acVs)). Please notice that, unlike English nouns, most German nouns are not commonly used as verbs and, vice versa, most verbs do not have homophonous common nouns. It is possible to generate nouns from verbs ("das Gehen" from the verb "gehen"), but these derived nouns are used rarely. On the basis of their frequency of occurrence (standardized lexical frequency according to Baayan et al. [1]), all of the words in the stimulus set could straightforwardly be classified into one of these lexical categories, with either rare or not even documented use as members of other categories.

To validate that the three word groups differed with regard to their visual and action associations, cognitive processes elicited by these items were assessed in a pre-experiment. The methods of the behavioral assessment are described in much detail in earlier studies (e.g. [46]). Subjects were asked to rate the stimulus words on five-point scales. The participants were asked:

(1) whether words reminded them of visually perceivable objects or scenes (visual association rating);
(2) whether words reminded them of activities they could perform themselves (action association rating), and;
(3) whether they considered the words as concrete or abstract (concreteness rating).

Note that a question about motor associations may leave it unclear whether associations of movement perceptions or actual actions performed by the subject are to be rated. Therefore, it was made clear by the instruction that motor activities performed by the experiment participants were meant.

Twelve volunteers (monolingual native speakers of German, aged 20–31 years; mean age 25 years) were paid for participating in a 1 h session during which they saw words followed by questions on a computer screen. The ratings were made by pressing a number key between 1 and 5 on the computer keyboard.

Preliminary analyses of the data showed that mean ratings significantly and strongly differed between the three rating scales, and that the variances were also different. To yield equal means and variances on each of the rating scales, the values were *z*-transformed. The mean rating on each scale was therefore 0, and positive or negative numbers indicate above- or below-average visual and action associations. After *z*-transformation, the variance on all scales is 1.

When the values obtained on the scales for action and visual association strengths were entered into an analysis of variance (ANOVA), a clearly significant interaction of the word-category factor with the rating scale factor emerged. This was the case for raw values ($F(1, 11) = 127.3$; $P < 0.0001$), and for *z*-transformed scores as well ($F(1, 11) = 55.7$; $P < 0.0001$). The ratings of action associations revealed the highest *z*-values for the group of action verbs (0.6), slightly slower values for the bimodal nouns (0.2) and a clear below-average outcome for the group of visually-related nouns (−0.8). These numbers document that the action associations of one of the noun categories was clearly below average. Post-hoc Scheffe-tests further confirmed these differences in action ratings between the visually-related noun category and both other categories ($P < 0.0001$ for both relevant comparisons). There was a marginally significant difference between action verbs and the group of bimodal nouns ($P = 0.05$). The visual ratings revealed reports of clearly stronger associations for both noun groups ($z = 0.2$) than for the action verbs ($z = -0.4$). Scheffe-tests confirmed this (*P* values were 0.01 and 0.03, respectively). Finally, the concreteness ratings revealed additional differences between the three word groups ($F(2, 22) = 7.4$; $P = 0.007$). The outcome here was very similar to that of the visual association ratings: nouns were rated as being substantially more concrete than verbs (the *z*-scores were again 0.2 for both noun categories, and −0.4 for the verbs). The correlation between visual-association ratings and concreteness ratings was significant ($r = 0.62$; $P < 0.0001$).

These results substantiate the claims that the present set of action verbs elicits stronger action associations but weaker visually-related associations than the nouns included in the visually-related group. In addition, the result shows that what we call the group of “bimodal” nouns indeed elicits both strong visual and action associations. Furthermore, there was good agreement between the concreteness and the visual ratings for the word groups under investigation.

The three word groups were matched for frequency of occurrence and for word length. All words were four–nine letters long. Average lengths were 6.4 (visually-related nouns), 6.2 (bimodal nouns) and 6.6 (action verbs) letters. As revealed by a *t*-test, these differences were not significant. All words consisted of two syllables. All are common words in German with moderate word frequency. According to the CELEX database [1] they occur between 1 and 50 times per million words. Group averages of word frequencies were 7.9 (visually-related nouns), 8.8 (bimodal nouns) and 7.3 (action verbs) per million words in standard text. The *t*-tests failed to reveal any significant between-group differences in word frequency.

It is important to match word length and frequency in studies of category-specific word processing deficits, because these factors are well known to have important neurophysiological and neuropsychological correlates (see, for example, [5]). This has not always been the case in earlier investigations (e.g. [52]), and earlier results must therefore be discussed in the light of the possibility that putative category effects can be due to differences in word length or frequency. The exact matching for length and frequency performed for the present stimulus set rules out these possible confounds in the first place.

Pronouncable and orthographically regular pseudowords were constructed by permutating letters within a word or by exchanging one letter between two words. All pseudoword stimuli were thus matched for length to the word sample. All pseudoword stimuli were two syllables long.

2.3.2. Apparatus

Data were collected with an IBM compatible Pentium computer. Subjects were seated approximately 50 cm from a 17 in. computer monitor, with their chin on a chin rest, and had to fixate the center of the screen. Two keys on the computer keyboard were used to collect subjects’ responses. One key was labeled with the letter ‘w’ for ‘word’, the other key was labeled with the letter ‘n’ for ‘not a word’. They had to press the ‘w’-key with the middle finger and the ‘n’-key with the index finger of their right unimpaired hand.

2.3.3. Procedure

The entire neuropsychological test battery and the experiments were carried out in three sessions, each of approximately 50 min duration. During the first session, the experiment was done, and during the second and third sessions the neuropsychological tests were administered. Before the experiment, the patients were instructed to decide whether they considered a certain letter string to be a real German word or a meaningless pseudoword and to press a button accordingly. Subjects were asked to respond as fast and as accurately as possible. They were given ample opportunity to practice with a set of practice stimuli not used in the subsequent experiment.

The experiment consisted of eight blocks. Each block contained 36–38 of the 300 stimuli. Between any two blocks the subjects could decide whether they would like to have a break. A new pseudo-random sequence of stimuli was made up for each subject.

During the experiment, a fixation cross was shown in the middle of the computer screen. The subjects were told to fixate their eyes on this cross. After a delay randomly varying between 2 and 2.5 s, a warning tone of 800 Hz was presented for 200 ms. One thousand milliseconds after the onset of the tone, the fixation cross disappeared and was replaced by a word or pseudoword stimulus. These stimuli were presented for 130 ms thus guaranteeing tachistoscopic stimulation. Subjects had to respond during the subsequent 3 s (otherwise trials were evaluated as incorrect). The stimuli were written horizontally in capital letters. Each stimulus appeared bilaterally, with two copies of the same word or pseudoword simultaneously flashed to the left and right visual field. The inner angle of the word was 0.9° away from fixation, and the outer angle was no more than 4.9° from fixation. The words were thus flashed to the perifoveal region.

The reason for presenting words bilaterally was the following. Such stimulation is necessary to guarantee that both hemifields, and, thus, both hemispheres receive the full information about each word under investigation. In this case, a putative deficit degrading visual processing in one hemifield may still affect the processing of words in some way, but, since the other hemisphere would always receive the full information about each stimulus word, a category-specific deficit could not be explained on the basis of this feature. All word categories should be affected in the same way.

3. Results

3.1. Neuropsychological assessment

Results of the neuropsychological assessment of the patients with right frontal lesions are shown in Table 4. Age-corrected values significantly below the average of the age-group are indicated by superscript letter 'a'. In about one half of the patients, the tested aspects of attention, visuo-spatial processing and short-term memory were in the normal range whereas in the other half there were deficits in these areas. None of the patients showed deficits in the tested aspects of praxia and neglect and none of them gave any indication of an aphasic language disturbance. three patients were ambidextrous and two of them had a left-handed family member. Visual and spatial memory deficits are frequently associated with lesions in the right hemisphere. However, these disturbances are unlikely to affect the performance on a lexical decision task, because this task does not have a visual or spatial short-term memory component. Furthermore, even if these deficits somehow affected the results on the lexical decision experiment, they would not provide a ready explanation of the category-specific effects reported below. Deficits on the d2 Test seen in three patients suggest that their selective attention is reduced, but one must keep in mind that only patients who performed well on the lexical decision experiment could be included in the present experiment. Successful participation in a lexical decision experiment proves an ability to focus attention on stimuli for a substantial time. And, again, given these patients' selective and sustained attention was not perfect, as the d2 Test results indicate, such deficient attention can not explain category-specific differences in processing words or their meaning.

Results of the neuropsychological assessment of the patients with right temporo-occipital lesions are shown in Table 5. Age-corrected values significantly below the average of the age-group are indicated by superscript letter 'a'. Two of the patients included in the temporo-occipital group did not show any deficit on the neuropsychological tasks tested here. Eight of the patients revealed deficits in attention, visuo-spatial processing and short-term memory but just as in the group of patients with lesions in motor areas, there is no reason why these deficits could lead to word-category specific impairments. And also in this group, all patients performed significantly above chance on the lexical decision experiment.

Table 4
Results of the neuropsychological assessments of the patients with right frontal lesions

No.	Benton Visual Retention Test	d2 Test	Corsi Block-Tapping Test	Token Test	Reading Test	Neglect screening	Apraxia screening	Handedness	Left-handed family members
1	7 (11)[a]	9.7[a]	3[a]	0	0	No neglect	0	Right	1
2	6[a] (5)	96.4	4[a]	0	0	No neglect	0	Ambidextrous	1
3	8 (6)	86.4	6	0	0	No neglect	0	Right	0
4	6[a] (5)[a]	95.5	5	0	0	No neglect	0	Right	0
5	8 (3)	75.8	6	0	0	No neglect	0	Right	0
6	2[a] (12)[a]	1.8[a]	4[a]	0	0	No neglect	0	Ambidextrous	0
7	9 (1)	90.3	6	0	0	No neglect	0	Right	0
8	8 (2)	99.2	6	0	0	No neglect	0	Right	0
9	4[a] (6)[a]	11.5[a]	5	0	0	No neglect	0	Ambidextrous	0
10	10 (0)	99.2	7	0	0	No neglect	0	Right	0
11	9 (1)	95.5	6	0	0	No neglect	0	Right	0
12	6[a] (5)[a]	65.5	3[a]	0	0	No neglect	0	Right	0

Values in parenthesis $\alpha = 0.05$.

[a] Test results below the normal performance range of the relevant age groups.

Table 5
Results of the neuropsychological assessments of patients with lesions in right inferior temporal and/or occipital areas

No.	Benton Visual Retention Test	d2 Test	Corsi Block-Tapping Test	Token Test	Reading Test	Neglect screening	Apraxia screening	Handedness	Left-handed family members
13	6[a] (6)[a]	3.5[a]	5	0	0	No neglect	0	Right	0
14	5 (5)	91.9	4[a]	0	0	No neglect	0	Right	0
15	6 (4)	81.6	6	0	0	No neglect	0	Right	0
16	2[a] (15)[a]	24.2	4[a]	0	0	No neglect	0	Right	1
17	9 (1)	97.7	5	0	0	No neglect	0	Right	0
18	9 (1)	27.4	4[a]	0	0	No neglect	0	Right	0

Values in parenthesis $\alpha = 0.05$.
[a] Test results below the normal performance range of the relevant age groups.

Table 6
Results of the neuropsychological assessments of the neurological control group

No.	Benton Visual Retention Test	d2 Test	Corsi Block-Tapping Test	Token Test	Reading Test	Neglect screening	Apraxia screening	Handedness	Left-handed family members
19	10 (1)	90.3	6	0	0	No neglect	0	Right	0
20	7 (4)	82.5	5	0	0	No neglect	0	Right	0
21	5[a] (7)[a]	24.2[a]	5	0	0	No neglect	0	Right	2
22	6[a] (4)	69.2	5	0	0	No neglect	0	Right	0
23	6[a] (5)	76.7	4[a]	0	0	No neglect	0	Right	0
24	6 (6)	50.0	4[a]	0	0	No neglect	0	Ambidextrous	0
25	4[a] (10)[a]	54.0	4[a]	0	0	No neglect	0	Right	0
26	9 (1)	99.0	6	0	0	No neglect	0	Right	0
27	9 (1)	46.0	5	0	0	No neglect	0	Right	0

Values in parenthesis $\alpha = 0.05$.
[a] Test results below the normal performance range of the relevant age groups.

Results of the neuropsychological assessment of the neurological control group are shown in Table 6. Superscript letter 'a' indicated age-corrected values significantly below the average of the age-group. Four out of nine neurological control subjects did not show any deficit on the tests administered, *but*, *surprisingly*, the other five subjects revealed deficits in attention, visuo-spatial processing and short-term memory. Neither the tested aspects of praxia and neglect nor the language tests revealed any deficits. One subject was ambidextrous and one had left-handed family members. These results of the neuropsychological testing of the control patients indicate that the tests administered were difficult even for subjects without any cortical lesion. ANOVAs did not reveal any significant differences between the two groups of cortical patients and the neurological control subjects with regard to the neuropsychological tests administered. This indicates that the category-specific deficits reported below cannot be attributed to neuropsychological deficits covered by these tests.

As expected, the patients with right-hemispheric lesions did not show deficits on clinical language tests. Most were error-free on the Token Test, a widely used clinical test distinguishing aphasics from patients without neurological language deficit, and the screening of language comprehension and naming abilities also failed to reveal any dysfunction. Furthermore, the patients acted as competent verbal communicators throughout the testing sessions and not a single one of them gave evidence of an aphasia-like language deficit.

3.2. Statistical evaluation

Response times and error scores were evaluated by ANOVA. The three word categories (visually-related nouns, bimodal nouns, action verbs) (factor 'word category', three levels) and the three groups (factor 'group', three levels) were compared. Only latencies of correct responses were analyzed. All patients' error scores were significantly better than chance. Accuracies (percentage of correct responses) and mean latencies of correct responses to words and pseudowords, and to words of different categories, are shown for the two groups of patients and for controls in Tables 7 and 8.

3.3. Accuracies

3.3.1. Word–pseudoword comparison

Average accuracy revealed a main effect for the factor 'wordness' ($F(1, 24) = 19.6$; $P = 0.0002$). Words were processed more accurately than pseudowords. Word superiority on the accuracy measure is a common finding in the lexical decision task (see, e.g. [31]). There was also a just significant main effect of the factor 'group' ($F(2, 24) = 3.5$; $P = 0.05$). Planned comparisons showed that patients with lesions in right temporo-occipital lobes made more errors than patients with right frontal lesions ($F(1, 24) = 6.3$; $P = 0.02$) and more errors than control patients ($F(1, 24) = 4.9$; $P = 0.04$). The less accurate responses in the temporo-occipital group may be a trivial

Table 7
Error scores and reaction times for words and pseudowords, obtained in patients with right-hemispheric lesions and in control subjects

	Words		Pseudowords	
	Mean	Standard error	Mean	Standard error
Accuracies (percentage of correct responses)				
Patients with right frontal lesions	83.7	3.7	80.2	3.7
Patients with right temporo-occipital lesions	78.2	5.3	61.2	3.4
Control patients	87.7	2.8	74.6	4.0
Latencies (ms)				
Patients with right frontal lesions	903	38	1015	41
Patients with right temporo-occipital lesions	909	70	1101	74
Control patients	903	27	1035	34

Table 8
Error scores and reaction times for the three word categories, visually-related nouns (viNs), bimodal nouns (biNs) and action verbs (acVs), obtained in patients with right-hemispheric lesions and in control subjects

	viNs		biNs		acVs	
	Mean	Standard error	Mean	Standard error	Mean	Standard error
Accuracies (percentage of correct responses)						
Patients with right frontal lesions	87.5	2.9	86.5	4.0	76.8	4.9
Patients with right temporo-occipital lesions	73.0	6.3	80.3	4.8	81.0	5.1
Control patients	89.1	3.1	88.0	2.7	86.0	3.1
Latencies (ms)						
Patients with right frontal lesions	896	38	878	34	939	47
Patients with right temporo-occipital lesions	904	75	891	67	929	74
Control patients	910	28	883	31	908	31

by-product of their visual processing deficit. This issue will be addressed further.

3.3.2. *Word category comparison*

The results for the three word categories: viNs; biNs; and acVs, for the three patient groups are summarized in Table 8. An ANOVA investigating the errors revealed a significant main effect of the factor word category ($F(2, 48) = 3.2$; $P = 0.05$). Planned comparisons indicated that, overall, bimodal nouns were processed more accurately than action verbs ($F(1, 24) = 6.3$; $P = 0.02$). The ANOVA also showed a significant interaction of the between-group factor with the within group variable word category ($F(4, 48) = 7.2$; $P < 0.0001$). This significant interaction is illustrated in Fig. 5.

Planned comparison tests were performed using one-tailed *t*-test to investigate differences between word categories in any of the patient groups. Patients with right frontal lesions showed significant differences between visually-related nouns and action verbs ($F(1, 24) = 20.5$; $P < 0.0001$) and between bimodal nouns and action verbs ($F(1, 24) = 21.9$; $P < 0.0001$), with better processing of nouns than verbs. There was no significant difference between subcategories of nouns. In patients with right inferior temporo-occipital lesions, there was a significant difference between visually-related nouns and action verbs ($F(1, 24) = 6.0$; $P = 0.02$) and between the two noun categories ($F(1, 24) = 8.0$; $P = 0.009$), but not between the bimodal nouns and action verbs. *The neurological control patients* did not show any significant word-category differences.

The significant between-group differences suggest that the performance on the lexical decision task was generally reduced after temporo-occipital lesions, as compared with both neurological control patients and patients with right-frontal lesions. Closer observation of the data, however, indicated that the observed between-group difference was mainly due to a few good performers, three in the right-frontal group and three in the control group, who showed an accuracy of lexical decisions on words above 95%, which is close to ceiling. To investigate the robustness of possible between-group differences, we found it important to perform a second analysis after removal of best performers. Such removal was further justified, because: (i) a ceiling effect masked possible word-category effects in best-performing patients; and (ii) lesions seen in the temporo-occipital group tended to be relatively large, whereas two out of the three best performers in the frontal group had particularly small lesions (patients nos. 8 and 11; cf. Table 4).

After exclusion of all good performers (three in the frontal group, three in the neurological control group; criterion: accuracy >95%), the interaction of the between-group variable with the factor word category persisted ($F(4, 36) = 9.2$; $P < 0.0001$), whereas the between-group difference was

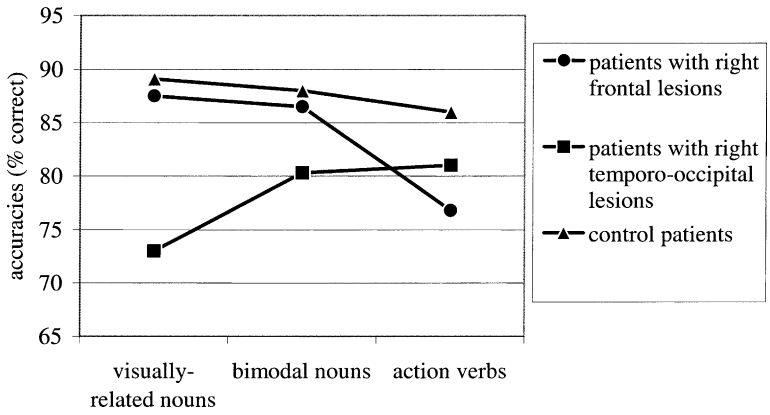

Fig. 5. Error scores of lexical decisions of patients with right frontal lesions, of patients with right temporo-occipital lesions and of neurological control patients. A significant group by word-category interaction ($F(4, 48) = 7.2$; $P < 0.0001$) was obtained. Planned comparisons of the word categories revealed that in patients with right frontal lesions there were significant differences between visually-related nouns and action verbs ($F(1, 24) = 20.5$; $P < 0.0001$) as well as between bimodal nouns and action verbs ($F(1, 24) = 21.9$; $P = 0.00009$). There was no significant difference between visually-related nouns and bimodal nouns. In patients with right temporo-occipital lesions, there were significant differences between visually-related nouns and action verbs ($F(1, 24) = 6.0$; $P = 0.02$) and between visually-related nouns and bimodal nouns ($F(1, 24) = 8.0$; $P = 0.009$). There was no significant difference between bimodal nouns and action verbs. Control patients did not show any word-category differences.

now far from significant ($F = 1.1$; $P > 0.3$) (see Fig. 6). Importantly, also the between-category differences in the three patient groups were still significant. The right-frontal group showed reduced performance on action verbs as compared with both other word groups ($F(1, 18) = 28.2$ and 31.9, respectively; $P < 0.0001$), the right-temporo-occipital group showed an impairment specific for visually-related nouns as compared with both other groups ($F(1, 18) = 6.1$ and 6.3, respectively; $P < 0.01$), and no category differences were seen in the neurological control group (all $P > 0.3$). This documents the robustness of the effects observed.

Between-group comparisons were performed separately for each word category. The best-performing subjects were also excluded from this analysis, because their performance had suggested a virtual between-group difference in global performance that may confound results on individual word categories. Action verbs led to more errors in frontal patients than in the temporo-occipital and control groups ($F(1, 18) = 3.8$ and 6.1; $P < 0.03$), whereas the visually-related nouns were processed less accurately in temporo-occipital patients as compared with both other patient groups ($F(1, 18) = 4.8$ and 6.1; $P < 0.02$). There were no significant between-group differences for the nouns with strong associations in more than one modality.

One may ask whether the category-specific effects seen in the two patient groups with *right-hemispheric* lesions were sufficient for yielding a significant interaction. Therefore

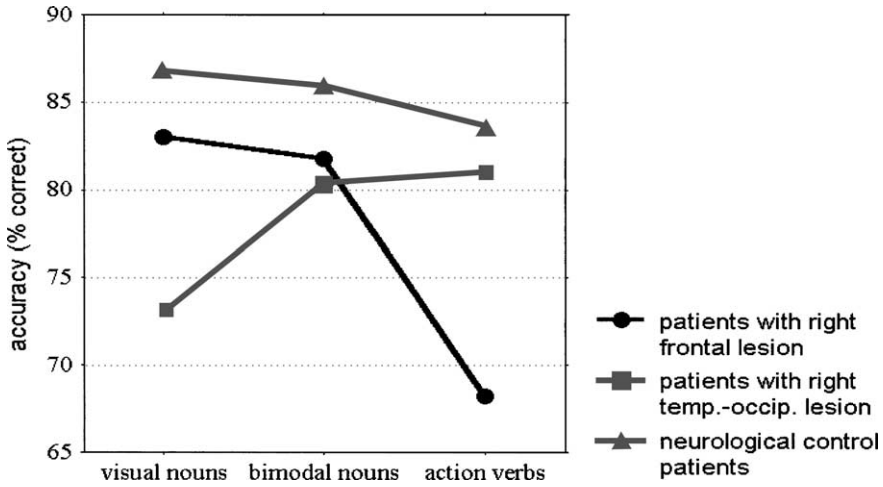

Fig. 6. Error scores of lexical decisions of patients with right frontal lesions, of patients with right temporo-occipital lesions and of neurological control patients after exclusion of best performers. The significant group by word-category interaction was markedly expressed ($F(4, 36) = 9.2$; $P < 0.0001$). This data display shows that the slightly better performance the right-frontal group compared with the right-inferior-temporal group was due to three good performers in the frontal groups.

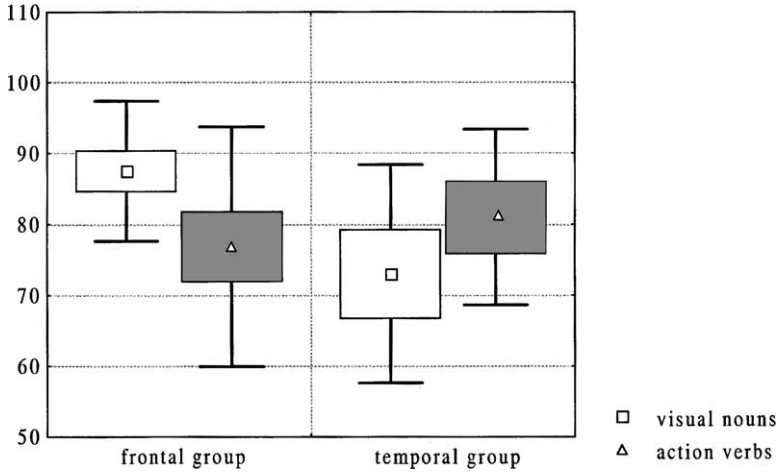

Fig. 7. Error scores of lexical decisions on visually related nouns and action verbs obtained from the patients with right frontal lesions and patients with right temporo-occipital lesions showed a significant group by word-category interaction ($F(2, 32) = 11.5$; $P = 0.0002$). Planned comparison tests revealed better performance on action verbs than visually-related nouns in patients with right temporo-occipital lesions ($F(1, 16) = 4.5$; $P = 0.05$), and the reverse, better performance on the nouns, in patients with right frontal lesions ($F(1, 16) = 16.0$; $P = 0.001$). The box plots give means, standard errors and ranges.

an additional ANOVA was carried out investigating error scores on visually-related nouns and action verbs in the two groups with right-hemispheric lesions alone. This analysis further confirmed the significant interaction of the between-group factor with the within group variable word category ($F(2, 32) = 11.5$; $P = 0.0002$). The box plot in Fig. 6 illustrates this interaction and presents additional statistical details (standard errors and ranges). The interaction was equally clear after exclusion of good performers ($F(1, 12) = 22.8$; $P = 0.0005$). Note that this interaction corresponds to a double dissociation of action verb and visually-related noun processing in patients with lesions in the frontal and temporo-occipital areas of their right hemisphere (Fig. 7).

3.4. Response times

Words led to faster responses than pseudowords ($F(1, 24) = 54.4$; $P < 0.0001$). The analysis of latencies also showed a significant main effect of the three-level factor word category ($F(2, 48) = 5.4$; $P = 0.008$). Planned comparisons showed faster responses to bimodal nouns than to action verbs ($F(1, 24) = 9.3$; $P = 0.005$), but no other significant effects. In particular, there was no statistically significant manifestation of any performance difference between patient groups on this measure.

4. Discussion

Twenty-seven neurological patients, 12 with lesions affecting the right frontal lobe, 6 with lesions in the right temporo-occipital lobes and 9 neurological controls without cortical damage, underwent neuropsychological testing and participated in a speeded lexical decision experiment. Whilst tests of aphasia, naming, reading and language comprehension failed to reveal any neurological language disorder, the lexical decisions performed by the patients gave evidence of category-specific word processing deficits. The analysis of accuracy data revealed a significant patient group by word-category interaction. Whereas neurological controls achieved equally high accuracies for all word categories tested, action verbs, visually-related nouns and bimodal nouns, both patient groups with cortical lesions exhibited relative degradation of performance on specific word categories. Patients with lesions in temporo-occipital areas did respond less accurately to visually-related nouns compared with both other word categories. In contrast, patients with frontal lesions processed action verbs least accurately. This double dissociation in the cortical patients makes it evident that lesions in different areas of the right hemisphere can affect the processing of different word categories to different degrees. Intactness of right frontal cortical areas appears to be necessary for the optimal processing of action verbs and that of right temporo-occipital areas appears to be essential for the processing of visually-related nouns.

4.1. Methodological issues: patient grouping, neuropsychological performance

In the group with right-frontal lesions, three patients were ambidextrous. One may argue that, because atypical hand preference is more frequently associated with right-hemispheric language dominance, these patients' results may not be representative. However, several studies (for example, [9,28]) found that about 70% of clear left-handers exhibited normal, that is, left-hemispheric language dominance, while in only about 20% of these subjects the right hemisphere was dominant for language. (The rest did not show language dominance.) From a statistical

perspective, not more than one out of our three ambidextrous patients in the frontal group should therefore be left-dominant. A single, or even 3, atypically lateralized subject(s) in a group of 12 cannot possibly produce the highly significant word-category effects reported here. To further ascertain that hand preference was not related to the observed category-specific deficits, we compared the ambidexters' performance on the three word categories to that of the right-handed frontal patients. Average accuracy values for action verbs was clearly lower than those of both other categories in both sub-groups (ambidextrous frontal patients: visually-related nouns—76.0%, bimodal nouns—72.0%, action verbs—61.3%; right-handed frontal patients: visually-related nouns—91.3%, bimodal nouns—91.3%, action verbs—82.0%). Thus, hand preference cannot account for the category differences observed in the present study.

The patient groups compared in this investigation differed in their cortical lesions. The "frontal" group included patients with small lesions in the fronto-central motor cortices, but also patients with large perisylvian lesions in whom inferior parietal and superior temporal areas were affected, in addition to frontal sites. We justify this grouping as follows: (1) in an earlier study on word-category specific deficits after right-hemispheric lesions, we found significant and equally pronounced processing deficits for action verbs in two patients with small fronto-central and larger perisylvian lesions [32]; (2) in the present study, similar patterns of action verb deficits were seen in the both subgroups (small fronto-central lesion: visually-related nouns—87.1%, bimodal nouns—85.3%, action verbs—74.9%; large perisylvian lesion: visually-related nouns—88.7%, bimodal nouns—90.0%, action verbs—81.7%). The grouping of patients with inferior temporal and occipital lesions was motivated by the what-stream of visual object processing (cf. [24]), which extends from the occipital areas to the anterior inferior temporal cortex. When comparing subgroups of patients in whom anterior parts of the temporal or occipital areas, respectively, were primarily affected, we found consistent category-specific processing deficits for visually-related nouns (primarily temporally-lesioned patients: visually-related nouns—69.3%, bimodal nouns—76.0%, action verbs—80.0%; primarily occipitally-lesioned patients: visually-related nouns—76.6%, bimodal nouns—84.6%, action verbs—82.0%). The consistency of the category-specific pattern over different sub-groups of the frontal and temporo-occipital groups confirms the proposed patient grouping. Further, the two patients with possible additional minor left-hemispheric involvement did show a similar word-category effect as the rest of the group with exclusively right-hemispheric involvement.

As mentioned in Section 3, one analysis indicated global reduction of word and pseudoword processing in our group of patients with inferior temporo-occipital lesions. However, as the analysis after exclusion of best performers revealed, this between-group difference was entirely due to three good performers in the frontal group, all of whom performed at ceiling (and therefore without clear category differences), and two of whom had particularly small lesions (patient nos. 8 and 11). The reanalysis confirmed all major results revealed by the entire group, with the exception of the between-group difference in accuracy, which had disappeared. Between-group difference suggested by the initial analysis of lexical decision performance should therefore not be interpreted.

The neurological control subjects who suffered from non-cortical lesions (e.g. slipped disc) did not show significant performance differences between word categories. This suggests that the obtained deficits in action verb and visually-related noun processing in the frontal and temporo-occipital groups are due to the cortical lesions and not, as one may want to argue from a psychological perspective, a psychological process such as what has been labeled "perceptual defense". Following Bruner and Postman [7,8], perceptual defense in control subjects could have been the result of motor and/or somatosensory deficits which could have made the patients feel threatened and tense when confronted with words related to actions. This, in turn, could have lead to a higher perception threshold for these items specifically. As we could not find degradation of action verb processing in control subjects who also suffered from motor and/or somatosensory deficits, this psychological approach can probably be ruled out as a possible explanation of the present category-specific processing deficits.

4.2. Comparison of the present results with earlier findings

Our results reveal a similar picture for the effect of right-hemispheric cortical lesions as has earlier been documented for left-hemispheric damage. Frontal lesions in the left-dominant hemisphere were sometimes found to lead to aphasias in which deficits in processing verbs dominated over the processing deficits for other content words (see, e.g. [14,27]). On the other hand, more posterior lesions involving visual areas or the temporal pole were found to underlie deficits in processing nouns [14,37]. We found a similar pattern for lesions in the right non-dominant hemisphere. Furthermore, Bak et al. [2], Bak and Hodges [3] recently reported that bilateral lesions of frontal areas, as present in motor neuron disease, can also have specific effects on the processing of action verbs. In addition, Cappa et al. [10] found most pronounced deficits in fronto-temporal dementia. These data are consistent with the view that the frontal cortices on the left and right both support the action associations of words, thereby facilitating word processing. The present results in patients with lesions in right-hemispheric motor areas are consistent with the earlier findings and further confirm the role of frontal cortices in verb processing.

The present results also replicate the finding reported earlier that right frontal lesions can impair the processing of action verbs more than that of visually-related nouns [32,45]. In the earlier studies, data obtained from patients

with right-hemispheric lesions were contrasted with the performance of a control group matched for age and level of education. A significant interaction of the word-category factor with the between-group factor revealed more errors on action verbs than nouns in the patients, but no pronounced differences in the controls. The present study replicates and extends these earlier findings. Consistent with them, the control group included in the present study failed to show word-category differences in the lexical decision task. Now, a double dissociation was observed in two patient groups defined on the basis of the locus of their right-hemispheric lesions.

As mentioned in the Section 1, temporo-occipital lesions in the right hemisphere have earlier been found to cause naming deficits for specific word categories, but no evidence was reported that right-frontal lesions could also be associated with category-specific naming deficits (e.g. [52]). This discrepancy of results can be explained in at least two ways, it can be attributed to the stimulus materials, the words selected for the experiments, or to the task administered, either naming or lexical decision. Of course, a cumulative effect of task and stimulus material is possible, too. One putative reason why Tranel et al. [52] did not find verb processing deficits after right-hemispheric lesions is the following. These authors used verbs with higher word frequency compared with their nouns. For example, their verbs were almost five times as frequent as their nouns referring to animals (the respective numbers being 69 versus 13). It is well known that more frequent and more familiar items are less vulnerable if disease of the brain affects cognitive processing (see, for example, [5,16]). The absence of a specific verb-processing deficit after right-hemispheric lesions in Tranel et al.'s study may therefore be due to the relatively high word frequency of their verbs.

As a second possibility, it may be that the naming task might not be sensitive enough to reveal the fine-grained language processing deficits arising from lesions of the non-dominant hemisphere. The speeded lexical decision task, a standard procedure in psycholinguistic research [25], proved to be sufficiently sensitive to uncover category-specific word processing deficits in patients with lesions in different areas of their right hemisphere. Because this task can be administered in clinical populations, even in patients with severe forms of aphasia [42], its application in clinical investigation appears fruitful.

The patients tested in the present study did not appear to be aware of their word processing difficulties. Apart from their unimpaired performance on clinical language tests (cf. Tables 4 and 5), they put great emphasis on that they never noticed any language deficits when being questioned about such possible problems. Also, the experimenter asked the patients whether they had noticed any difficulty with action verbs during the experiment, or in everyday language use, but all patients gave negative answers here. Together with the perfect performance on the clinical language tests applied, this suggests that there was no pronounced difficulty in everyday language use, although category-specific deficits were clearly documented by the lexical decision experiment. It may therefore be that category-specific deficits in patients with right-hemispheric lesions can best be revealed by a demanding and highly sensitive psycholinguistic test such as lexical decision (cf. [26]).

4.3. Origin of the dissociation between word categories

Word-category differences were obtained using a lexical decision experiment. In earlier work (e.g. [19,21,38,49,53–55]) category-specific deficits were revealed by other tests, e.g. naming or verbal definitions of the meaning of words. Impaired performance on these tasks can, in principle, be explained by different cognitive deficits, including retrieval of word forms, semantic processes, or the analysis of the visual images of to-be-named objects. In contrast, perceptual differences and other differences in pre-lexical processing [12] are unlikely in a lexical decision task using visually similar written words matched for their length and word frequency. A locus of the effect at the lexical level appears more likely, because the lexical decision can be carried out on the basis of the orthographic and phonological knowledge of word forms. No semantic knowledge is *necessary* for deciding whether a letter string is a word or not, and a deficit in performing lexical decisions may therefore arise at the lexical level [12], at the level of word form processing. However, Chumbley and Balota [13] found an effect of word meaning on lexical decisions. They argued that a post-lexical process, the word–pseudoword decision, may have been influenced by semantic processes, which differed between their word categories. Our data could also be tentatively explained along this line of thought. The different semantic systems in right-frontal or right-temporo-occipital areas were differentially affected and this, in turn, led to a lack of facilitation at the post-lexical decision stage. Instead, we would propose that the word form representation itself is strongly and reciprocally connected with the semantic representations in visual and action-related areas, and this explains the differential involvement of word categories by focal lesions in these areas. We admit that, at this stage, the alternative views (serial processing and post-lexical locus of the category effect versus interactive processing of word form and meaning and lexical locus of the effect) both provide possible explanations of the present results. Still, with a wider scope that also incorporates neurophysiological data we would believe that more evidence scores in favor of the interactive view [41].

It has been suggested that the primary factors determining deterioration of word processing caused by disease of the brain may be the frequency of lexical items and their imageability (see, for example, [5]). Therefore, it is relevant to examine whether the present data can, in part, be explained by these factors. Since, as we note again, word frequency was exactly matched between the word categories tested, this variable is not a plausible confound. Imageability ratings were not available for the words under investigation.

However, concreteness ratings were obtained for all words and, since there is a strong (>0.8) correlation between imageability and concreteness [36], it is likely that the higher concreteness for both our noun categories compared to the action verbs (see Section 2) yielded the same difference with regard to imageability. Still, whereas, a difference in concreteness or imageability between word categories can account for the degradation of action verb processing in the frontal group, it does not explain the specific impairment of visually-related noun processing in the temporo-occipital patients. Further, the dissociation between the two noun categories cannot be due to the imageability factor, because these stimulus groups did not differ in their concreteness and there is therefore no evidence that their imageability differed. The factors word frequency and imageability alone cannot account for the full range of data reported in this study.

Although the control group did not show word significant category differences, their average performance on visually-related nouns was slightly better than that on the action verbs (maximum difference: 3.1%; 3.0% after exclusion of good performers). On the basis of this putative difference, one may postulate that there are differences in the difficulty level between word categories that may also account, in part, for the deterioration of the frontal patients' impaired performance on verbs. Such deterioration may, as one may hold, also be present in the temporo-occipital group, with further deterioration for visually-related nouns due to the temporal involvement. However, this view would not be consistent with the better average performance on action verbs of the temporo-occipital group as compared with the frontal group (difference: 4.2%; 13% after exclusion of best performers). Further, the significant word-category differences between patient groups argue in favor of an account in terms of word categories.

The present results suggest that neural systems devoted to the programming of actions and visually perceivable objects, respectively, are woven into the representations of action- and visually-related word forms, such that the two parts of the distributed representation, the word form and the semantic part, are mutually dependent [40,41]. This view can be traced to Freud's monograph on aphasia published in 1891 (see Section 1). If word form and meaning-related actions and perceptions of objects are frequently processed at the same time, the neurons involved will frequently fire together and will therefore wire together, thus yielding distributed representations by which word form and meaning representations are held together. Because the meaning-related processes likely involve neuronal firing in both hemispheres, the relevant distributed word representations have been postulated to involve neurons in both hemispheres. Therefore, lesions in the action-related semantic areas in both hemispheres should have the potential of causing specific deficits in accessing word forms characterized by action-related meanings. An analogous argument holds for visually-related semantic areas. Areas involved in the programming of actions or visually perceivable objects, may therefore be *particularly* relevant for the storage of the meaning of action words or visually-related nouns, respectively. Lesions in these areas may therefore cause deficits in the access to the forms of action verbs or visually-related nouns, respectively. In other words, not only lesions in core language areas, but, in addition, lesions in right-hemispheric complementary language areas involved in category-specific semantic processing can have an effect on the processing of word forms. The data obtained for bimodal nouns are consistent with this view. They yielded relatively accurate lexical decisions in both patients groups. This can be explained by their more extended and therefore less vulnerable cortical representations.[1] This proposal accounts for the present data set and is consistent with a large body of neuropsychological, neurophysiological, and neuroimaging work [22,41].

5. Conclusions

This study demonstrates that lesions in the non-dominant right hemisphere and not leading to an overt aphasia can cause word-category specific processing deficits. Category-specific deficits were revealed by an attention-demanding speeded lexical decision task. Our results are consistent with the view that the right hemisphere not only contributes to but, in addition, is necessary for word processing. The right frontal lobe is particularly relevant for processing one specific word category, action verbs, and the right inferior temporo-occipital areas are specifically necessary for processing visually-related nouns. Our findings support a neurobiological model of language according to which word processing is based on cell assemblies distributed over both hemispheres whose right-hemispheric parts constitute aspects of word meaning and are necessary for the optimal processing of word forms.

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[1] As an alternative, the bimodal nouns, which included a large proportion of tool names, may have more strongly left-lateralized representations, as pointed out in a recent publication in this journal by Ilmberger et al. [23], and may therefore be affected less by lesions in the right hemisphere.

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