# NEUROANATOMICAL CORRELATES OF LOCATIVE PREPOSITIONS

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Very little research has explored which neural systems may be important for retrieving the meanings of locative prepositions (e.g., *in, on, around*). To begin to address this knowledge gap, we conducted a lesion study in which we tested the hypothesis that processing the meanings of locative prepositions depends on neural structures in the left inferior prefrontal cortex and left inferior parietal cortex. Seventy-eight subjects with focal, stable lesions to various parts of the telencephalon and a comparison group of 60 normal participants were studied with tasks that require production, comprehension, and semantic analysis of locative prepositions. In support of our hypothesis, we found that in subjects with impaired knowledge of locative prepositions, the highest region of lesion overlap was in the left frontal operculum and the left supramarginal gyrus, and in the white matter subjacent to these two areas. In a second study, focused on six subjects who had pervasive defects for locative preposition knowledge, we confirmed that such defects were associated specifically with damage to the posterior left frontal operculum, white matter subjacent to this region, and white matter underneath the inferior parietal operculum. These subjects did not have basic impairments in spatial processing or working memory, and they had relatively well-preserved processing of conceptual knowledge for actions and various categories of concrete entities (e.g., persons, animals, tools). All six subjects, however, had defects in naming actions, and some of them also had defective naming of some categories of concrete entities. Overall, the findings converge nicely with recent results from functional imaging approaches, and with classic studies from the aphasia-based literature, and suggest that the left inferior prefrontal and left inferior parietal regions have crucial—albeit not exclusive—roles in processing knowledge associated with locative prepositions.

## INTRODUCTION

A great deal of research in linguistics and cognitive science has been devoted to understanding the complex meanings of locative prepositions—specifically, words like *in, on,* and *around.* In contrast, very little research in cognitive neuroscience has addressed the question of which neural systems may be important for retrieving the semantic structures and lexical forms for these kinds of words. To

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Supported by Program Project Grant NINDS NS19632.

Ralph Adolphs, PhD, provided generous and substantial assistance with the lesion overlap analyses, and with the production of the lesion overlap figures. His input was critical to the completion of this study. We thank Ken Manzel for assistance with data collection and analysis, and with help in preparing Figure 1. Denise Krutzfeldt and Kathy Jones provided assistance in scheduling the subjects and coordinating their assessments.



http://www.tandf.co.uk/journals/pp/02643294.html
DOI:10.1080/02643290342000627

begin to fill this knowledge gap, we conducted two studies. In Study 1, we administered a set of tests that require production, comprehension, and semantic analysis of locative prepositions to 78 brain-damaged subjects with focal, stable lesions distributed throughout the left and right cerebral hemispheres, and then compared the lesion sites of the subjects who were impaired on the tests with the lesion sites of the subjects who were not impaired. In Study 2, we explored the nature and specificity of these findings by investigating in detail the ability of a selected subgroup of subjects—namely, those with pervasive defects in processing knowledge for locative prepositions—to process conceptual knowledge and retrieve lexical forms for actions and various categories of concrete entities. We investigated the general spatial processing and working memory capacities of the subjects in this subgroup, and conducted detailed follow-up analyses of their lesions. Before reporting the two studies, we review pertinent background information about the semantic properties of locative prepositions and the brain areas that might be involved in representing and processing them.

## The semantic properties of locative prepositions

The literature on the meanings of locative prepositions is now so vast that it would resist even book-length review, so what follows is only intended to be a brief summary of the main semantic factors that we attempted to take into account in designing our neuropsychological study (for a sample of recent research, see Bloom, Peterson, Nadel, & Garrett, 1996; Garrod, Ferrier, & Campbell, 1999; Herskovits, 1986; Landau & Jackendoff, 1993; Levinson, 1996, 2003; Lindstromberg, 1998; Sandra & Rice, 1995; Talmy, 1983; Zelinsky-Wibbelt, 1993).

Locative prepositions constitute a small class of grammatical morphemes that speakers use to describe static spatial relationships between objects.[1] Two objects are typically involved—the "figure," which is the thing to be located, and the "ground" or "landmark," which is an object that serves as a point of reference. For example, in the sentence *The beer is in the refrigerator,* the noun-phrase *the beer* specifies the figure, the noun-phrase *the refrigerator* specifies the landmark, and the preposition *in* specifies the nature of the spatial relationship between them. For the most part, locative prepositions express spatial relationships in terms of very sketchy or schematic structural properties of the objects involved; metrical details are usually ignored, such as the exact sizes, shapes, and orientations of the objects, or the precise distances between them. For instance, in the example given above, the real-world situation that the sentence refers to might consist of a geometrically rich, idiosyncratic, three-dimensional spatial layout, perhaps involving a Corona longneck standing upright on the top shelf of a big refrigerator with many levels and compartments; yet the semantic structure of *in* is very austere and skeletal, since it abstracts away from these spatial particularities and instead treats the beer bottle as just a dimensionless point and the refrigerator as simply an idealised container. Hence, locative prepositions designate what Kosslyn (1994) calls "categorical" as opposed to "coordinate" spatial relationships—a distinction that we elaborate in greater detail in the Discussion.

The meanings of many locative prepositions are difficult to define precisely because these words can accommodate a tremendous variety of geometric situations in a spatially complex world. For instance, *in* prototypically describes a spatial relation of containment in which (1) the landmark is a three-dimensional object, (2) the landmark is hollow, and (3) the landmark completely encloses the figure. But each of these conditions can be violated, thereby yielding extended meanings as exemplified in the following situations: (1) a person standing inside a circle painted on the floor (landmark is two-dimensional), (2) a nail that has been pounded into a board (landmark is solid), and (3) an apple in a bowl, even though it rests on top of other fruit so that it is technically above the

[1] Another set of prepositions describe paths (e.g., *into, onto, toward*). We do not deal with those in the current investigation.

horizontal upper edge of the bowl (figure not enclosed by landmark). Some linguists argue that the remarkable adaptability of locative prepositions to a wide range of situations should be explained in terms of polysemy—i.e., networks of distinct but closely related submeanings—whereas others attempt to explain it in terms of monosemy—i.e., a single extremely general meaning that is integrated into particular contexts by construal rules or pragmatic inferences of some kind. Whether one approach is superior to another, or whether some combination of both approaches is necessary, is a topic of ongoing research (Sandra & Rice, 1995).

Although our focus is on English, it is important to note that, according to recent crosslinguistic research, the majority of other languages in the world have prepositions—or some other closed-class category like postpositions, case-markers, or a restricted set of verbs—that express spatial relationships in terms of fairly schematic structural properties of figure and landmark objects; however, this research also demonstrates that languages vary greatly in the details of the spatial concepts they encode (e.g., Bickel & Gaenszle, 1999; Danziger, 1998; Haviland & Levinson, 1994; Levinson, 1996, 2003; Senft, 1997). For instance, instead of having prepositions corresponding to English *in* and *on,* Finnish has case-markers that distinguish between so-called "intimate" and "nonintimate" types of spatial relationships (Bowerman, 1996). Relationships involving containment (an apple in a bowl) and attachment (a handle on a door) are treated as intimate and coded by one case-marker, *-ssa,* whereas relationships involving loose horizontal support (a cup on a table) are treated as nonintimate and coded by a different case-marker, *-lla.* More radically, Zapotec, a language in Mexico, describes locations by metaphorically imposing the schematic body-part organisation of a bipedal or quadrupedal animal onto an inanimate landmark object, and then identifying the figure object as being at, say, its face, arm, leg, or belly (MacLaurey, 1989). Substantial crosslinguistic diversity is also found in the domain of "front–back" spatial relationships. For example, in Hausa, a West African language, the front of a tree is not construed as the side facing the observer, but rather as the side facing away from the observer—a strategy that employs an egocentric "orientation-preserving" frame of reference (Hill, 1982). Even more surprising is Arrernte, an Australian language that lacks terms like *front, back, left,* and *right* and instead has only cardinal direction terms like (in rough translation) *north, south, east,* and *west,* which are based on an absolute, allocentric frame of reference anchored in celestial azimuths (Pederson, Danziger, Wilkins, Levinson, Kita, & Seuft, 1998). Remarkably, speakers regularly use these words to describe spatial arrays at every level of scale, from inches to miles. Other languages around the world have sets of regularly used cardinal direction terms that are grounded in salient environmental features like mountain slopes ("uphill" vs. "downhill"), river drainages ("upriver" vs. "downriver"), and prevailing wind patterns ("upwind" vs. "downwind") (Levinson, 1996, 2003).

This crosslinguistic diversity is important because it indicates that when people talk about the spatial world, they must conceptualise their experience in ways that reflect the unique perspective captured by the inventory of expressions in the given language—a process that Slobin refers to as "thinking for speaking" (Slobin, 1996). Indeed, the meanings of locative prepositions may be distinct from the kinds of spatial representations that are used for nonlinguistic purposes such as perceptual categorisation and motor control. This idea has recently been supported by psycholinguistic as well as neuropsychological studies (Chatterjee, 2001; Crawford, Regier, & Huttenlocher, 2000; Kemmerer & Tranel, 2000a; Munnich, Landau, & Dosher, 2001), and we elaborate this topic in greater detail in the Discussion.

## The neuroanatomical correlates of locative prepositions

Very little is currently known about the neural systems that are responsible for retrieving the semantic structures and lexical forms for locative prepositions. Some indirect evidence comes from studies of agrammatic aphasic patients, who characteristically manifest impairments in the use of closed-class lexical items, often but not always including prepositions (e.g., Caplan, 1991; Friederici, 1982, 1985; Friederici, Schönle, & Garrett, 1982; Froud, 2001; Grodzinsky, 1988, 1991; Saffran, Schwartz, & Marin, 1980; Schwartz, Saffran, & Marin, 1980; Tesak & Hummer, 1994; Zurif & Caramazza, 1976). Agrammatism is frequently associated with left perisylvian lesions (e.g., Vanier & Caplan, 1990), and thus it can be postulated that neural structures in this large region might play an important role in processing locative prepositions. This view is supported by several detailed case studies of brain-damaged subjects who clearly exhibit impaired production, comprehension, and semantic analysis of locative prepositions and whose lesions are within the left perisylvian region, especially the frontoparietal sector (Kemmerer, 2004; Kemmerer & Tranel, 2000a, 2003). Recent functional imaging studies have yielded some additional preliminary findings that are anatomically more precise. Damasio, Grabowski, Tranel, Ponto, Hichwa, and Damasio (2001) found in a PET study that naming static spatial relationships with locative prepositions activated regions in the left inferior prefrontal cortex and the left supramarginal gyrus. A similar result was reported by Emmorey et al. (2002) in a PET study that used hearing native American Sign Language signers as subjects (see also Emmorey et al., 2003). But in general, the question of which neural structures are important operators of locative prepositions has received little research attention, and the goal of the study reported here was to begin to fill this lacuna in the cognitive neuroscience literature.

## The current report

We report here on two studies, aimed at exploring the neural correlates of processing locative prepositions, and the nature and specificity of this relationship.

Study 1 addressed the following hypothesis: Processing the meanings of locative prepositions depends on neural structures in the left inferior prefrontal cortex, and on neural structures in the left inferior parietal cortex. We tested this hypothesis using the lesion method in a group of 78 brain-damaged subjects.

Study 2 addressed the following questions regarding the nature and specificity of the relationship hypothesised in Study 1 above: (1) In subjects with impaired processing of the meanings of locative prepositions, what is the status of processing conceptual knowledge and lexical forms for actions? (2) In subjects with impaired processing of the meanings of locative prepositions, what is the status of processing conceptual knowledge and lexical forms for various categories of concrete entities? (3) Are locative preposition processing defects accompanied by impairments in (a) basic aspects of spatial processing, and (b) working memory? (4) What are the lesion correlates of pervasive impairments of locative preposition processing? These questions were addressed in a subset of the subjects who participated in Study 1.

# STUDY 1

## Method

### *Subjects*

Seventy-eight subjects with circumscribed unilateral left (*n* = 48) or right (*n* = 30) hemisphere brain damage were selected from the Patient Registry of the University of Iowa's Division of Cognitive Neuroscience. All gave informed consent in accordance with the Human Subjects Committee of the University of Iowa. The distribution of lesions allowed us to probe most of the left hemisphere and a substantial portion of the right hemisphere. It should be noted that although Study 1 was hypothesis driven, as elaborated earlier, the broad-based lesion sampling approach we utilised here allowed a powerful test of which brain regions are, and are not, crucial for performance of the experimental tasks. That is, by sampling many different brain regions, we could determine not only whether our main hypothesis was supported (i.e., that processing the meanings of locative prepositions depends on neural structures in left inferior prefrontal cortex and left inferior parietal cortex), but also whether there might be other brain regions that are also important for processing the meanings of locative prepositions. This is an important rationale for using a broad-based lesion sampling approach in Study 1.

The subjects' lesions were caused by either cerebrovascular disease ($n$ = 61), surgical treatment of arteriovenous malformation ($n$ = 3), or temporal lobectomy ($n$ = 14). To be eligible for the study, subjects had to have lesions that could be analysed with our MAP-3 technique (see below), and they had to have left-hemisphere language dominance (as determined from neurological, WADA, and neuropsychological testing). Handedness, measured with the Geschwind-Oldfield Questionnaire, which has a scale ranging from full right-handedness (+100) to full left-handedness (–100), was distributed as follows: 73 subjects were fully right-handed (+90 or greater); 3 were primarily right-handed (+80, +50, +40); 1 was fully left-handed (–100); and 1 was mixed-handed (+10).

All subjects had been extensively characterised neuropsychologically and neuroanatomically, according to standard protocols (Damasio & Frank, 1992; Frank, Damasio, & Grabowski, 1997; Tranel, 1996). All subjects had normal intelligence (as measured by the Wechsler Adult Intelligence Scale-III), and no difficulty attending to or perceiving visual stimuli, as determined by detailed neuropsychological assessment. None of the subjects had defects in discriminating red and green, as judged from standard assessment of colour vision (see Tranel, 2003). Some of the subjects with left hemisphere lesions were recovered aphasics. However, none of the subjects had residual aphasia of such a degree so as to preclude their comprehension of the experimental tasks. We were very careful to exclude subjects who could not comprehend the tasks, or who had any difficulty understanding the content of the queries used in the tasks (3 subjects were excluded on this basis, prior to forming the group of 78 noted above; the determination of exclusion was made by a clinical neuropsychologist who was not involved in the planning or execution of the current study).

All data, including standard neuropsychological measures, neuroanatomical data, and the experimental tasks, were obtained in the subjects' chronic phase, at least 3 months post lesion onset. In regard to the experimental tasks for prepositions, the average time at which subjects were tested was 71 months ($SD$ = 56) post lesion onset.

A comparison group of normal subjects was also studied. These were 60 persons who were selected so as to be free of neurological or psychiatric disease. They participated in the experiments on a voluntary basis, and were compensated financially for their time. The comparison group (CG) and the brain-damaged group (BD) had the following general demographic characteristics: female/male gender ratio (CG = 33/27; BD = 26/52); average age (CG = 31, $SD$ = 9; BD = 52, $SD$ = 14); average educational level (CG = 16, $SD$ = 2; BD = 14, $SD$ = 3); preponderance of right-handedness (CG = 92% right-handed, 8% non-right-handed; BD = 97% right-handed, 3% non-right-handed); and racial composition (CG = 90% white, 10% nonwhite; BD = 94% white, 6% nonwhite). Overall, the comparison group is somewhat younger, and slightly better educated, than the brain-damaged group; otherwise, the groups are demographically similar (we note that both groups were drawn from a rural midwestern population whose overall demographic characteristics are comparable to those of the study groups). Since the key contrasts in the analyses utilised in this study involve subsets of brain-damaged subjects (and not the normal comparison group), the age and education differences are not considered to be of any direct consequence for the primary objectives of the study. The comparison group was studied so that we would have data from normal individuals regarding performances on the various experimental tests, and to inform our interpretations of test scores in the brain-damaged subjects.

### *Stimuli and procedures*

Four tests were used to evaluate subjects' production, comprehension, and semantic analysis of English locative prepositions. All of the tests require semantic processing of prepositions as well as visual processing of pictures, but the tests vary along the following parameters: (1) whether the phonological output forms of prepositions must be produced, (2) whether the orthographic and/or phonological input forms of prepositions must be recognised, (3) whether the pictures show real objects or abstract shapes, and (4) whether each item has one picture or three pictures. The primary rationale for including these various tests derived from our desire to have broad coverage of different ways of processing locative prepositions, in a manner akin to the strategy we have utilised previously (Kemmerer, 2004; Kemmerer & Tranel, 2000a, 2003; Kemmerer, Tranel, & Barrash, 2001). In general, our goal was to assess carefully and extensively the subjects' knowledge of the meaning of locative prepositions, and we felt that multiple tests, with partially nonoverlapping processing requirements, would provide a reasonable means of such assessment.

For three of the tests, the stimuli were drawn from a set of black-and-white objects in various spatial relationships. Some of these came from the Photo Resource Kit (Pro-Ed, 8700 Shoal Creek Blvd., Austin, TX 78758), and others were specially constructed by the authors. In each picture, the *figure object* was explicitly indicated by a thinner arrow, and the *landmark object* by a thicker arrow (see Figure 1 for examples). These pictures were initially pilot tested in a large group of normal subjects ($n$ = 120). We used the responses from these subjects to determine which pictures had high name agreement, specifically, 90% or greater (using formulae provided by Snodgrass & Vanderwart, 1980, and Fiez & Tranel, 1997), and for which the pilot subjects provided either a single preposition or two very similar prepositions (e.g., *behind* and *in back of*). We eventually ended up with a set of 80 pictures that conformed to these criteria. The pictures showed spatial relationships corresponding to the following prepositions: *on* (13), *in* (13), *around* (3), *through* (3), *above/over* (13), *below/under* (13), *in front of* (6), *in back of/behind* (6), *next to/beside* (6), and *between* (4).[2] For many of these prepositions, prototypical as well as nonprototypical situations were illustrated in the pictures.

*Test #1: Naming*. The Naming Test is made up of 80 pictures. The pictures were presented to the subject one at a time on a Caramate 4000 slide projector in free field. For each, the subject was asked a question designed to elicit the preposition that best describes the depicted spatial relationship—e.g., "Where is the fork?" (Figure 1a; target response = *in*). The subject was instructed to avoid nouns, verbs, adjectives, and prepositional phrases, and to be as precise as possible in selecting a preposition response.

*Test #2: Matching*. The Matching Test is made up of 50 sets of three pictures each, with each set arranged vertically on a legal-size page. The subject's task was to choose which picture in each set best represents a given preposition. For example (Figure 1b), one item features the preposition *in*, and the three pictures show (1) a toothbrush *in* a glass, (2) a balloon *above* a barrel, and (3) a pencil *on* a book. The prepositions were presented in written format and were also read aloud to the subject, i.e., input was both orthographic and phonological, and short-term memory demands were negligible. In addition, the pictures were carefully chosen so that in each item, one of the distractors was more closely related to the target (e.g., *in* vs. *on*), while the other was more distantly related (e.g., *in* vs. *above*). Pictures showing *between* relationships were not included in this test, because they necessarily involve three key objects, whereas pictures for all of the other prepositions involve only two key objects. The numbers of pictures representing each preposition were as follows: *on* (8), *in* (8), *around* (3), *through* (3), *above/over* (8), *below/under* (8), *in front of* (4), *in back of/behind* (4), *next to/beside* (4).

[2] For some of the pictures showing relations of superiority, the preposition favoured by the pilot subjects was *above* rather than *over*, and for others it was the reverse; these items were scored accordingly (i.e., for some items, *above* was correct and *over* was not, and for other items, the reverse was true). However, for all of the pictures showing relations of inferiority, the two prepositions *below* and *under* were treated as equivalent, because the pilot subjects used these terms interchangeably (see Kemmerer & Tranel, 2000a, for further details).

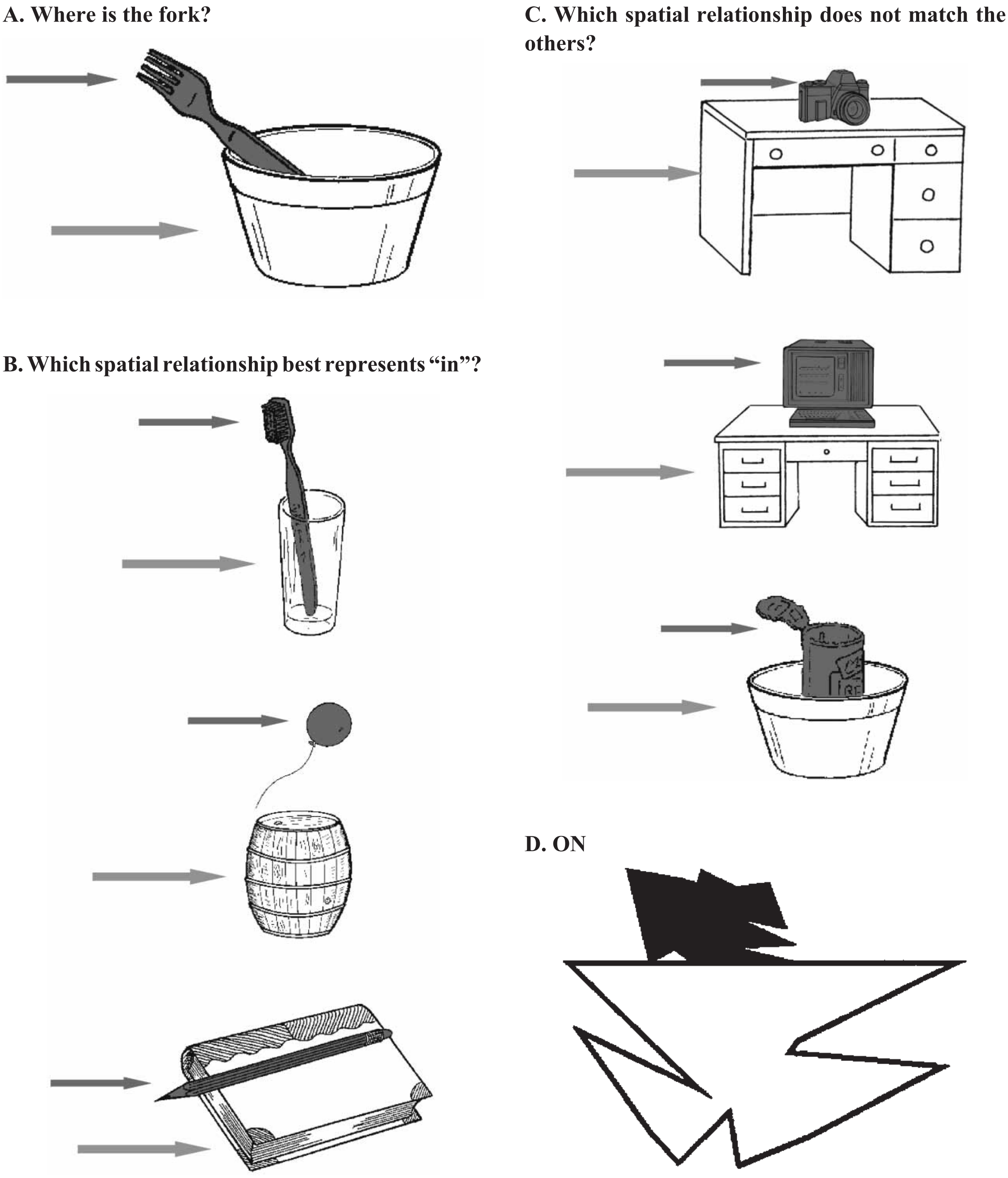


**Figure 1.** *Examples of the types of stimuli used in the four spatial relationship tests. (A) Naming Test. The subject is asked to name the relationship between the figure object (fork) and ground object (bowl) (in). (B) Matching Test. The subject is asked to choose which picture best represents in (1, top picture). (C) Odd One Out Test. The subject is asked to determine which picture shows a spatial relationship that is different from the other two (3, bottom picture). (D) Verification Test. The subject is asked to determine whether the meaning of the preposition correctly describes the relationship of the dark object, relative to the light one (correct answer = yes).*

*Test #3: Odd One Out*. The Odd One Out Test is made up of 45 items. Each item has three pictures, composed and presented as in the Matching Test described above. Here, though, the subject's task was to determine which picture in each set shows a spatial relationship that is different from the others (Figure 1c). For some of the picture sets, the two similar pictures both represented prototypical instances of the same preposition (e.g., a camera *on* a desk, a computer *on* a desk), whereas for other picture sets, one of the two similar pictures represented a prototypical instance and the other a non-prototypical instance of the same preposition (e.g., a cat *on* a kitchen counter, a fingernail *on* a finger). Pictures showing *between* relationships were not included, for the same reason as in the Matching Test. We note that many of the items in the Odd One Out Test probably require access to the crosslinguistically unique semantic structures of English prepositions, in order to be solved correctly. For example, one item on the test has the following three pictures: (1) a design *on* the side of a coffee cup; (2) a boy *on* a tricycle; and (3) eggs *in* a carton. In order to determine that the first two pictures are similar, and that the third one is the "odd one out," the subject has to recognise that the first two pictures both represent spatial relationships that involve "contact" but not "containment," whereas the third picture represents a spatial relationship that involves both of these features, especially the latter. These are the language-specific semantic features that distinguish *on* from *in*.

*Test #4: Verification*. The Verification Test employs a different set of stimuli than the first three tests.[3] The subject is shown 44 line drawings of abstract shapes in various spatial relationships (Figure 1d). Each spatial relationship is shown on a separate page. One shape is dark and the other is light (for the *between* items, there were two light shapes and one dark shape), and there is a preposition written at the top of the page (the prepositions were also read aloud to the subject so that input was both orthographic and phonological, just like in the Matching Test). The subject's task was to determine whether the meaning of the preposition correctly describes the location of the dark object, relative to the light one(s). The numbers of pictures representing each preposition were as follows: *in* (6), *on* (6), *around* (4), *across* (4), *above/over* (6), *below/under* (6), *next to/beside* (6), *between* (6). This test is considered a fairly "pure" measure of the subject's knowledge of the topological and projective meanings of locative prepositions, since the shapes in the stimuli do not represent real objects and the visual processing of object-internal features is minimised.

## Data quantification

*Neuropsychological data*. For all items on the four tests, subjects' answers were compared to those that had been established as correct based on the pilot testing, and then scored as correct or incorrect. Then, for each subject and for each test, a percentage correct score was calculated by dividing the number of correct responses by the number of items on the test, and multiplying by 100.

The following method, which we have used previously in a similar context (see Tranel, Adolphs, Damasio, & Damasio, 2001; Tranel, Kemmerer, Damasio, Adolphs, & Damasio, 2003), was used to determine a cutoff score for each test—i.e., a level above which subjects' scores were considered unimpaired, and below which subjects' scores were considered impaired. For each test, data from the 78 brain-damaged subjects were plotted according to percentage correct scores. To explore whether these scores were drawn from one or from more than one Gaussian normal distribution, we obtained quantile-quantile plots (actual data vs the scores that would be expected if the data were normally distributed, or "N-scores"), as follows. Typically, the *i*th N-score for a sample of size *N* is obtained from the mean of the sampling distribution of the *i*th order statistic in a sample of N values

[3] We thank Karen Emmorey for providing the materials for this test; some of these stimuli were also used in the PET study by H. Damasio et al. (2001).

drawn from a standard normal distribution. (In order to increase resistance to skewness, we conducted the analysis using the medians of the sampling distributions, rather than the means.) The *i*th median order statistic of a sample size *N* was approximated by the function:

$$\text{InvGaussian}((i-1/3)/(N+1/3)),$$

where InvGaussian is the inverse Gaussian (or normal) cumulative distribution function. We used a dynamic least-squares regression of actual scores versus N-scores to isolate those scores that are most likely to belong to the same distribution. Beginning at each extreme of the score range (the lowest score and the highest score), we calculated the least-squares fit continuously as additional scores were added, until a maximum was reached. At this point, a cutoff score was set. All of the four tests were subjected to this analysis, and cutoff scores were set for all of the tests. For each test, scores below the cutoff were designated as impaired, and scores above the cutoff were designated as unimpaired.

To validate further the procedure for determining impairment, we compared the findings obtained from the method described immediately above to those from the normal comparison group. In particular, we were interested in the contrast between the brain-damaged subjects who were classified as unimpaired (based on the method described above), and the normal comparison subjects. As the summary data in Table 1 indicate, the two groups had very similar scores on all four tests, an outcome that supports the validity of our classification procedure. Also, the between-group effect sizes ($d$) for the unimpaired brain-damaged subjects versus the normal comparison subjects indicated relatively minimal differences between the groups (Table 2), as would be expected based on the mean group performances (average $d$ = 0.31; average Confidence Interval: 0.03 – 0.67).

*Neuroanatomical data*. The neuroanatomical analysis was based on magnetic resonance (MR) data obtained in a 1.5 Tesla scanner with an SPg sequence of thin (1.5 mm) and contiguous $T_1$ weighted coronal cuts, and reconstructed in three dimensions using Brainvox (Damasio, 2000; Damasio & Frank, 1992; Frank et al., 1997). (In a few subjects in whom an MR could not be obtained, the analysis was based on computerised

**Table 1.** *Summary of group performances on the four spatial relationship tests (means and standard deviations)*

| | *Test* | | | |
|---|---|---|---|---|
| *Group*[a] | *Naming* | *Matching* | *Odd One Out* | *Verification* |
| Impaired Ss, N | 21 | 15 | 15 | 16 |
| Mean | 64.3 | 82.3 | 70.0 | 81.6 |
| *SD* | 24.6 | 13.8 | 15.1 | 7.5 |
| Unimpaired Ss, N | 57 | 62 | 62 | 45 |
| Mean | 95.9 | 98.9 | 96.2 | 92.8 |
| *SD* | 3.5 | 1.5 | 3.9 | 2.8 |
| Normal comparison ($n$ = 60) | 93.3 | 99.4 | 95.2 | 91.6 |
| Mean | 6.6 | 1.2 | 6.5 | 8.9 |
| *SD* | | | | |
| Cutoff score | <89 | <95 | <87 | <89 |

[a] Not every brain-damaged subject had every test, which is why there are differences in the total numbers of impaired plus unimpaired subjects. The Verification Test, in particular, was missing for a number of subjects. However, given that (1) most of the subjects with deficits on this test also had deficits on some of the other tests, and (2) most of the subjects for whom this test is missing did very well on the other tests, we do not believe that the missing data here are problematic for interpreting the available results.

**Table 2.** *Effect sizes (d) and confidence intervals for between-group comparisons on the four spatial relationship tests*

| | Group contrast | | |
|---|---|---|---|
| *Test* | *Imp vs. Unimp* | *Imp vs. Nml* | *Unimp vs. Nml* |
| *Naming* | | | |
| Effect size | 2.44 | 2.13 | 0.49 |
| Confidence interval | 1.78–3.04 | 1.51–2.70 | 0.12–0.85 |
| *Matching* | | | |
| Effect size | 2.72 | 2.79 | 0.37 |
| Confidence interval | 1.98–3.39 | 2.04–2.79 | 0.01–0.72 |
| *Odd One Out* | | | |
| Effect size | 3.53 | 2.86 | 0.19 |
| Confidence interval | 2.71–4.29 | 2.10–3.55 | –0.17–0.54 |
| *Verification* | | | |
| Effect size | 2.50 | 1.16 | 0.17 |
| Confidence interval | 1.74–3.18 | 0.57–1.73 | –0.22–0.56 |

*Imp. = brain-damaged subjects who were impaired on the test, as indicated in Table 1; Unimp = brain-damaged subjects who were unimpaired on the test, as indicated in Table 1; Nml = the 60 normal subjects in the Comparison group.

axial tomography, or CT, data.) The final anatomical description of the lesion overlap and of its placement relative to neuroanatomical landmarks was performed with Brainvox, using the MAP-3 technique. All lesions in this set were transposed and manually warped into a normal 3-D reconstructed brain, so as to permit the determination of the maximal overlap of lesions relative to subjects grouped by neuropsychological defect according to the method specified above.

A detailed description of MAP-3 is provided in Damasio (2000); in brief, it entails the following: (1) A normal 3-D reconstructed brain is resliced so as to match the slices of the MR/CT of the subject and create a correspondence between each of the subject's MR/CT slices and the slices of the normal brain. (2) The contour of the lesion on each slice is then transposed onto the matched slices of the normal brain, taking into consideration the distance from the edge of the lesion to appropriate anatomical landmarks. (3) For each lesion, the collection of contours constitutes an "object" that can be co-rendered with the normal brain. The objects in any given group can intersect in space, and thus yield a maximal overlap relative to both surface damage and depth extension. The number of subjects contributing to this overlap is calculated and recorded.

***Data analysis***

To analyse the data in regard to our hypothesis, we grouped the subjects according to their performances on the four tests, and analysed the neuroanatomical results. We utilised a lesion analysis approach that we have used previously with comparable datasets (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Tranel et al., 2001, 2003). Specifically, for each test, we contrasted the group of subjects who fell in the "impaired" partition of the distribution of scores, with a like-sized group of subjects who fell in the "unimpaired" partition of the distribution. A MAP-3 lesion overlap was calculated for each group, and then the two MAP-3 overlaps were contrasted by subtracting one from the other (impaired minus unimpaired). Thus, neuropsychological performance (test performance) served as the independent variable, and lesion overlap (according to MAP-3) served as the dependent variable. To compare neuropsychological performances of groups of subjects, we calculated point estimates, effect sizes, and confidence intervals (see below).[4]

The lesion subtraction proceeded arithmetically for each brain voxel (see Adolphs et al., 2000, for additional details about this method). We took the number of subjects with unimpaired test scores who had lesions at a given voxel, and subtracted this from the total number of subjects with impaired test scores who had lesions at that same voxel. Thus, the subtraction yields a difference in the number of lesions at each voxel, reflecting the proportion of subjects with impaired scores, compared with the proportion of subjects with unimpaired scores, who had damage at that voxel. This arithmetic subtraction of subject numbers was applied to all voxels in the brain.

The standard we used for defining a region of voxels as "significant" was a difference in the overlap subtraction of five subjects or more. That is, if subtracting unimpaired subjects from impaired subjects yielded a difference of five subjects or more for a particular region of voxels, that region was considered to be involved crucially in the experimental test performance. The overlap subtraction results were color coded, and the volumes were depicted on lateral and coronal brain views.

The use of a five-subject threshold in the overlap subtraction analysis is based on extensive prior investigations in our laboratory, which have determined that this is a valid criterion for identifying, with a high degree of specificity and sensitivity, brain regions that are important for experimental task performance (see Damasio et al., 2004). For instance, in H. Damasio et al., we determined that the probability of obtaining by chance an overlap subtraction difference of 5 or more was smaller than .001 in a sample of 139 brain-damaged subjects with widely varying lesion sizes and locations. H. Damasio et al. also addressed this issue by creating 10 random lists of 139 brain-damaged subjects, again, subjects with widely varying lesion sizes and locations. In each list, the first 20 subjects were selected to stand in for the random "abnormal" group, and the next 90 were selected to stand in for the random "normal" group. For eight of these combinations, no overlap of 5 subjects was detected. For the other two lists, there were no more than a few clusters of contiguous overlapping voxels, and the largest volume of such contiguous clusters was at least 12 times smaller than the volume of contiguous clusters in the actual overlap subtraction maps. In short, multiple overlap subtractions of randomly grouped subjects demonstrated that overlap differences of 5 or more were rare, and never yielded a large or functionally meaningful set of contiguous voxels in the outcome.

## Results

Results are presented for each of the four tests, in terms of the subjects' performances on the tests (Table 1) and in terms of the neuroanatomical findings (Figures 2–5). Table 2 provides between-group comparisons on the four tests, as a function of pair-wise contrasts of the three groups. For each comparison (impaired vs. unimpaired; impaired vs. normal; unimpaired vs. normal), effect sizes (*d*) and confidence intervals are provided according to recommendations set forth by the American Psychological Association (2001; Wilkinson & the Task Force on Statistical Interference, 1999).

### *Naming*

There were 21 brain-damaged subjects with impaired scores on the Naming Test (Table 1). As a group, the performance of these subjects was well below that of the unimpaired brain-damaged subjects ($d = 2.44$) and of the normal comparison group ($d = 2.13$) (Table 2). The unimpaired brain-damaged group and the normal comparison group had similar mean scores. As the data in Table 2 show, the lower bounds on the confidence intervals

[4] Parametric statistical approaches would not be inappropriate here, but they are relatively uninformative given that the subjects were classified in the first place according to their test performances. The group means and standard deviations (Table 1), and effect sizes with confidence intervals (Table 2), provide a more complete picture of the relative group test performances.

for the contrasts of the impaired group to the unimpaired group and comparison group were very large effect sizes (1.78 and 1.51, respectively), indicating that the impaired subjects were in fact quite defective on the Naming Test.

The MAP-3 subtraction of 21 unimpaired subjects from the 21 impaired subjects indicated maximal lesion overlap in the left inferior prefrontal region, specifically, in the pars opercularis, pars triangularis, and underlying white matter (Figure 2). As shown on the coronal cuts, the overlap extends posteriorly into the anterior insular cortex, and into the anterior part of the white matter underneath the inferior parietal operculum. The overlap is seen in as many as eight subjects in parts of the prefrontal region and white matter.

### *Matching*

There were 15 brain-damaged subjects with impaired scores on the Matching Test (Table 1). As a group, their performance was well below that of the unimpaired brain-damaged subjects ($d$ = 2.72) and of the normal comparison group ($d$ = 2.79) (Table 2). The unimpaired brain-damaged group and the comparison group did not differ substantially from one another. The differences between the impaired group and the other two groups were large, reflected in the lower bounds of the

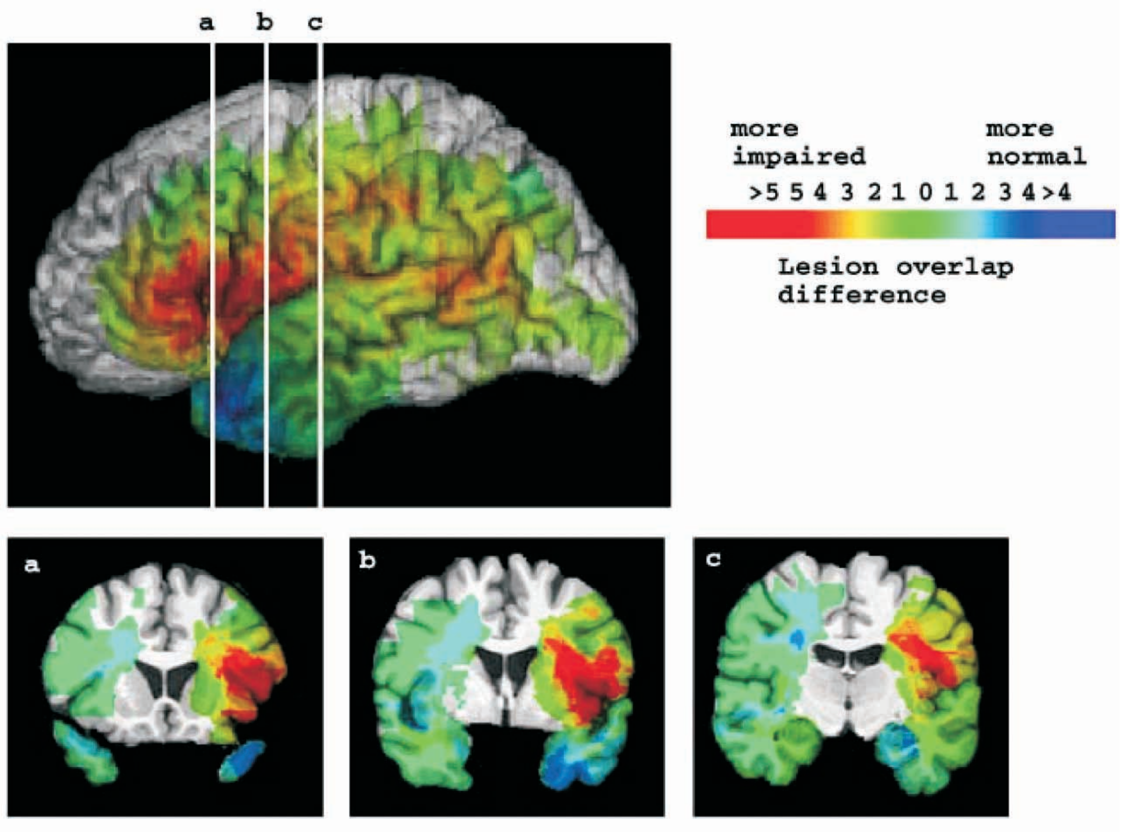


**Figure 2.** *Naming Test: Subtraction of lesion overlaps for 21 unimpaired subjects from the lesion overlaps for 21 impaired subjects, derived from MAP-3. The colour bar indicates the number of lesions in the overlap difference. (Red depicts the threshold criterion of 5 or more impaired than unimpaired subjects; this difference reached as high as 8 within the red-coded zone.) The white lines denote the planes of coronal sections depicted in the figure (sections a–c). The subtraction image shows that the area of highest lesion overlap specific to the impaired subjects is in the left hemisphere, in the pars opercularis and pars triangularis of the frontal operculum, the underlying white matter, and extending posteriorly into the anterior sector of the white matter underneath the inferior parietal operculum.*

confidence intervals being very large effect sizes for both contrasts (*d*s 1.98 and 2.04, respectively).

The MAP-3 subtraction of 15 unimpaired subjects from the 15 impaired subjects indicated maximal lesion overlap in the left frontal operculum (pars opercularis and pars triangularis) and the supramarginal gyrus (Figure 3). As shown in the coronal cuts, the overlap involves the white matter underneath the inferior prefrontal region, and much of the white matter underneath the supramarginal gyrus and the inferior parietal operculum. The posterior extent of the overlap reaches as far back as the white matter underneath the posterior tip of the sylvian fissure. Most of the overlap region involves as many as seven subjects.

### *Odd One Out Test*

There were 15 brain-damaged subjects with impaired scores on the Odd One Out Test (Table 1). As a group, their performance was well below that of the unimpaired brain-damaged subjects ($d = 3.53$) and of the normal comparison group ($d = 2.86$) (Table 2). The unimpaired brain-damaged group and the comparison group performed very similarly. The magnitude of the differences between the impaired group and the other two groups was again quite substantial, as the lower bounds of the confidence intervals were effect sizes of 2.71 and 2.10 for the unimpaired and normal groups, respectively.

The MAP-3 subtraction of 15 unimpaired subjects from the 15 impaired subjects indicated maximal lesion overlap in the left inferior prefrontal region, specifically, in the pars opercularis, pars triangularis, and underlying white matter (Figure 4). As shown on the coronal cuts, the overlap extends posteriorly into a bit of the anterior insular cortex, and into the anterior part of the white matter underneath the inferior parietal operculum. The overlap involves as many as seven subjects in parts of the prefrontal region and white matter.

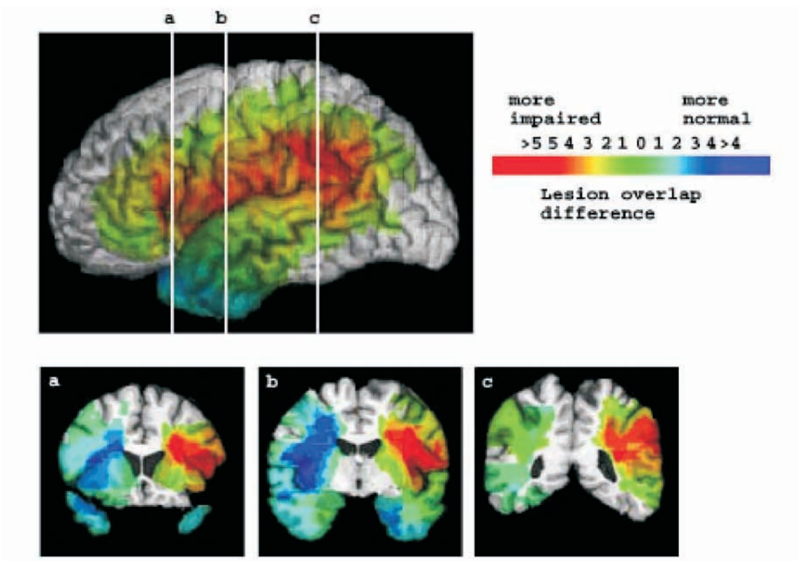


**Figure 3.** *Matching Test: Subtraction of lesion overlaps for 15 unimpaired subjects from the lesion overlaps for 15 impaired subjects, derived from MAP-3. The colour bar indicates the number of lesions in the overlap difference. (Red depicts the threshold criterion of 5 or more impaired than unimpaired subjects; this difference reached as high as 7 within the red-coded zone.) The white lines denote the planes of coronal sections depicted in the figure (sections a–c). The subtraction image shows that the area of highest lesion overlap specific to the impaired subjects is in the left hemisphere, in the frontal operculum (pars opercularis and pars triangularis) and the supramarginal gyrus. The overlap involves the white matter underneath the inferior prefrontal region, and much of the white matter underneath the supramarginal gyrus and the inferior parietal operculum.*

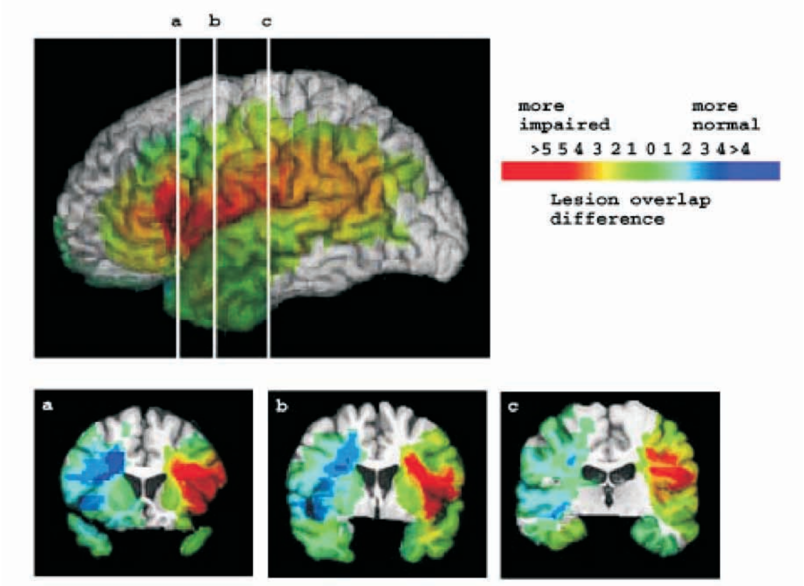


**Figure 4.** *Odd One Out Test: Subtraction of lesion overlaps for 15 unimpaired subjects from the lesion overlaps for 15 impaired subjects, derived from MAP-3. The colour bar indicates the number of lesions in the overlap difference. (Red depicts the threshold criterion of 5 or more impaired than unimpaired subjects; this difference reached as high as 7 within the red-coded zone.) The white lines denote the planes of coronal sections depicted in the figure (sections a–c). The subtraction image shows that the area of highest lesion overlap specific to the impaired subjects is in the left hemisphere, in the pars opercularis and pars triangularis of the frontal operculum, the underlying white matter, and extending posteriorly into the anterior sector of the white matter underneath the inferior parietal operculum.*

### *Verification*

There were 16 brain-damaged subjects with impaired scores on the Verification Test (Table 1). As a group, their performance was well below that of the unimpaired brain-damaged subjects ($d$ = 2.50) and of the normal comparison group ($d$ = 1.16) (Table 2). The unimpaired brain-damaged group and the comparison group did not differ from one another. The impaired group was very different from both the unimpaired group (effect size for lower bound of confidence interval = 1.74) and the normal comparison group (effect size for lower bound of confidence interval = 0.57).

The MAP-3 subtraction of 16 unimpaired subjects from the 16 impaired subjects indicated maximal lesion overlap in the left inferior prefrontal region, specifically, in the pars opercularis, pars triangularis, and underlying white matter (Figure 5). As shown on the coronal cuts, the overlap extends posteriorly into the anterior insular cortex and into the anterior part of the white matter underneath the inferior parietal operculum. The overlap involves as many as seven subjects in parts of the prefrontal region and white matter.

# STUDY 2

## Method

### *Subjects*

To explore the nature and specificity of the findings reported in Study 1, we conducted a detailed investigation focused on a subset of the subjects from Study 1. Specifically, we singled out the subjects who demonstrated the most consistent and severe impairments on the four locative preposition tests, namely, those subjects who performed defectively on all four tests, as defined in Study 1. There were six subjects (all with left hemisphere lesions; see below) who failed all four locative preposition tests.

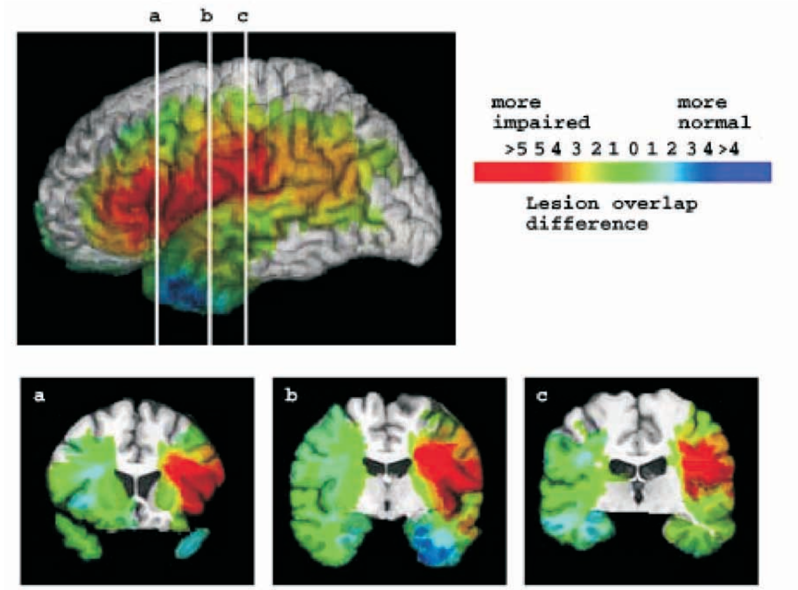


**Figure 5.** *Verification Test: Subtraction of lesion overlaps for 16 unimpaired subjects from the lesion overlaps for 16 impaired subjects, derived from MAP-3. The colour bar indicates the number of lesions in the overlap difference. (Red depicts the threshold criterion of 5 or more impaired than unimpaired subjects; this difference reached as high as 7 within the red-coded zone.) The white lines denote the planes of coronal sections depicted in the figure (sections a–c). The subtraction image shows that the area of highest lesion overlap specific to the impaired subjects is in the left hemisphere, in the pars opercularis and pars triangularis of the frontal operculum, the underlying white matter, and extending posteriorly into the anterior sector of the white matter underneath the inferior parietal operculum.*

These subjects are the focus of the investigations reported in the current section, as part of Study 2, and we refer to these subjects as the "target" subjects in this section.

We would like to emphasise that by focusing on subjects who failed all four of the locative preposition tests, there is some assurance that such subjects have reliable and valid impairments in their knowledge of locative prepositions, and not just isolated defects in certain processing operations that might be necessary for some of the tests but not others (cf. Kemmerer et al., 2001). For example, the Naming Test depends heavily on retrieving phonological forms; by contrast, the Odd One Out Test depends heavily on comparing the meanings of different prepositions; and so on. As we noted earlier, the use of multiple tests—and in this study, the focus on subjects who failed all of these tests—supports the contention that we are tapping into genuine disorders of lexicosemantic knowledge for locative prepositions.

***Experimental procedures***

A primary goal was to assess the status of conceptual knowledge and retrieval of lexical forms for actions and concrete entities. We also sought to investigate the status of basic spatial functions and working memory in the six target subjects. The following procedures were utilised to accomplish these objectives.

*Actions*. To measure *naming* of actions, we used the Action Naming Test, a 100-item test that requires the retrieval of verbs to name various ongoing and completed actions (Fiez & Tranel, 1997; also see Kemmerer & Tranel, 2000b, 2000c; Tranel et al., 2001). To measure *conceptual* knowledge for actions, we used a set of five tests designed to assess this type of knowledge (Fiez & Tranel, 1997; also see Kemmerer et al., 2001; Tranel et al., 2003).

1. The Picture-Word Matching Test, which has 69 items. Each item is made up of two pictures

of ongoing or completed actions, along with a verb; the subject is asked to choose the picture that best matches the meaning of the verb.

2. The Picture Attribute Test, which comprises 72 items showing two pictures of ongoing or completed actions. For each item, the subject is asked to choose which picture best satisfies a certain criterion, e.g., "Which action would make the loudest sound? Which action would take the longest to complete?"

3. The Word Attribute Test, which has 62 items and is parallel to the Picture Attribute Test except that the stimuli are verbs instead of pictures.

4. The Picture Comparison Test, which comprises 24 items, each consisting of three pictures of ongoing actions. On each item, the subject is asked to choose the picture that shows an action that is "different" from the other two.

5. The Word Comparison Test, which has 44 items and is parallel to the Picture Comparison Test except that the stimuli are verbs instead of pictures.

*Concrete entities*. We assessed recognition and naming of concrete entities from six different conceptual categories: persons, animals, fruits/vegetables, tools, musical instruments, and vehicles. The stimuli and procedures for this have been published in detail previously (Damasio et al., 2004; Tranel, Damasio, & Damasio, 1997), but to summarise briefly, they entail the following. The stimuli are photographs and line drawings (selected from the Snodgrass & Vanderwart, 1980, set and from stimuli developed in our laboratory), distributed across the various categories as follows: persons (famous faces; $n$ = 133); animals ($n$ = 90); fruits/vegetables ($n$ = 67); tools ($n$ = 104); musical instruments ($n$ = 16); vehicles ($n$ = 23). The stimuli were shown as slides on a Caramate 4000 slide projector, in random order, in free field. For each stimulus, the subjects' task was to identify the stimulus, by telling the experimenter what (or who) the stimulus was. The subject was prompted to be more specific if they gave a vague or superordinate-level response. Time limits were not imposed. Responses were audiotaped and prepared as typewritten transcriptions, and the transcriptions were then scored by two raters who were blind to the experimental hypotheses.

For each subject, two measures were derived from this assessment: a recognition score (denoting retrieval of conceptual knowledge) and a naming score (denoting lexical retrieval). Each subject's response to each stimulus was scored as follows: If the stimulus was named correctly, the subject was given credit for a correct recognition response and for a correct naming response. If the stimulus was not named correctly, the subject's response was presented to two raters (as a typewritten transcription, as indicated above), and the raters were asked to determine what the stimulus was from the description alone, without having in front of them either the stimulus or its name. If either or both raters could identify the stimulus correctly based on the subject's description, the item was scored as a correct recognition response. Two scores were then calculated for each subject, for each of the six categories: (1) the recognition score was the number of items recognised correctly, divided by the total number in the category (and multiplied by 100 to yield a percentage correct score); (2) the naming score was the number of items named correctly, divided by the number of items recognised correctly (i.e., subjects were not penalised for failing to name items that they did not recognise). Again, the result was multiplied by 100 to yield a percentage correct score.

*Spatial processing*. Spatial processing was assessed with a battery of standardised neuropsychological tests, including three subtests from the Wechsler Adult Intelligence Scale-III (Matrix Reasoning, Block Design, Object Assembly), the Benton Facial Recognition Test, the Benton Judgment of Line Orientation Test, the Hooper Visual Organization Test, the Complex Figure Test (copy administration), and the Benton 3-Dimensional Block Construction Test (see Benton, Hamsher, Varney, & Spreen, 1983; Tranel, 1996). A full discussion of the processing requirements of these tests is well beyond the scope of this report, but it can be noted that the tests provide comprehensive and stringent assessment of a wide range of visual perceptual and visual constructional functions (see also Benton & Tranel, 1993).

*Working memory*. Verbal and spatial working memory were assessed with the following battery of standardised neuropsychological tests: the Digit Span and Arithmetic Reasoning subtests from the WAIS-III; the Benton Visual Retention Test; and the Wechsler Memory Scale-III (Working Memory Index). Again, we do not have space to discuss fully the processing requirements of these tests, but collectively, they provide a detailed assessment of working memory for both verbal and nonverbal material (see Tranel, 1996).

*General linguistic functioning*. All of the six target subjects were studied extensively in terms of their basic speech and linguistic functions (see Study 1, Methods). To give a more detailed picture of their linguistic profiles, we selected several key measures from the Multilingual Aphasia Examination, including the Token Test, Sentence Repetition, Aural Comprehension, and Reading Comprehension. Data for these measures are presented below as part of Study 2.

## Results

### *Knowledge for locative prepositions*

The individual performances of the six target subjects on the various locative preposition tests are enumerated in Table 3. It can be seen that all of the subjects produced highly impaired performances on the four tests. This subgroup stands out from the larger brain-damaged population studied in the current project (Study 1). While there were a few other subjects (four, to be exact) who failed three of the preposition tests, none of those subjects had highly defective scores (specifically, below 86% correct) on more than two tests, and all of those subjects had nearly perfect scores on one or two of the tests. And in the remaining subjects, 23 failed one or two tests, but performed very well on the others. In sum, based on the locative preposition test performances, one can clearly draw out a subgroup of six subjects who manifest considerably more severe and pervasive deficits in processing the meanings of locative prepositions than do any of the other brain-damaged subjects. The consistency and severity of the locative preposition processing impairments in these subjects are illustrated clearly in Table 3, where it can be seen that the target subjects performed, on average, anywhere from nearly 9 to more than 25 *SD*s below normal.

We also analysed the error profiles of the six target subjects with regard to the Naming Test. For each of the target subjects, we classified their errors on the Naming Test into one of four categories: *semantic* (incorrect prepositions, e.g., "on" for "in"), *phonological*, *omission*, and *other* (nonprepositional linguistic responses, e.g., "upper" for "above"). The errors were distributed in these categories in the following manner: semantic (19%), phonological (0%), omission (39%), other (4%). For two subjects

**Table 3.** *Knowledge for locative prepositions % correct (z-score in parentheses[a])*

| *Subject* | *Naming* | *Matching* | *Odd One Out* | *Verification* | *Average z-score*[b] |
|---|---|---|---|---|---|
| 1076 | 48 (−13.7) | 68 (−20.6) | 47 (−12.6) | 82 (−3.9) | −12.7 |
| 1726 | 66 (−8.5) | 72 (−17.9) | 73 (−5.9) | 84 (−3.1) | −8.9 |
| 1760 | 0 (−27.4) | 44 (−36.6) | 36 (−15.4) | 61 (−11.4) | −22.7 |
| 1962 | 68 (−8.0) | 74 (−16.6) | 62 (−8.8) | 72 (−7.4) | −10.2 |
| 1978 | 45 (−14.5) | 72 (−17.9) | 73 (−5.9) | 70 (−8.1) | −11.6 |
| 2054 | 0 (−27.4) | 34 (−43.3) | 27 (−17.7) | 52 (−14.6) | −25.8 |

[a] *z*-scores were calculated in relation to the mean (and *SD*) of the unimpaired brain-damaged subjects from Study 1. Following the definition of "impairment" presented in Study 1, every score on every test in the six subjects presented in Table 3 falls in the impaired range.
[b] The average *z*-score is the average across the four preposition tests, for each subject.

**Table 4.** *Knowledge for actions (% correct)*

| *Subject* | *Naming* | *Picture–Word matching* | *Picture attribute* | *Word attribute* | *Picture comparison* | *Word comparison* |
|---|---|---|---|---|---|---|
| 1076 | 31 | 83 | 83 | 66 | 88 | 66 |
| 1726 | 62 | 97 | 88 | 87 | 46 | 70 |
| 1760 | 0 | 90 | 83 | 83 | 80 | 70 |
| 1962 | 22 | 99 | 89 | 94 | 58 | 64 |
| 1978 | 62 | 84 | 83 | 85 | 40 | 70 |
| 2054 | 0 | 84 | 88 | 87 | 76 | 80 |
| Mean | 29.5 | 89.5 | 85.7 | 83.7 | 64.7 | 70.0 |
| (*SD*) | (28.0) | (7.1) | (2.9) | (9.4) | (19.5) | (5.5) |
| *Brain-damaged comparison subjects (n = 120)* | | | | | | |
| Mean | 81.0 | 94.7 | 91.2 | 92.2 | 80.3 | 83.6 |
| (*SD*) | (17.7) | (7.2) | (7.1) | (8.1) | (17.9) | (13.3) |
| *Fiez/Tranel comparison subjects*[a] | | | | | | |
| Mean | 85.2 | 92.1 | 91.7 | 94.8 | 83.6 | 88.7 |
| (*SD*) | (5.0) | (4.6) | (4.8) | (3.6) | (8.3) | (8.1) |

[a] Slight modifications of the tests were implemented by Kemmerer et al. (2001), and the means and *SD*s shown here are derived from the modified versions of the tests.

(1760, 2054), all of the errors were omissions, whereas in the other four subjects (1076, 1726, 1962, 1978), the semantic error type was most common. As the data indicate, phonological errors were nonexistent in this group.

### *Knowledge for actions*

The results of the investigation of retrieving words and conceptual knowledge for actions are presented in Table 4. As a point of comparison, we have provided the average performances (means and *SD*s) of a group of 120 brain-damaged subjects who have been studied with this same battery of tests in connection with our ongoing research projects concerning the neural correlates of knowledge retrieval (see Tranel et al., 2001, 2003). (Those 120 subjects had lesions outside the neural sectors targeted by the hypothesis in the current investigation; for example, they had lesions in ventromedial prefrontal regions, occipital regions, or in right hemisphere structures.) We also provide comparison data from the normal subjects originally studied by Fiez and Tranel (1997).

In regard to action naming, all six target subjects performed defectively, achieving scores on the Action Naming Test that were well below the mean of the brain-damaged comparison group. A different picture emerges, though, in regard to conceptual knowledge for actions. On the five action knowledge tests, many of the scores for the six target subjects were within 1 *SD* of the brain-damaged comparison subjects. In fact, on three of the tests (Picture-Word Matching, Picture Attribute, Word Attribute), the six target subjects as a group produced scores that were close to those of the brain-damaged comparison subjects. On the other two tests (Picture Comparison, Word Comparison), the target subjects tended to have more difficulty, and three of the subjects (1726, 1962, 1978) demonstrated significant impairments on both of these tests.[5]

[5] Given the wide disparity in *N*s for the groups (6 vs. 120), we did not perform between-group statistical comparisons. The availability of two comparison groups (brain-damaged and normal) allows a clear, reliable interpretation of the scores from the target subjects, without formal statistical analyses.

To summarise, all six target subjects with severe locative preposition processing impairments had action naming defects, but none had pervasive impairments in processing conceptual knowledge for actions.

*Knowledge for concrete entities*

The results regarding *recognition* of concrete entities from six conceptual categories are presented in Table 5. Again, for purposes of comparison, we have included data from the 120 brain-damaged subjects mentioned immediately above. We also included data from a group of 55 normal subjects who have been tested with this same battery of stimuli (cf. Damasio et al., 2004; Tranel et al., 1997).

It can be seen that none of the target subjects had substantial, pervasive defects in recognition of concrete entities. There are scattered instances of relatively low scores, but none of the subjects performed poorly in the majority of categories assessed. Moreover, as a group, the six target subjects performed at a level quite comparable to that of the brain-damaged comparison group. In three categories (persons, musical instruments, vehicles), in fact, the target subjects actually slightly outperformed the brain-damaged comparison subjects. (For the same reasons mentioned above for the action stimuli, we did not compare the groups with formal statistical tests.)

In regard to *naming* of concrete entities in the six different conceptual categories, the results for the six target subjects are presented in Table 6, along with summary data from the comparison groups of 120 brain-damaged subjects and 55 normal subjects. The results indicate that most of the target subjects had naming defects in multiple categories. The exception is subject 1726, who performed fairly well on naming of most nonunique categories (his proper naming was defective). As a group, the target subjects performed substantially below the level of the brain-damaged comparison group, and below the normal comparison group.

To summarise, the six target subjects manifested relative preservation of conceptual knowledge for concrete entities from six different categories, including persons, animals, fruits/vegetables, tools, musical instruments, and vehicles. However, most

**Table 5.** *Recognition of concrete entities (% correct)*

| | *Category* | | | | | |
|---|---|---|---|---|---|---|
| *Subject* | *Persons* | *Animals* | *Fruits/ Vegetables* | *Tools* | *Musical instruments* | *Vehicles* |
| 1076 | 93 | 78 | 84 | 85 | 100 | 100 |
| 1726 | 73 | 82 | 74 | 100 | 75 | 100 |
| 1760 | 83 | 65 | 78 | 89 | 75 | 100 |
| 1962 | 86 | 96 | 97 | 83 | 100 | 100 |
| 1978 | 67 | 83 | 75 | 91 | 81 | 91 |
| 2054 | 78 | 82 | 85 | 93 | 100 | 100 |
| Mean | 80.0 | 81.0 | 82.2 | 90.2 | 88.5 | 98.5 |
| (*SD*) | (9.3) | (10.0) | (8.6) | (6.1) | (12.8) | (3.7) |
| *Brain-damaged comparison subjects (n = 120)* | | | | | | |
| Mean | 70.5 | 85.2 | 82.6 | 95.0 | 86.5 | 98.4 |
| (*SD*) | (17.4) | (13.2) | (14.3) | (11.5) | (14.3) | (5.2) |
| *Normal comparison subjects (n = 55)*[a] | | | | | | |
| Mean | 75.7 | 91.9 | 92.6 | 96.2 | 96.3 | – |
| (*SD*) | (6.7) | (2.8) | (3.9) | (3.3) | (3.4) | – |

[a] Taken from Damasio et al. (2004); these subjects were not studied with the "vehicles" category.

**Table 6.** *Naming of concrete entities (% correct)*

| | *Category* | | | | | |
|---|---|---|---|---|---|---|
| *Subject* | *Persons* | *Animals* | *Fruits/ Vegetables* | *Tools* | *Musical instruments* | *Vehicles* |
| 1076 | 23 | 22 | 11 | 10 | 6 | 30 |
| 1726 | 56 | 90 | 80 | 78 | 100 | 100 |
| 1760 | 35 | 27 | 8 | 28 | 33 | 33 |
| 1962 | 6 | 64 | 65 | 47 | 25 | 58 |
| 1978 | 39 | 57 | 58 | 52 | 31 | 76 |
| 2054 | 42 | 76 | 67 | 63 | 51 | 73 |
| Mean | 33.5 | 56.0 | 48.2 | 46.3 | 41.0 | 61.7 |
| (*SD*) | (17.2) | (26.9) | (30.8) | (24.4) | (32.3) | (27.0) |
| *Brain-damaged comparison subjects (n = 120)* | | | | | | |
| Mean | 81.1 | 91.8 | 92.3 | 92.4 | 89.4 | 97.7 |
| (*SD*) | (17.1) | (11.8) | (13.3) | (11.5) | (16.2) | (9.6) |
| *Normal comparison subjects (n = 55)*[a] | | | | | | |
| Mean | 92.3 | 95.7 | 94.3 | 97.2 | 96.9 | – |
| (*SD*) | (6.2) | (3.1) | (3.7) | (3.9) | (4.5) | – |

[a] Taken from Damasio et al. (2004); these subjects were not studied with the "vehicles" category.

of the subjects had naming defects in at least some categories of concrete entities.

***Neuropsychological profiles***

*Spatial processing*. Results from the comprehensive assessment of visuospatial and visuoconstructional functioning are presented in Table 7A. The six target subjects manifested very few impairments on the various measures, and overall, performed extremely well in these domains. In fact, only two scores, out of the 48 listed in Table 7A, were formally classified as impaired. It can be seen that the subjects performed very well for the most part, and in many cases, were well above average. These data indicate conclusively that the subjects did not have defects in basic aspects of visuospatial processing.

*Working memory*. The results of the working memory assessment are presented in Table 7B. There are some instances of missing data, due to subjects having impairments that precluded valid administration of the measure. Based on the available data, though, it can be concluded that working memory defects in these subjects were rare, if present at all. Most of the subjects, in fact, performed very well on the tests; four of them (all who could be tested) generated average to high average performances on the Working Memory Section of the Wechsler Memory Scale-III.

*Linguistic functioning*. The results from the four selected subtests of the Multilingual Aphasia Examination are presented in Table 7C. Most of the six target subjects had defects on some of these measures, in keeping with their general profile of aphasia: for example, four had defects in sentence repetition, all but one failed the Token Test, and one had a defect in reading comprehension. It must be emphasised here, though, that the subjects did not have comprehension defects that precluded valid administration of the experimental measures (see Study 1).

***Neuroanatomical profiles***

To explore further the lesion correlates of defective performance on the locative preposition tests, we computed a MAP-3 overlap for the six target subjects (i.e., those who were impaired on all four preposition tests). All of the target subjects had left

**Table 7.** *Neuropsychological measures*[a]

| | *Subject* | | | | | |
|---|---|---|---|---|---|---|
| *Measure* | *1076* | *1726* | *1760* | *1962* | *1978* | *2054* |
| *A. Spatial processing* | | | | | | |
| WAIS-III (age-corrected scaled score) | | | | | | |
| Matrix reasoning | 12 | 9 | 7 | 17 | 12 | *6* |
| Block design | 10 | 11 | 9 | 12 | 8 | 8 |
| Object assembly | 10 | *6* | 9 | 15 | 10 | 8 |
| Facial Recognition Test (raw score/54) | 44 | 42 | 45 | 54 | 47 | 42 |
| Judgment of Line Orientation Test (raw score/30) | 25 | 29 | 22 | 24 | 22 | 28 |
| Visual Organisation Test (*t*-score) | 50 | 50 | 50 | 50 | 43 | 50 |
| Complex Figure Test, copy (raw score/36) | 32 | 33 | 31 | 31 | 31 | 24 |
| 3-Dimensional Block Construction Test (raw score/29) | 29 | 29 | 27 | 29 | 29 | 28 |
| *B. Working memory* | | | | | | |
| WAIS-III (age-corrected scaled score) | | | | | | |
| Digit span | | *7* | | | *7* | |
| Arithmetic reasoning | | 9 | | | 3 | |
| Visual Retention Test | | | | | | |
| No. correct (raw score) | 5 | 6 | 5 | 8 | 6 | *3* |
| No. errors (raw score) | *7* | 6 | *7* | 3 | 5 | *13* |
| Wechsler Memory Scale-III | | | | | | |
| Working Memory Index | | 96 | 90 | 110 | 100 | |
| *C. Linguistic functioning* | | | | | | |
| Multilingual Aphasia Examination | | | | | | |
| Token Test (raw score/44) | *17* | 44 | 11 | 12 | *33* | *12* |
| Sentence Repetition (raw score/14) | *2* | 9 | *0* | *0* | 9 | *0* |
| Aural Comprehension (raw score/18) | *13* | 17 | 18 | *11* | 17 | 18 |
| Reading Comprehension (raw score/18) | *11* | 18 | 18 | 18 | 18 | 17 |

[a] Italic scores are defective; blanks indicate missing data.

hemisphere lesions; moreover, in all six subjects the lesions involved the left frontal region, the left parietal region, or both. The results of the overlap computation are presented in Figure 6. The areas of highest lesion overlap include the posterior left frontal operculum, the inferior parietal operculum, and the white matter subjacent to these regions. Individual lesion analysis indicated that in five of the six target subjects, the lesion involved the frontal operculum and underlying white matter. Also, in five of the six target subjects there was significant involvement of the inferior parietal operculum, including the anterior part of the supramarginal gyrus and the underlying white matter. (The two sets of five subjects mentioned in these ratios were not exactly the same; four were in common, and the other two fit one ratio or the other.)

To determine the specificity of these findings, we calculated a MAP-3 lesion overlap for nine subjects who were impaired on only one test and had left hemisphere lesions, and then contrasted this with the lesion overlap for the six target subjects by subtracting the MAP-3 overlaps from each other (the overlap for the nine subjects with one test impairment was subtracted from the overlap for the six subjects with four test impairments). This showed that the highest area of lesion overlap *specific* to the subjects who failed all four tests was in the posterior sector of the left frontal operculum and in the white matter subjacent to this region, extending posteriorly into the anterior sector of the white matter underneath the inferior parietal operculum (Figure 7). Together with the findings depicted in Figure 6, this result indicates that not only do the target subjects share a considerable

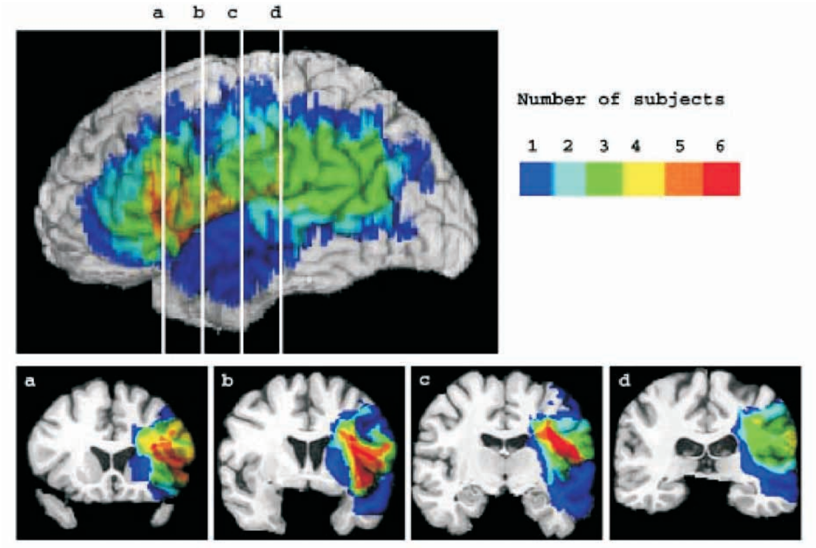


**Figure 6.** *The figure shows a MAP-3 lesion overlap composite for the six target subjects, i.e., the subjects who had severe and pervasive defects on all four of the locative preposition tests. The colour bar indicates the number of lesions in the overlap, and the white lines denote the planes of coronal sections depicted in the figure (sections a–d). All of the target subjects had left hemisphere lesions. The area of highest lesion overlap includes the posterior left frontal operculum, the inferior parietal operculum, and the white matter subjacent to these regions.*

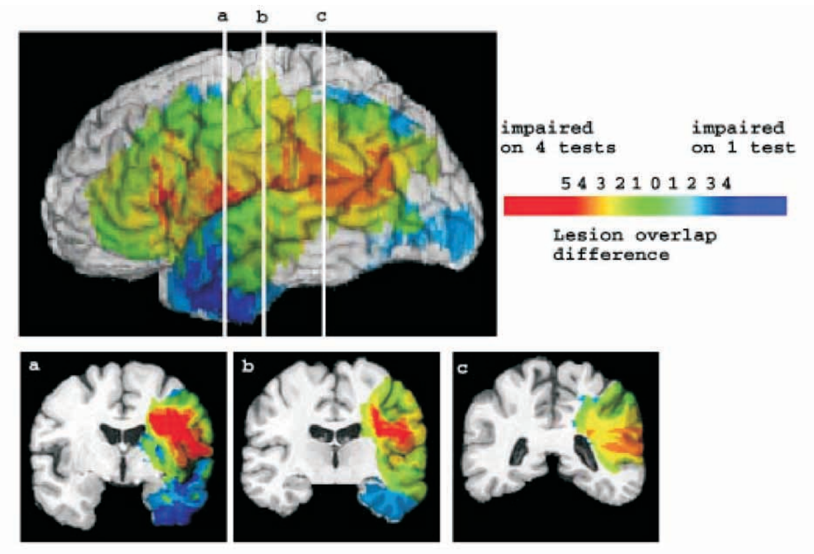


**Figure 7.** *The lesion overlaps for subjects with left hemisphere lesions who failed only one of the four spatial relationship tests (*n = 9*) were contrasted with the lesion overlaps for the subjects who failed all four of the tests (*n = 6*), by subtracting the former from the latter. The colour bar indicates the number of lesions in the overlap difference. The white lines denote the planes of coronal sections depicted in the figure (sections a–c). The subtraction image shows that the highest area of lesion overlap* specific *to the subjects who failed all four tests is in the posterior sector of the left frontal operculum, and especially in the white matter subjacent to this region. The overlap extends posteriorly into the anterior sector of the white matter underneath the inferior parietal operculum. At its highest extent, the subtraction difference is as many as five subjects.*

degree of common lesion locus in the left frontal opercular and inferior parietal regions, but also that damage in this sector is likely to produce pervasive defects in processing the meanings of locative prepositions. Subjects who failed only one of our preposition tests tended not to have lesions in this region.

# DISCUSSION

## Neuropsychological issues

We found, in a large series of 78 brain-damaged subjects, a subgroup of 6 subjects who had severe, pervasive defects in processing the meanings of locative prepositions. Detailed investigation of the spatial processing capacities of these six subjects indicated that the subjects had well-preserved basic visuospatial and visuoconstructional abilities. This was clearly evident in a set of demanding neuropsychological tests, where test failures were almost nonexistent in the target subjects. On a comparable note, we did not find consistent or convincing evidence of working memory impairments in the six target subjects, again based on conventional neuropsychological assessment. Thus, it is reasonable to conclude that the defects these subjects manifested on the locative preposition tests cannot be explained by basic impairments in spatial processing or working memory.

The six "target" subjects did manifest varying degrees of impairment in linguistic functions, as indexed by standard tests from an aphasia battery. This was not unexpected, as the subjects all had clinically significant aphasia in the acute phase of their neurological illness, of such severity that a full recovery in the chronic epoch would have been unlikely. For the purposes of the current set of studies, though, the key consideration is that the subjects were able to cooperate with the experimental procedures sufficiently to produce valid responses on the tasks. In fact, this determination was made by a clinical neuropsychologist who was blind to the hypotheses being addressed in these studies, and who was not involved in the basic research we are reporting here. Thus, we have no reason to believe that residual linguistic defects in the target subjects would explain, per se, the subjects' performances on the experimental measures.

Another issue that deserves comment is the fact that the six target subjects did not have impairments in the recognition of concrete entities, which would explain their poor performances on the locative preposition tests. Direct evidence for this comes from the subjects' performances in the recognition of concrete entities, including such entities as tools and vehicles. These objects (along with furniture) were the most common items utilised in the locative preposition tests, and none of the six target subjects had severe recognition impairments for any of these categories of entities (this is true of the furniture category as well, which we have tested previously but do not report here). Moreover, one of the locative preposition tests (verification) does not utilise any real objects, and the pattern of findings for this test turned out to mirror quite closely the patterns we found for the other preposition tests that did utilise real objects.

A more challenging issue concerns the distinction between phonological processing, on the one hand, and the processing of "meaning" (conceptual knowledge, semantics), on the other. This is a thorny issue, especially in the domain of prepositions (cf. Froud, 2001). Our tests were not designed to tease this apart, nor do we believe this is a readily tractable issue. What we can say is the following. We found four subjects who failed only the Naming Test, which arguably provides—out of the four tests in our battery—the "purest" measure of phonological processing independently from processing of meanings. Two of these subjects had lesions confined to the left inferior prefrontal region, with no encroachment into parietal sectors. (One of the other subjects has a left occipitotemporal lesion, and the other has a right-sided prefrontal lesion. Neither of these cases contributed to the lesion overlap outcomes depicted in Figures 2–5.) This can be proffered as tentative evidence that the left prefrontal region may be relatively more specialised for encoding the phonological forms of prepositions, and the parietal region may be relatively more specialised for processing the meanings of these words. But this issue obviously demands further study, and we are making no claims here that our data can do anything more than provide some preliminary hints. (We take up these points again later on in the Discussion.)

## Neuroanatomical issues

The neuroanatomical findings from our study converge nicely with recent results from functional imaging approaches, and with studies from the aphasia-based literature, suggesting that the left inferior prefrontal and left inferior parietal regions have important roles in the processing of knowledge associated with locative prepositions. We will discuss the possible functions of the frontal and parietal components separately.

As indicated in the Introduction, we showed in a PET study that naming static spatial relationships with locative prepositions activated the left inferior prefrontal region (Damasio et al., 2001). There is evidence for a number of related functional roles of this region, with respect to various kinds of linguistic information. First, this region may contribute to the phonological processing of prepositions during language production (Indefrey & Levelt, 2000). Some support for this interpretation comes from our finding, mentioned above, that two subjects whose lesions were restricted to the left inferior prefrontal region were impaired on just the Naming Test. Second, the left inferior prefrontal region may contribute to semantic processing by facilitating the retrieval of prepositional meanings and guiding the comparison of different meanings so that the most appropriate one can be selected (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Third, the same region may also be involved in processing the syntactic properties of prepositions (Friederici, 1982, 1983).

Regarding this last point, we suspect that if syntactic factors influenced the performance of our subjects, it was probably to only a minor extent. There are several reasons for this, beginning with the fact that none of the tests explicitly requires syntactic processing in either the stimuli or the responses. Even if subjects were inclined to generate full prepositional phrases, either covertly or overtly, the syntactic processing requirements were probably negligible. This is because the locative prepositions that are the focus of our study are all predicative, which is to say that they license the nominal argument they mark, and their selection is determined solely by semantic considerations derived from the spatial arrays being referred to. If the spatial arrays shown in the pictorial stimuli for our tests were to be described in complete sentences, the sentences would probably be very simple intransitive clauses containing noun-phrases for the figure and landmark objects, a locative preposition specifying the spatial relationship between the objects, and a copula to carry tense (e.g., *The spoon is in the cup*). Predicative prepositions are quite different from nonpredicative prepositions, since the latter neither license the nominal argument they mark nor add substantial semantic information to the clause, but instead have exclusively syntactic functions.[6] Some non-predicative prepositions are selected purely on the basis of the idiosyncratic subcategorisation specifications of particular verbs (e.g., *believe in/*on, rely on/*in*), while others are essentially case-markers whose selection is determined by general syntactic rules (e.g., dative *to,* as in *She handed her ticket to the flight attendant*). There is some evidence that agrammatic Broca's aphasics are more impaired on nonpredicative than predicative prepositions (Friederici, 1982, 1983; Grodzinsky, 1988; but see also Tesak & Hummer, 1994), which is in accord with their broader morphosyntactic difficulties. This is also consistent with our view that the left inferior prefrontal region is more important for processing the syntactic properties of nonpredicative than predicative prepositions.

[6] The terms "predicative" and "nonpredicative" come from *Role and Reference Grammar* (Jolly, 1993; Van Valin & LaPolla, 1997). They correspond, respectively (and also rather loosely), to the terms "nongoverned" and "governed" in Chomsky's *Government and Binding Theory.*

Turning to the left inferior parietal region, the PET study by Damasio et al. (2001) also found left supramarginal gyrus activation, in a contrast that involved the subtraction of naming tools from naming static spatial relationships. There is other convergent evidence supporting the notion that this region, and the left inferior parietal region more generally, is involved in processing knowledge about spatial relationships. A starting point is the classic notion of a dorsal "visual pathway" that projects from the occipital lobe to the parietal lobe. This pathway has traditionally been called the "where" system because it appears to be fundamentally involved in spatial localisation, as shown by a wide range of data reviewed by Ungerleider and Mishkin (1982). In an influential article, Landau and Jackendoff (1993) used this literature as a springboard for speculating that the meanings of locative prepositions are represented in the parietal lobe. Damasio et al.'s PET study and the current lesion study not only corroborate this proposal but allow it to be made more precise by suggesting that the critical neuroanatomical structure may be the left supramarginal gyrus.

Landau and Jackendoff's proposal can be refined further by taking into account the distinction between "categorical" and "coordinate" spatial relationships.[7] Categorical spatial relationships involve generalisations at a rather abstract level of analysis (e.g., "connected to," "left of," "above"), similar to the degree of schematicity found in prepositional meanings. Representations of categorical spatial relationships are useful for specifying the rough locations of objects relative to each other and to the observer, and for recognising flexible objects when their parts are in contorted configurations—for instance, a person's forearm remains "connected to" the upper arm regardless of how the person twists and turns. In contrast, coordinate spatial relationships involve much more precise specifications (e.g., 4 cm, 60° angle) that are essential for the efficient visuomotor control of object-directed reaching, grasping, and throwing actions—for instance, picking up a coffee mug requires encoding very precise and rapidly updated metric representations of the exact position of the mug relative to one's hand during the reaching phase, and of the mug's handle relative to one's fingers during the grasping phase. Several sources of evidence suggest that the left parietal lobe is dominant for categorical spatial processing, whereas the right parietal lobe is dominant for coordinate spatial processing. Lesion studies have demonstrated a double dissociation such that left parietal damage produces relatively severe impairments in categorical spatial processing (e.g., left/right confusion), whereas right parietal damage produces relatively severe impairments in coordinate spatial processing (e.g., inaccurate judgment of line orientation) (Goldenberg, 1989; Hannay, Falgout, Leli, Katholi, Halsey, & Willis, 1987; Kemmerer & Tranel, 2000a; Laeng, 1994; Mayer, Martory, Pegna, Landis, Delavelle, & Annoni, 1999; Mehta & Newcombe, 1991; Taylor & Warrington, 1973; Warrington & Rabin, 1970). Also, divided visual field studies have shown a left-hemisphere advantage for processing categorical spatial relationships and a right-hemisphere advantage for processing coordinate ones (Kosslyn, Koenig, Barrett, Cave, Tang, & Gabrieli, 1989). More recently, functional imaging studies have shown that although both left and right inferior parietal lobes are activated during both types of spatial processing tasks, the left-sided activation is significantly stronger for categorical tasks and the right-sided activation is significantly stronger for coordinate tasks (Baciu, Koenig, Vernier, Bedoin, Rubin, & Segebarth, 1999; Kosslyn, Thompson, Gitelman, & Alpert, 1998). Overall, these findings about the categorical/coordinate distinction provide a useful context for situating the notion that the meanings of locative prepositions depend on the left supramarginal gyrus.

These considerations are also relevant to the issue raised in the Introduction regarding the

[7] The terms categorical and coordinate come from Kosslyn (1994), but similar dichotomies have been proposed by other authors, such as discrete (symbolic) versus continuous (dynamic) (Turvey & Carello, 1986), prototypical versus fine-grained (Huttenlocher, Hedges, & Duncan, 1991), topological versus metric (Poucet, 1993), and low-frequency versus high-frequency (Ivry & Robertson, 1998).

autonomy of prepositional meanings vis-à-vis other types of spatial representations. On both functional and anatomical grounds, the meanings of locative prepositions are clearly independent of coordinate spatial representations. However, a more theoretically subtle and empirically challenging question is whether the meanings of locative prepositions are also independent of the kinds of categorical representations used for perceiving the general locations of objects and the internal meronymic (i.e., part-whole) organisation of objects. This question has only begun to be investigated, but several lines of research support the autonomy view. For example, psycholinguistic studies suggest that there are divergences between the linguistic and perceptual encoding of spatial location, and that the unique language- and culture-specific semantic structures captured by prepositions (and by other closed-class morphemes, such as the Finnish case-markers for the intimate/nonintimate distinction) are employed primarily when a person has to package his or her conceptualisations of space in a manner that can easily be expressed in words (Crawford et al., 2000; Munnich et al., 2001).

Additional evidence comes from a recent neuropsychological study that found a double dissociation between linguistic and perceptual representations of spatial relationships (Kemmerer & Tranel, 2000a). This study showed that knowledge of the meanings of locative prepositions can be selectively impaired or preserved relative to a variety of nonlinguistic tasks that require categorical spatial representations, such as recognising multicomponent objects whose parts are in contorted configurations, copying geometrically complex line drawings, and assembling three-dimensional block structures based on a model. And in the current study, we found that in subjects who were severely defective on all of the tests involving locative prepositions, but who were robustly intact on conventional neuropsychological tests of visuospatial and visuoconstructional skills, the highest density of lesions was in the left inferior prefrontal region and left inferior parietal region, including the anterior part of the supramarginal gyrus.[8]

## Other considerations

Returning to the findings reported in the current investigation, there are two important results that warrant additional consideration. First, we found that all six of the subjects with pervasive, severe defects in processing the meanings of locative prepositions also had defects in retrieving verbs to name actions. Previous work in our laboratory, and by others, has demonstrated a reliable relationship between the left ventrolateral prefrontal region and the retrieval of words for actions (Cappa, Sandrini, Rossini, Sosta, & Miniussi, 2002; Hillis, Wityk, Barker, & Caramazza, 2003; Pulvermüller, Lutzenberger, & Preissl, 1999; Tranel et al., 2001). Given that five of the six target subjects in the current study had lesions that included this neural sector, it is not surprising to find that these subjects also had action naming impairments; in fact, this outcome is very consistent with our previous work and that of others. Taken at face value, the finding implies that there is substantial overlap between the neural systems that are important for retrieving words for actions, and those that are important for processing locative prepositions. Those systems may not even be all that different, and in any event, it may not be possible using a lesion approach to easily disentangle them. The current results certainly do not allow us to tease apart this potential difference; on the contrary, the findings can be taken to suggest that there is substantial commonality in the neural systems required for operating verbs and locative prepositions.

Second, most of the target subjects had some degree of impairment in retrieving nouns to name concrete entities, at least for some categories. This was also not greatly surprising, given the fact that some of these subjects have fairly broad residual impairments in generating phonological forms per se. This may be seen as reducing the intrigue of the

[8] We have reported previously on brain-damaged subjects who exhibited a similar correlation between neuropsychological and neuroanatomical data (Kemmerer, 2004; Kemmerer & Tranel, 2003).

finding that these subjects cannot retrieve the lexical forms for locative prepositions, although we would still argue that this is an important result to have been established empirically in a large-scale lesion study. What cannot be discounted, though, is the finding that the target subjects had very severe defects in processing the semantic structures of locative prepositions, despite having manifestly intact spatial processing capacities (as noted earlier). The subjects did not have consistent impairments in processing conceptual knowledge for other categories, including actions and concrete entities. Thus, the defect for processing the meanings of locative prepositions, which goes well beyond a problem with generating phonological forms, stands out in these subjects. And the fact that this defect correlates with damage to the left posterior frontal operculum, or to the left inferior parietal region, or both, is of considerable importance in light of the pertinent literature we have reviewed above. To recapitulate, our findings do not allow the conclusion that these left prefrontal/inferior parietal structures are *exclusively* important for processing the meanings of locative prepositions, but the findings do indicate that these structures are critically involved in this process.

## Future directions

A great deal of research in cognitive neuroscience has focused on how information about the spatial locations of objects is represented in multiple brain systems that are anatomically organised according to functional considerations such as perception, action, and navigation (Burgess, Jeffrey, & O'Keefe, 1999; Milner & Goodale, 1996; Thier & Karnath, 1997). However, very little research has explored how information about the spatial locations of objects is neurally represented for the purpose of linguistic communication. Hence this field of inquiry remains wide open, and there are many interesting questions that can be pursued.

For example, the tests we designed included two different subclasses of locative prepositions: topological, which encode notions such as containment, contiguity, encirclement, and penetration (e.g., *in, on, around, through*); and projective, which specify the location of the figure object as being within a search-domain extended from one of the major dimensional axes of the landmark object (e.g., *in front of, in back of, above/over, below/under*). In analysing our data, we lumped these two subclasses together and did not investigate whether they dissociate from each other neuropsychologically and neuroanatomically. But since the two subclasses are in fact semantically distinct (Herskovits, 1986; for refinements, see Levinson, 2003), it is certainly possible that their meanings are represented by separate neural networks. This issue could be addressed in future studies using both the lesion method and functional neuroimaging techniques.

In this same vein, we should emphasise that our study investigated one type of preposition—namely, locative prepositions—and our findings have to be interpreted with this qualification. Other types of prepositions—e.g., path prepositions such as *into* and *toward*—may or may not require the same neural systems that we have identified here as being important for locative prepositions. It could turn out to be the case, for example, that path prepositions, by virtue of their inherent basis in real or implied movement, would be more dependent on temporal lobe structures, including motion-related sectors in the posterior part of the middle temporal gyrus (so-called area MT). This remains an open question, and one very much worth exploring in future work.

Another topic that warrants attention involves the neural correlates of certain words that are like locative prepositions insofar as they encode schematic information about spatial relationships, but are unlike locative prepositions insofar as they belong to other morphosyntactic categories—e.g., nouns (*inside*), verbs (*enter*), adjectives (*inner*), and adverbs (*inwards*) (Bennett, 1993; Kemmerer, 1999; Sinha & Kuteva, 1995). Because the meanings of these words are qualitatively similar to those of locative prepositions, we predict that they too might be implemented in the left supramarginal gyrus. In this context, body-part nouns like *head, belly, arm, leg, front,* and *back* are of special interest for the following reasons: (1) crosslinguistic research has demonstrated that they are frequently the historical sources of locative prepositions (Svorou, 1994); (2) many languages currently use them as either the principal device for describing spatial locations (e.g., Zapotec) or as an ancillary device for this function (as in the English expressions *at the foot of the mountain, on the face of the cliff, in the mouth of the cave,* etc.); and (3) neurological disorders that affect the conceptual representation of the body, such as autotopagnosia, finger agnosia, and left/right disorientation are linked primarily to disturbances of the left inferior parietal cortex (Denburg & Tranel, 2003; Felician, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 2003). Thus, it would be quite interesting to investigate the relation between the neural underpinnings of locative prepositions on the one hand and body-part nouns on the other.

Many other possibilities for future research come to mind, but we will conclude by mentioning one particular topic that we regard as especially worthy of investigation. Recent advances in cognitive science and linguistics suggest that spatial schemas provide a foundation for metaphorically structuring abstract conceptual domains (for review, see Gattis, 2001). The semantics of locative prepositions constitute an important source of evidence for this view, since many of these words are not restricted to describing static spatial relationships but instead have a multiplicity of meanings (Dirven, 1993; Haspelmath, 1997; Kuteva & Sinha, 1994; Lindstromberg, 1998; Radden, 1985; Rice, 1993). For example, *at* can refer not just to a point in space (*Bill is at the post office*) but also to a moment in time (*Your plane departs at 5:10*), an emotional state (*She's at peace*), a specific subject-matter (*He's an expert at chess*), a focus of attention *(They laughed at the joke*), a directed activity (*Those two countries have been at war for years*), and a causal linkage or near-simultaneity of events (*At that he exploded*). Moreover, spatial schemas are routinely projected into abstract arenas such as graphs, mathematics, musical notation, measures of close and distant kin and of high and low social groups, and so forth (Gattis, 2001; Lakoff & Johnson, 1999; Lakoff & Núñez, 2001; Pinker, 1990). These findings led Gentner, Bowdle, Wolff, and Boronat (2001) to propose that spatial representation is so important for analogical thought that it should be granted "universal donor" status. The neural basis of this remarkable human trick is, however, unknown. We hope that other researchers in cognitive neuroscience will share our enthusiasm for exploring the question of exactly how and why spatial schemas have such a profound influence on human cognition (Kemmerer, 2004).

Manuscript received 15 January 2003
Revised manuscript received 15 August 2003
Revised manuscript accepted 24 September 2003

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