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BEHAVIORAL PATTERNS AND LESION SITES ASSOCIATED WITH IMPAIRED PROCESSING OF LEXICAL AND CONCEPTUAL KNOWLEDGE OF ACTIONS

David Kemmerer[1,2,3], **David Rudrauf**[1,4], **Ken Manzel**[1], and **Daniel Tranel**[1]

[1]Department of Neurology Division of Cognitive Neuroscience University of Iowa College of Medicine

[2]Department of Speech, Language, and Hearing Sciences Purdue University

[3]Department of Psychological Sciences Purdue University

[4]Laboratory of Brain Imaging and Cognitive Neuroscience University of Iowa

Abstract

To further investigate the neural substrates of lexical and conceptual knowledge of actions, we administered a battery of six tasks to 226 brain-damaged patients with widely distributed lesions in the left and right cerebral hemispheres. The tasks probed lexical and conceptual knowledge of actions in a variety of verbal and non-verbal ways, including naming, word-picture matching, attribute judgments involving both words and pictures, and associative comparisons involving both words and pictures. Of the 226 patients who were studied, 61 failed one or more of the six tasks, with four patients being impaired on the entire battery, and varied numbers of patients being impaired on varied combinations of tasks. Overall, the 61 patients manifested a complex array of associations and dissociations across the six tasks. The lesion sites of 147 of the 226 patients were also investigated, using formal methods for lesion-deficit statistical mapping and power analysis of lesion overlap maps. Significant effects for all six tasks were found in the following left-hemisphere regions: the inferior frontal gyrus; the ventral precentral gyrus, extending superiorly into what are likely to be hand-related primary motor and premotor areas; and the anterior insula. In addition, significant effects for 4-5 tasks were found in not only the regions just mentioned, but also in several other left-hemisphere areas: the ventral postcentral gyrus; the supramarginal gyrus; and the posterior middle temporal gyrus. These results converge with previous research on the neural underpinnings of action words and concepts. However, the current study goes considerably beyond most previous investigations by providing extensive behavioral and lesion data for an unusually large and diverse sample of brain-damaged patients, and by incorporating multiple measures of verb comprehension. Regarding theoretical implications, the study provides new support for the Embodied Cognition Framework, which maintains that conceptual knowledge is grounded in sensorimotor systems.

Address for correspondence: David Kemmerer Department of Speech, Language, and Hearing Sciences 1353 Heavilon Hall Purdue University West Lafayette, IN 47907-1353 Phone: (765) 494-3826 Fax: (765) 494-0771 kemmerer@purdue.edu.

1. INTRODUCTION

In recent years, significant progress has been made in understanding the areas of brain injury that are most often associated with impaired production of verbs, especially in tasks that require the participant to name actions (for reviews see Mätzig et al., 2009; Vigliocco et al., in press). However, much less is known about the areas of brain injury that are most often associated with impaired comprehension of verbs—for example, in tasks that require the participant to match verbs with pictures of actions, answer questions about the meanings of verbs, or sort verbs according to their meanings. In addition, research is only beginning to reveal the neural underpinnings of non-verbally encoded action concepts—for example, the kinds of action concepts that enable us to recognize and make intelligent inferences about the bodily movements of other people. Here we describe a study that not only adds to the existing literature on the neural correlates of defective verb production, but also provides a wealth of new information about the neural correlates of defective verb comprehension; moreover, the study includes parallel data on the neural correlates of defective non-verbal processing of action concepts.

Specifically, we report data for 226 brain-damaged patients, all of whom received six standardized tasks that assess, in a variety of verbal and non-verbal formats, the processing of lexical and conceptual knowledge of actions. We and our colleagues have employed different subsets of these tasks in a number of previous group studies and case studies (Damasio et al., 2001; Kemmerer & Tranel, 2000a, 2000b, 2003; Kemmerer et al., 2001a, 2001b, 2007; Tranel et al., 2001, 2003, 2005, 2008). However, this is the first time that we present both behavioral and lesion data for a large cohort of brain-damaged patients, all of whom received the entire battery of tasks. In particular, we describe the behavioral patterns manifested by all 226 patients, 61 of whom failed one or more of the six tasks; and we describe the lesion sites of 147 of those patients, 37 of whom failed one or more of the six tasks. By analyzing the range of associations and dissociations across the six tasks, not only in the patients' neuropsychological performance profiles but also in their neuroanatomical lesion sites, we are able to shed new light on the networks of brain regions that are most critical for various forms of verbal and non-verbal processing of action concepts.

1.1. A battery of tasks for investigating lexical and conceptual knowledge of actions

Fiez and Tranel (1997) developed and normed a battery of six tasks that probe the participant's ability to retrieve lexical and conceptual information pertaining to actions. Brief descriptions of these tasks are provided below. For further details, see Fiez and Tranel (1997) and Kemmerer et al. (2001a).

- Naming Task (*N* = 100 items): For each item, the participant is shown a photograph of an action, and the task is to orally name each one with a specific verb. Normative data: *M* = 85.0% correct; *SD* = 5.0.
- Word-Picture Matching Task (*N* = 69 items): For each item, the participant is shown a printed verb together with two photographs of actions, and the task is to determine which action the verb describes. Normative data: *M* = 92.1% correct; *SD* = 4.6.
- Word Attribute Task (*N* = 62 items): For each item, the participant is shown two printed verbs, and the task is to indicate which one designates a type of action that satisfies a certain value for a single attribute (e.g., which one would be more tiring). Normative data: *M* = 94.8% correct; *SD* = 3.6.

- Word Comparison Task (*N* = 44 items): For each item, the participant is show three printed verbs, and the task is to determine which one is most different in meaning from the other two. Normative data: *M* = 88.7% correct; *SD* = 8.1.
- Picture Attribute Task (*N* = 72 items): This task is analogous to the Word Attribute Test, but the stimuli are photographs of actions instead of verbs. Normative data: *M* = 91.7% correct; *SD* = 4.8.
- Picture Comparison Task (*N* = 24 items): This task is analogous to the Word Comparison Test, but the stimuli are photographs of actions instead of verbs. Normative data: *M* = 83.6% correct; *SD* = 8.3.

Altogether, this battery includes one verb production task (Naming), three verb comprehension tasks (Word-Picture Matching, Word Attribute, and Word Comparison), and two non-verbal tasks (Picture Attribute and Picture Comparison). At the same time, the battery has some limitations. For example, in the four tasks that necessarily require verb processing, the verbs are not carefully controlled for “nuisance variables” like frequency, age of acquisition, length, imageability, and noun/verb homophony, nor are they controlled for syntactic/semantic factors like transitivity and the range of argument structure constructions that are possible. In addition, none of the six tasks involve systematic manipulations of conceptual factors like the following: whether the action consists mainly of arm/hand movement, leg/foot movement, or face/mouth movement; whether the action involves one, two, or three core entities; whether the action involves tool use; whether the action causes an entity to undergo a change of spatial location; whether the action causes an entity to undergo a change of physical state; etc. Furthermore, none of the tasks can be said to provide a completely “pure” measure of either verbal or non-verbal processing, since all of them involve various mixtures of these two ways of thinking about actions.

Despite these limitations, the tasks have many important advantages. For example, even though Fiez & Tranel (1997) did not equate the target verbs in the Naming Task for the nuisance variables mentioned above, they did provide several kinds of normative data for all of the items, including two separate measures of name agreement for the target verbs, as well as distinct measures of visual complexity, familiarity, and image agreement for the pictorial stimuli (see Kemmerer & Tranel, 2000a, for an investigation of how these variables, among others, influenced the action naming performances of 53 brain-damaged patients). In addition, the shortcoming of not controlling for specific conceptual factors is offset by the virtue of covering a wide range of action categories, thereby affording a well-rounded assessment of a person's ability to retrieve and process information in this domain. Another noteworthy virtue is that when the six tasks are considered collectively as a composite battery, it should be clear that they constitute a powerful research tool for probing, in heterogeneous verbal and non-verbal formats, the retrieval of lexical and conceptual knowledge of actions. In fact, as we discuss in greater detail below, one of the main benefits of evaluating action knowledge from many different angles, especially in a neuropsychological setting, is that it helps the investigator distinguish between, on the one hand, patients who fail only a small number of tasks and hence are likely to have deficits restricted to relatively task-specific ways of processing action concepts, and on the other hand, patients who fail a large number of tasks and hence are more likely to have deficits that directly affect the core content of action concepts. Finally, is worth emphasizing that the six tasks were carefully normed, and that none of them have ceiling effects, thereby facilitating the discrimination of mild, moderate, and severe levels of impairment on any given task.

1.2. Previous studies

As already noted, one or more of the six tasks described above have been employed in previous studies that we and our colleagues have conducted with both healthy subjects and brain-damaged patients. In what follows, we briefly summarize some of these studies, emphasizing how the results bear on issues regarding the neural substrates of verb production, verb comprehension, and the non-verbal processing of action concepts.

1.2.1. Studies focusing on the Naming task—Tranel et al. (2001) administered the Naming task to 75 patients with focal, stable lesions in the left or right hemisphere, and then contrasted the lesion sites of the patients who failed the task ($N = 22$) with the lesion sites of an equal number of patients who passed it. Lesions linked with impaired oral naming of actions overlapped maximally in the following left-hemisphere regions: the inferior frontal gyrus (IFG), including Brodmann areas (BAs) 44, 45, and, to a lesser degree, 47; the inferior sectors of the precentral and postcentral gyri; the supramarginal gyrus (SMG); portions of the posterior middle temporal gyrus (pMTG); and the white matter underlying all of these regions. Notably, many of the patients who failed the action naming task passed a separate object naming task, and many of them also performed well on the Picture Attribute task, which, as described above, is one of our methods for probing knowledge of action concepts in a non-verbal manner. These findings suggest that many of the patients' action naming impairments were due to lexical access disturbances that selectively compromised some aspect(s) of the process of mapping verb meanings onto verb forms, while preserving the meanings themselves. Importantly, additional data from a closely related study support this interpretation, but only for some of the relevant patients. In particular, most of the patients in the study by Tranel et al. (2001) that focused on the Naming task also participated in a separate study by Kemmerer et al. (2001a, 2001b) that included the entire battery of tasks (see section 1.2.3 below). Ten patients in the latter study were reported to have failed the Naming task but passed the Picture Attribute task, just like in the former study; however, of that group of ten patients, only three passed all four of the other tasks (and hence exhibited highly selective action naming deficits), which suggests that the remaining seven patients had mild to moderate semantic disorders in the domain of action concepts.

To explore the possible influence of stimulus factors on action naming performance, Tranel et al. (2008) developed a new task that uses dynamic rather than static presentations of actions as stimuli. Specifically, the participant is shown 158 videoclips 3-5 sec in length, and is asked to produce the most appropriate verb for each one. This dynamic action naming task was administered to 78 patients with focal, stable lesions in the left or right hemisphere. Of those 78 patients, 71 also received the original Naming task for statically depicted actions (i.e., the Naming task described above), but only two were among the 75 patients in Tranel et al.'s (2001) study. Patients with impaired naming of dynamic actions ($N = 16$) almost invariably had impaired naming of static actions as well, and performances on target verbs that were the same across the two tasks ($N = 60$) were highly correlated ($r = .91$). These strong behavioral correspondences across the two tasks suggest that dynamic and static action naming depend on largely overlapping neural networks.[1] More direct support for this view comes from the finding that the lesion sites that were most reliably linked with impaired dynamic action naming in this study were remarkably similar to those that were most reliably linked with impaired static action naming in Tranel et al.'s (2001) study: the left IFG (particularly BAs 44 and 45), the left SMG, and the left pMTG, plus the white matter underlying all of these regions. Given that the two studies employed almost entirely

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[1] It is noteworthy, however, that Tranel et al. (2008) did find some dissociations between the two types of action naming tasks, and a few other studies have reported similar differences, not only in the behavioral performances of brain-damaged patients (Druks & Shallice, 2000; D'Hononcthun & Pillon, 2008), but also in the activation patterns of heathly subjects (den Ouden et al., 2009).

different groups of patients, the convergence of the neuroanatomical results is especially significant and compelling.

1.2.2. Studies focusing on the Picture Attribute and Picture Comparison tasks—In a study with 90 patients, Tranel et al. (2003) sought to elucidate the neural substrates of action concepts by concentrating on just the Picture Attribute and Picture Comparison tasks—that is, the two tasks that circumvent the overt processing of verb forms and hence tap fairly directly into the kinds of action concepts that verbs typically encode. The investigators contrasted the lesion sites of the patients who failed one or both tasks (*N* = 22) with those of the patients who passed both tasks (*N* = 64), and found that the greatest lesion overlap densities associated with defective non-verbal processing of action concepts were, once again, in the left IFG (BAs 44, 45, and 47), the left inferior precentral and postcentral gyri, the left SMG, and, to a lesser extent, the left pMTG, plus the white matter underlying all of these regions. When considered together with Tranel et al.'s (2001, 2008) naming studies, this outcome suggests that the neural mechanisms that mediate the non-verbal processing of action concepts may be tightly intertwined with those that mediate the retrieval of the verb forms that express those concepts.

1.2.3. Studies using all six tasks—We have conducted a few detailed case studies in which we administered the entire battery of tasks to certain carefully selected patients and then analyzed both the behavioral data and the lesion data (Kemmerer & Tranel, 2003; Kemmerer et al., 2007). Up to now, however, we have only reported one study in which all six tasks were given to a large group of patients, and that study did not address neuroanatomical issues, but instead focused on the behavioral data (Kemmerer et al., 2001a, 2001b). Nevertheless, the 2001 study did yield some important insights that are worth highlighting here, since they help set the stage for the new experiment described below. Of the 89 patients who received the battery, 30 were impaired on at least one of the six tasks. Remarkably, these patients manifested a total of 22 distinct performance profiles—i.e., unique combinations of passes and failures across the tasks. A principal components analysis revealed that 93% of the variance could be accounted for by just a few factors that were interpretable in terms of the following task dimensions: voluntary verb retrieval (required only by the Naming task); verbal stimuli (grouping together the Word-Picture Matching, Word Attribute, and Word Comparison tasks); and pictorial stimuli (grouping together, independently of the Naming task, the Word-Picture Matching, Picture Attribute, and Picture Comparison tasks). Despite these generalizations, however, the most salient finding was the tremendous diversity of the patients' performance profiles. This variability clearly demonstrates that in order to get a well-balanced sense of a given patient's ability to process lexical and conceptual knowledge of actions, it is worthwhile to use a variety of tasks that evaluate this general capacity in different ways. In addition, the fact that each of the six tasks dissociated from all the others—with at least a 2-point (i.e., 2 standard deviations) difference between normal and defective *z*-scores for any two tasks (see Kemmerer et al., 2001b)—raises the possibility that each one may have at least some idiosyncratic computational requirement(s) that can be independently disrupted. And this in turn may have implications for brain organization, because even though the neuroanatomical analyses conducted by Tranel et al. (2001, 2003, 2008) revealed fairly comparable lesion correlates for defective verb production and defective non-verbal processing of action concepts, the complex patterns of associations and dissociations between tasks that Kemmerer et al. (2001a, 2001b) discovered suggest that defective performances on particular tasks, or combinations of tasks, may actually co-occur with at least partially non-overlapping lesion maps. One of the aims of the current investigation was to explore this possibility in greater detail.

1.3. The current investigation

The overarching goal of this investigation was to further illuminate the neural substrates of lexical and conceptual knowledge of actions by building substantially on the previous studies reviewed above. To that end, we gathered and analyzed data from a sample of 226 patients, all of whom had stable, focal lesions in either the left or right hemisphere, and all of whom received the entire battery of tasks developed by Fiez and Tranel (1997).

Study 1 focused on the behavioral patterns of normal and impaired performances across the six tasks. Because the group of 226 patients investigated here subsumes all but one of the 89 patients investigated by Kemmerer et al. (2001a, 2001b), we expected to replicate the major behavioral outcomes of that previous study. However, we also predicted that those discoveries would be robustly reinforced and further enriched by the addition of 137 new cases.

Study 2 focused on the lesion sites of 147 of the 226 patients whose behavioral data are presented in Study 1. These analyses employed formal methods for statistical thresholding and power analysis of lesion overlap maps (Rudrauf et al., 2008). Based on Tranel et al.'s (2001, 2003, 2008) findings, as well as on other studies that we consider in the Discussion, we anticipated that in the group of patients investigated here, defective performances on the Naming, Picture Attribute, and Picture Comparison tasks would be associated with damage to the left IFG, ventral precentral and postcentral gyri, SMG, pMTG, and underlying white matter. In addition, we extrapolated from our earlier findings to further predict that lesions in these same regions, or in subsets of them, would also be present in a significant number of patients with defective performances on the other three tasks in the battery, all of which require verb comprehension—namely, Word-Picture Matching, Word Attribute, and Word Comparison. This prediction is one of the most novel aspects of the current study, since we have not reported the lesion correlates of impaired verb comprehension in any of our previous group studies, and since this topic has only been explored in a few other large-scale neuropsychological group studies, most of which involved patients with various progressive neurodegenerative diseases (Rhee et al., 2001; Cotelli et al., 2006; Hillis et al., 2006; Yi et al., 2007; Grossman et al., 2008; for two studies involving stroke patients see Hillis et al., 2002b, and Kalénine et al., in press). Finally, given the wide range of task dissociations described by Kemmerer et al. (2001a, 2001b), and the likelihood of observing similarly complex patterns of selective deficits in the current study, we predicted that the lesion maps associated with the different tasks would not be identical, but would instead be at least somewhat heterogeneous in terms of the extent and/or degree of involvement of not only the main regions of interest—i.e., the left IFG, SMG, and pMTG—but perhaps other regions as well.

2. STUDY 1: BEHAVIORAL PATTERNS

2.1. Methods

2.1.1. Participants—We studied 226 brain-damaged patients drawn from the Patient Registry of the Division of Behavioral Neurology and Cognitive Neuroscience at the University of Iowa. The patients were included in the current study if they could participate validly in the experimental procedures, and an effort was made to cover a variety of different lesion loci—i.e., lesions to either hemisphere, and to different sites within a hemisphere. Under the auspices of their enrollment in the Patient Registry, the patients have been screened to be free of mental retardation, learning disability, psychiatric disorder, substance abuse, and dementia. The patients in our Patient Registry have been extensively characterized neuropsychologically and neuroanatomically, following the neuropsychology (Tranel, 2007) and neuroanatomy (Damasio & Frank, 1992) protocols for our program. The neuropsychological and neuroanatomical data were collected when the patients were in the chronic phase of recovery, defined as three or more months post-lesion onset. The patients provided informed consent to participate in these studies, in accordance with university and federal regulations.

To be enrolled in our Patient Registry, patients must have focal, stable cerebral lesions. In the sample of 226 patients included in the current study, lesion etiologies were as follows: cerebrovascular disease (*N* = 150); surgical intervention to alleviate epileptic seizures (*N* = 39); tumor resection (*N* = 17); herpes simplex encephalitis (*N* = 8); anoxia (*N* = 8); traumatic brain injury (*N* = 4). Of the group, 129 patients had unilateral left hemisphere lesions, 67 had unilateral right hemisphere lesions, and 30 had bilateral lesions. Handedness was measured with the Geschwind-Oldfield Questionnaire, which has a scale ranging from full right-handedness (+100) to full left-handedness (−100), and in the current sample this variable was distributed as follows: 193 subjects were fully right-handed (+90 or greater); 15 were mostly right-handed; 10 were fully left-handed (−90 or lower); 7 were mostly left-handed; and 1 had mixed handedness (−10). There were 122 men and 104 women in the sample. Overall, they had a mean education level of 13.6 years (*SD* = 2.8). When the neuropsychological and neuroanatomical data for this study were gathered, the patients had a mean age of 56.3 years (*SD* = 14.3) and were on average 9.3 years post lesion onset (*SD* = 7.2).

The participants did not have basic impairments in intellectual functioning, perception, or attention that would confound their performances on the experimental tasks. Notably, some of the patients were fully or partially recovered aphasics. However, we only included such patients if they were capable of understanding the directions for the tasks and providing valid responses. We have extensive experience with these patients, and thus we could ascertain carefully, for every case, whether they were able to participate appropriately in the experiments. Summary data for several benchmark neuropsychological measures are as follows: verbal IQ (*M* = 99.3, *SD* = 13.5); performance IQ (*M* = 100.2, *SD* = 14.4); full-scale IQ (*M* = 99.6, *SD* = 13.1); Boston Naming Test (*M* = 50.6, *SD* = 11.0); Token Test (*M* = 40.8, *SD* = 7.5); Benton Judgment of Line Orientation Test (*M* = 25.9, *SD* = 3.9).

2.1.2. Stimuli and procedures—The stimuli consisted of the six tasks described in section 1.1. These tasks were given to each patient individually in a quiet examination room by a trained technician. The stimuli were presented either on a computer monitor (using PowerPoint) or via a Caramate slide projector. The tasks were consistently administered in the following sequence: Naming, Picture Comparison, Picture Attribute, Word-Picture Matching, Word Comparison, and Word Attribute. Patients were given an unlimited amount of time to respond to each item, and were encouraged to think carefully about each item before making a decision. All of the tasks were administered in a single session, although breaks were provided if the patient became tired. As noted above, we were careful during the test administration to make sure that patients were providing valid responses and understood fully the instructions for each task, and we relied on our extensive experience administering these tasks to our brain-damaged patients to make this determination. For tasks requiring comparisons and “odd one out” choices, we used practice items to make sure that patients understood the task demands.

2.1.3. Neuropsychological data quantification and analysis—With only two minor exceptions,[2] complete data sets for all six tasks were obtained from all 226 patients. Each patient's performance on each task was calculated as percent correct. Scoring of items

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[2] Case 129 did not receive the Naming task, and case 1976 did not receive the Word Comparison task.

was based on the normative data indicated in section 1.1 (for details see Fiez & Tranel, 1997). To define impairment, we used the conventional approach of classifying as “impaired” or “defective” all scores that were two or more standard deviations (*SD*s) below the mean of normal performance, as in previous work (e.g., Kemmerer et al., 2001a; Tranel et al., 2001, 2003, 2008; see Damasio et al., 2004, for a detailed discussion of the rationale for a 2 *SD* threshold for defining impairment).

Additional analyses involved just the patients who failed one or more of the six tasks (N = 61). To determine whether their average performance on each task was significantly below normal, we focused on their mean z-scores. And to determine whether the tasks differed in difficulty for these patients, we conducted a series of repeated measures ANOVAs comparing each pair of tasks in terms of percent correct. Also, to investigate dissociations between tasks in greater detail, we adopted the strategy employed by Kemmerer et al. (2001b). Specifically, in order for a difference between an impaired score and a normal score to qualify as a genuinely significant dissociation, it must be at least 2.0 z-score points in magnitude. Using this approach, we calculated the number of patients who manifested each of the 30 possible one-way dissociations between the six tasks in the battery.

2.1.4. Comparison of action naming and object naming—For the patients who exhibited action naming deficits, we investigated the extent to which their impairments were specific to the domain of actions by also administering, when possible, object naming tasks that included the following three categories of concrete entities: animals (N = 18), fruits/vegetables (N = 16), and tools (N = 35). For further information about the stimuli and scoring procedure, see Damasio et al. (2004).

2.2. Results

A total of 61 patients were impaired on one or more of the six tasks. Their lesion etiologies were as follows: non-hemorrhagic stroke (N = 37); hemorrhagic stroke (N = 6); aneurysm rupture/clipping (N = 5); surgical intervention to alleviate epileptic seizures (N = 5); tumor resection (N = 1); herpes simplex encephalitis (N = 4); traumatic brain injury (N = 3). **Table 1** shows each patient's percent correct and z-score on each task, and **Figure 1** shows the mean percent correct and standard errors for all 61 patients on all six tasks. 30 of the 61 patients were originally described by Kemmerer et al. (2001a); they are highlighted in Table 1 by asterisks after their case numbers, and their scores in Table 1 are identical to the corresponding scores in Table 3 of Kemmerer et al. (2001a). The data for the remaining 31 patients in Table 1 are reported here for the first time, with the sole exception of case 2762, whose scores are reproduced from Kemmerer et al. (2007).

The 61 patients listed in Table 1 are organized in blocks of rows according to the number of tasks that they failed. As shown in the first block, four patients were impaired on all six tasks: 1172, 1709, 1808, and 1699. Interestingly, these are the same four patients who Kemmerer et al. (2001a) reported as failing the whole battery (see the first block of rows in Table 3 of that paper). The other blocks of rows indicate that four patients failed five tasks, eleven patients failed four tasks, ten patients failed three tasks, twelve patients failed two tasks, and twenty patients failed just one task.

As indicated at the bottom of Table 1, the average performance of the entire group of 61 patients was significantly below normal, as measured by z-scores of −2.0 or lower, for three of the six tasks—specifically, Naming (M = −3.3, SD = 4.6), Word Attribute (M = −2.5, SD = 3.0), and Picture Comparison (M = −2.6, SD = 2.1). Moreover, the patients’ average performance approached the cut-off point for impairment on a fourth task—specifically, Word Comparison (M = −1.9, SD = 1.8). However, their average performance was within normal limits for the other two tasks—specifically, Word-Picture Matching ($M = -0.2$, $SD = 1.9$) and Picture Attribute ($M = -1.1$, $SD = 1.7$).

The relative difficulty of the six tasks was calculated for the 61 patients by conducting statistical comparisons of the percent correct scores for all possible pairs of tasks. These analyses revealed the following hierarchy of difficulty: Picture Comparison ($M = 62.3$, $SD = 17.6$), Naming ($M = 68.5$, $SD = 22.8$), and Word Comparison ($M = 73.1$, $SD = 14.8$) were the hardest; Picture Attribute ($M = 86.4$, $SD = 8.1$) and Word Attribute ($M = 85.8$, $SD = 10.6$) were in the middle; and Word-Picture Matching ($M = 91.1$, $SD = 8.7$) was the easiest. Focusing first on the three hardest tasks, performances on the Picture Comparison and Naming tasks were not significantly different from each other, but performance on the Picture Comparison task was significantly worse than on all four of the other tasks [Word Comparison, $F(1,59) = 19.1$, $p < 0.01$; Picture Attribute, $F(1,60) = 109.6$, $p < 0.01$; Word Attribute, $F(1,60) = 106.9$, $p < 0.01$; Word-Picture Matching, $F(1,60) = 191.9$, $p < 0.01$], and performance on the Naming task was significantly worse than on three of the other four tasks, the exception being Word Comparison [Picture Attribute, $F(1,59) = 50.0$, $p < 0.01$; Word Attribute, $F(1,59) = 34.2$, $p < 0.01$; Word-Picture Matching, $F(1,59) = 73.9$, $p < 0.01$]. Also, the Word Comparison task yielded significantly worse performance than the three remaining tasks [Word Attribute, $F(1,59) = 67.8$, $p < 0.01$; Picture Attribute, $F(1,59) = 68.8$, $p < 0.01$; Word-Picture Matching, $F(1,59) = 145.4$, $p < 0.01$]. Second, the Picture Attribute and Word Attribute tasks fell in the middle of the hierarchy of difficulty. They were not significantly different from each other, but performance on the Picture Attribute task was significantly worse than on the Word-Picture Matching task [$F(1,60) = 33.1$, $p < 0.01$], and performance on the Word Attribute task was too [$F(1,60) = 20.7$, $p < 0.01$]. Overall, then, the Picture Comparison, Naming, and Word Comparison tasks tended to be harder than the Picture Attribute and Word Attribute tasks, which in turn tended to be harder than the Word-Picture Matching task. Importantly, this hierarchy of relative difficulty across the six tasks is very similar to the one manifested by healthy participants (see the normative data in section 1.1). We would like to emphasize, however, that, as noted in the previous paragraph, the 61 patients performed, on average, significantly below normal on three of the most challenging tasks—Naming, Picture Comparison, and Picture Attribute—and came very close to performing, on average, significantly below normal on a fourth—Word Comparison.

Even though the six tasks seem to fall along a continuum of difficulty, each of them dissociated from all the others in at least some patients. **Table 2** shows how many patients manifested each of the 30 possible one-way dissociations between tasks, with a dissociation being defined as a difference of at least 2.0 z-score points between defective and normal performances. Of the 30 possible dissociations, 27 were exhibited by at least one patient. Thirteen of those 27 dissociations were exhibited by 1-10 patients, eleven were exhibited by 11-20 patients, and three were exhibited by more than 20 patients. Only three types of dissociation were unattested: impaired Word-Picture Matching and normal Word Attribute; impaired Word-Picture Matching and normal Word Comparison; and impaired Picture Attribute and normal Naming. Interestingly, these three unattested dissociations are identical to three of the four unattested dissociations reported by Kemmerer et al. (2001b). The fourth dissociation that was unattested in the data analyzed by Kemmerer et al. (2001b)—namely, impaired Word Attribute and normal Word Comparison—was exhibited by one patient (2589) in the current study.

Finally, **Table 3** shows which of the 34 patients who failed the Naming task were also impaired at naming various categories of concrete entities—specifically, animals, fruits/vegetables, and tools. Overall, 15 patients had defective naming of all three object categories; four patients had defective naming of just two object categories (although one of those patients was not tested on the third category); five patients had defective naming of just one object category; six patients were not impaired at naming any of the object categories (although two of those patients were not tested on one of the categories); and four patients were not administered any of the object naming tasks. Taking into account only the 27 patients who received all of the object naming tasks, paired *t*-tests revealed that action naming was significantly worse than animal naming ($p < 0.00001$), fruit/vegetable naming ($p < 0.00001$), and tool naming ($p < 0.00001$). However, no significant differences were found between any of the categories of concrete entities.

3. STUDY 2: LESION SITES

3.1. Methods

3.1.1. Participants—This study included 147 of the 226 patients described above. The remaining patients were excluded because their lesions have not been analyzed using the MAP3 technique, this being a prerequisite for incorporation in the types of lesion overlap investigations that we conducted. Of the 147 patients whose lesions were in fact taken into account, 37 failed one or more of the six tasks in the battery. These 37 patients are indicated by grey shading in Tables 1 and 3.

3.1.2. Neuroanatomical data quantification and analysis

3.1.2.1. Lesion mapping: MRIs of the brains of most patients were acquired using a 1.5 Tesla General Electric Signa scanner with a 3D SPGR sequence yielding 1.5 – 1.7 mm contiguous T1-weighted coronal cuts. In some patients for whom an MRI could not be acquired, computerized axial tomography (CT) was used.

Lesion delineation and transfer onto a reference brain was achieved using the MAP3 method (Frank et al., 1997; Damasio, 2000) in which the boundaries of the lesion of a given patient are identified and manually transferred onto a normal reference brain based on the delineation of homologous anatomical landmarks. This procedure requires anatomical expertise, but circumvents the problems of inter-individual registration encountered with lesion data, and the problems of combining patients scanned with different imaging modalities. It has been used to generate lesion overlap and lesion overlap difference maps between groups of patients with and without a deficit of interest, across a variety of domains (e.g., Adolphs et al., 2000; Barrash et al., 2000; Tranel et al., 2001, 2003, 2008; Damasio et al., 2004; Kemmerer & Tranel, 2008). Lesion delineation and transfer were done using Brainvox (Frank et al., 1997).

The general procedure is as follows (Damasio et al., 2004): (1) a normal template is reconstructed in three dimensions from thin contiguous MR slices; (2) major sulci are identified and color-coded in the template brain and the lesioned brain; (3) the template brain is resliced so as to match the MR slices (or CT slices) of the lesioned brain; (4) the slices in the template brain are matched in orientation and thickness to those of the lesioned brain, taking into consideration the intersection of the slices with the color-coded sulci; (5) the lesion contour on each slice is manually traced by an expert on the template brain, taking into consideration the distance of the lesion contour to identifiable landmarks, such as sulci and subcortical structures, and respecting the grey and white matter components of the lesion; (6) the collection of transferred traces defines a volume that can be saved as a binary mask of lesion. One advantage of this time-consuming approach is that it preserves anatomical boundaries and tissue compartments in the mapping of the lesions onto the reference brain.

3.1.2.2. PM3 and ECM analysis: We performed whole-brain lesion-deficit statistical mapping analyses using lesion proportion difference maps (PM3s) for each of the six tasks

(Rudrauf et al., 2008). For each voxel, the PM3 statistic is defined as the difference between, on the one hand, the proportion of patients with a lesion at that voxel and a deficit (N_{LD}) among those patients with a deficit (N_D), and on the other hand, the proportion of patients with a lesion at that voxel and no deficit (N_{LnD}) among those patients with no deficit (N_{nD}). Lesion proportion difference maps between groups of patients with and without a deficit of interest are a normalized version of the kinds of lesion overlap difference maps used in many previous studies in our laboratory.

We pragmatically determined the statistical thresholds based on preliminary power analyses. Voxelwise lesion studies are prone to low and heterogeneous statistical power (Rudrauf et al., 2008), a problem which is exacerbated by attempting to control for type I error due to multiple tests over the cerebral space. For whole brain studies, it is often necessary to use a "realistic" threshold based on a trade-off between sensitivity and specificity. In order to do so, we have introduced the concept of "effective coverage" (Rudrauf et al., 2008). Effective coverage is defined as the map of locations where effects can possibly be detected at a given significance threshold, if the maximal lesion-deficit relationships authorized by the sample would be observed (which depends on the overall number of patients, the number of patients with a lesion at a given voxel, and the number of patients with a deficit). A satisfying effective coverage implies the ability to detect effects over a substantial percentage of the brain (or within regions for which hypotheses have been formulated). To build effective coverage maps (ECMs), we first construct maps of the maximum lesion-deficit relationship permitted by the sample. Maps of such maximally permitted statistics are then thresholded according to the statistical analysis used (e.g., PM3 exact statistic). ECMs select significance thresholds that are not associated with overly restricted effective coverage, and describe the regions where no effects could have been found even under the strongest lesion-deficit relationships, so as to guide the interpretation of results.

Because high thresholds lead to an important loss in effective coverage, we selected a liberal threshold for the voxelwise analyses: $p < 0.05$, uncorrected. We opted for this threshold based on preliminary ECMs analyses. The main results are presented using mapping of significant effects across the six tasks, only in the voxel space where ECMs were significant at 0.05 for all tasks. This is to ensure that possible differences in location of effects across tasks are not confounded with trivial heterogeneity of statistical power (Rudrauf et al., 2008).

3.2. Results

3.2.1. Conjunction and disjunction analyses across the six tasks—

Figure 2A shows the number of tasks with significant effects in regions where effective coverage was observed for all six tasks. Significant effects for all six tasks (red) were found in the following left-hemisphere regions: the cortex and underlying white matter of the IFG (especially BA47, but also portions of BA45 and BA44); the cortex and underlying white matter of the inferior precentral gyrus, extending superiorly into what are likely to be hand-related primary motor and premotor areas; and the anterior insula. Significant effects for five tasks (purple) were found in the same areas implicated in all six tasks, but with more posterior involvement of the IFG and greater overall white matter involvement beneath the ventral and lateral sectors of the precentral gyrus; in addition, significant effects appeared in the white matter subjacent to the left pMTG. Significant effects for four tasks (dark blue) were found around the borders of many of the frontal areas implicated in five or six tasks, and were also found in the following left-hemisphere regions: the ventral and lateral sectors of the postcentral gyrus; the cortex and underlying white matter of the anterior SMG; and the cortex and underlying white matter of the pMTG. Significant effects for three tasks (light blue) were largely similar to those for four tasks. Significant effects for two tasks (green) were found in the left SMG, in much of the left posterior temporal lobe, and in the right posterior fusiform/lingual gyri. Finally, significant effects for one task (orange) were found in numerous widely distributed areas in the left hemisphere, as well as in a few areas in the right hemisphere.

Figure 2B shows regions where significant effects were uniquely found for particular tasks. The Naming task (orange) was independently associated with several left-hemisphere regions: the SMG, the angular gyrus, and the middle fusiform and inferior temporal gyri. The Word-Picture Matching task (green) was independently associated with the right posterior collateral sulcus. The Word Attribute task (light blue) was independently associated with the right IFG (especially BA47) and the bilateral anterior cingulate cortex. The Word Comparison task (dark blue) was independently associated with a few small areas in the left anterior superior temporal gyrus, left anterior fusiform gyrus, and left anterior intraparietal sulcus. The Picture Attribute task (purple) was independently associated with a small area in the left posterior orbital gyrus, and with a large, mostly ventral, left temporo-occipital region comprising sectors of the fusiform, parahippocampal, lingual, and lateral occipital gyri. Last of all, the Picture Comparison task (red) was independently associated with the left posterior cingulate cortex and precuneus, and with the right mesial lingual and retrosplenial areas.

3.2.2. Lesion sites of patients impaired on all six tasks—**Figure 3** shows the lesions of three of the four patients who failed all six tasks. 1172's lesion is in the heart of Broca's area (BAs 44 and 45) in the left posterior IFG (**Figure 3A**; for a more detailed figure that includes seven coronal sections, see Kemmerer & Tranel, 2003). The lesion extends anteriorly into the orbital sector of the IFG, and superiorly into the middle part of the premotor region. The anterior insula is damaged, too; however, the precentral gyrus and basal ganglia are minimally affected. Posteriorly, there is no significant cortical involvement past the Rolandic sulcus, but some of the white matter underneath the postcentral gyrus and inferior parietal lobule is affected. 1709's lesion is very similar to 1172's, being centered in Broca's area (**Figure 3B**; a more detailed figure could not be provided because the MRI was obtained in 1993 and contains a considerable amount of motion artifact). The majority of the damage is confined to the left IFG, but a portion of the premotor/prefrontal cortex immediately superior to the IFG is affected as well. Moreover, the lesion spreads into the ventral precentral gyrus and through the superior portions of the insula and internal capsule. In contrast to both 1172 and 1709, 1808 had damage in the left pMTG and underlying white matter, with extension through the white matter ventrally to the fusiform gyrus (**Figure 3C**; see also Figure 3A in Tranel et al., 2003). Finally, 1699 had right hemisphere damage affecting mostly the white matter in the right inferior parietal lobule. The lesion is not shown in Figure 3.

3.2.3. Lesion sites linked with impairment on each individual task—**Figure 4** shows regions with significant effects for each individual task. As indicated in **Figure 4A**, the Naming task was linked with the cortex and underlying white matter of several exclusively left-hemisphere regions, including the IFG, inferior precentral and postcentral gyri, insula, SMG, angular gyrus, superior temporal gyrus, pMTG, posterior inferior temporal and lateral occipital gyri, and posterior fusiform and lingual gyri. As indicated in **Figure 4B**, the Word-Picture Matching task was linked with a much more restricted range of left-hemisphere regions—specifically, the cortex and underlying white matter of the IFG (especially BA47 and BA45), the lateral, perhaps hand-related, precentral gyrus, the anterior insula, and portions of the fusiform gyrus. In addition, the Word-Picture Matching task was associated with the right posterior collateral sulcus. As indicated in **Figure 4C**, the Word Attribute task was linked with a variety of left-hemisphere regions, including the cortex and

underlying white matter of the entire IFG, the lateral, perhaps hand-related, precentral gyrus, the posterior superior frontal gyrus, and the pMTG. Furthermore, the Word Attribute task was associated with the right IFG (especially BA47) and the bilateral anterior cingulate cortex. As indicated in **Figure 4D**, the Word Comparison task was linked with a network of left-lateralized brain regions that is almost identical to the one that was linked with the Naming task. The most conspicuous difference is that the Word Comparison task did not have as much posterior ventral temporal and ventrolateral temporo-occipital involvement as the Naming task. As indicated in **Figure 4E**, the Picture Attribute task was linked with the cortex and underlying white matter of the left IFG, inferior precentral and postcentral gyri, SMG, and pMTG. This task was also associated with an unusually large ventral temporal and ventrolateral temporo-occipital region in the left hemisphere. Finally, as shown in **Figure 4F**, the Picture Comparison task was linked with essentially the same left frontal and parietal regions as the Naming and Word Comparison tasks. In addition, it was linked with the white matter subjacent to the left pMTG. Notably, there was greater posterior ventral temporal involvement in the right than the left hemisphere, analogous to the Word-Picture Matching task. Last of all, the Picture Comparison task was associated with the left posterior cingulate cortex and precuneus, and with the right mesial lingual and retrosplenial areas.

4. DISCUSSION

The aim of this investigation was to explore the behavioral patterns (Study 1) and lesion sites (Study 2) of a large number of brain-damaged patients, all of whom received a battery of six tasks that probe lexical and conceptual knowledge of actions in a variety of verbal and non-verbal ways, including naming, word-picture matching, attribute judgments involving both words and pictures, and associative comparisons involving both words and pictures. In the following discussion, we first consider the major behavioral outcomes of the investigation, and then we examine the major neuroanatomical outcomes.

4.1. Major behavioral outcomes

The 61 patients who had deficits on one or more of the six tasks varied greatly in terms of the exact number of tasks that they failed, with some failing just one, others two, others three, others four, others five, and others all six. From both a clinical and a theoretical perspective, it is especially interesting that only four of the 61 patients failed the entire battery of tasks—namely, 1172, 1709, 1808, and 1699. It is also notable that all of these cases were originally described by Kemmerer et al. (2001a, 2001b), and not a single one of the 137 new cases in the current investigation had comprehensive, across-the-board impairments on the whole battery of tasks. Indeed, the four patients who are indicated at the top of Table 3 in Kemmerer et al.'s (2001a) paper as failing all six tasks are the same ones who are indicated at the top of Table 1 in the current paper as failing all six tasks. This outcome is significant for at least two reasons. It suggests that deep, pervasive, and severely debilitating defects in the domain of action concepts are relatively uncommon. And it underscores the advantages of employing a heterogeneous collection of tasks to carefully assess any given patient's competence in this domain. After all, patients who fail a relatively large number of tasks are more likely to have impairments that directly affect the core content of action concepts, whereas patients who fail a relatively small number of tasks are more likely to have superficial or process-specific impairments that affect particular ways of retrieving or analyzing those concepts.[3]

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[3] In this context, another relevant factor is whether or not a patient tends to fail items involving the same types of actions across tasks, since such consistency would constitute evidence for a representational deficit rather than a processing deficit. We did not address this issue in the current investigation; however, its potential importance is revealed by neuropsychological studies that have taken it into account (e.g., Hillis et al., 1990; Jeffries & Lambon Ralph, 2006; Tranel et al., 2008).

Another major behavioral outcome is that the six tasks were not evenly distributed, but instead fell along a continuum of difficulty, for the 61 patients who failed at least one of them. The Picture Comparison, Naming, and Word Comparison tasks were the most challenging, and in fact the average performance of the 61 patients was significantly below normal for the first two of those tasks, and was very close to the cut-off point for the third. In this context, it is notable that although the Picture Comparison task is non-verbal insofar as it does not require the participant to overtly process words in either the stimuli or the responses, it may nevertheless have much in common with the Naming task. This is because the most natural, reflexive strategy for carrying out the task is to first determine, for each item, which two of the three depicted actions can be covertly named with the same verb, and then select the remaining action as the "odd one out." For example, one item includes the following three pictures: a person *carving* a pumpkin with a knife, a person *carving* a bar of soap with a knife, and a person *spreading* jam over a slice of bread with a knife. As revealed by the italicized verbs in these descriptions, the first two pictures show similar kinds of actions, whereas the third shows a different kind of action and hence is the "odd one out." Thus, successful performance on the Picture Comparison task may, to some extent, be facilitated by categorizing the action stimuli in terms of the semantic structures of English verbs, and it is likely that healthy English-speaking participants often adopt such an approach.[4] At the same time, however, it is unlikely that a high level of accuracy on the Picture Comparison task necessarily requires the capacity to retrieve all of the appropriate verbs. Evidence supporting this view comes from the fact that many patients—15, according to Table 1—passed the Picture Comparison task yet failed the Naming task.

Returning to the topic of differential task difficulty, the Picture Attribute and Word Attribute tasks turned out to be significantly easier than the Naming, Picture Comparison, and Word Comparison tasks. The two "attribute" tasks may have been easier than the two "comparison" tasks because they only involve semantic analysis of two action concepts per item, and moreover the pertinent parameters are provided by the experimenter (e.g., "Which action would be more tiring?"); in contrast, the two "comparison" tasks involve semantic analysis of three action concepts per item, and the participant must discover the relevant dimensions. Finally, the Word-Picture Matching task was the easiest one in the battery. This is consistent with neuropsychological research on object concepts which suggests that matching paradigms often elicit better performance than more complex naming and associative paradigms (e.g., Jeffries & Lambon Ralph, 2006; Corbett et al., 2009).

Yet another important behavioral outcome is that, despite the evidence for a continuum of difficulty among the six tasks, almost all of the 30 possible one-way dissociations between tasks were manifested by at least some of the 61 patients who failed one or more tasks. Of course, because the current investigation included the 30 impaired patients from Kemmerer et al.'s (2001a, 2001b) study, this result was guaranteed at the outset. However, it is worth emphasizing that the addition of 31 new patients who failed one or more tasks led to a larger number of cases representing each of the various types of dissociation, thereby strengthening the original findings and lending further support to the notion that each task may have idiosyncratic processing requirements, or combinations of processing requirements, that can be selectively disrupted by focal brain damage. Although many of the dissociations are not especially striking or surprising, others warrant closer attention. Of greatest interest, perhaps, is the somewhat counterintuitive finding that the ability to name actions with appropriate verbs can be preserved while the ability to perform a variety of other tasks involving action concepts is impaired. Kemmerer et al. (2001a, 2001b) reported 13 patients

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[4] An open question is whether the stimuli would be categorized in similar ways by non-English-speaking participants, such as people who routinely use languages with very different kinds of event coding systems, such as serial verbs (Aikhenvald & Dixon, 2006; Bisang, 2009), coverbs (Wilson, 1999; Schultze-Berndt, 2000, 2006; McGregor, 2002), or figure-incorporating verbs (Talmy, 2000).

like this, and here we report 26 more. For example, case 1362, originally described by Kemmerer et al. (2001a, 2001b), achieved a score of 87% correct ($z = 0.4$) on the Naming task, but was significantly impaired on Word-Picture Matching (80%, −2.6), Word Attribute (47%, −13.3), Word Comparison (39%, −6.1), and Picture Comparison (42%, 5.0). Similarly, case 3050, described here for the first time, achieved a score of 89% correct ($z = 0.8$) on the Naming task, but was significantly impaired on Word Attribute (85%, −2.7), Word Comparison (66%, −2.8), and Picture Comparison (50%, −4.0). Cases like these are of clinical and theoretical importance because they demonstrate that intact verb retrieval for purposes of action naming cannot be interpreted as a reliable sign that the regulation of action concepts is completely normal. As suggested by Kemmerer et al. (2001a; see also Brennen et al., 1996; Marconi, 1997), referential processing, which involves mapping words onto the world, may have partially distinct neurocognitive underpinnings from analytic processing, which involves decomposing the meanings of words into their component features and exploring the networks of featural relations that exist both within and between concepts.

The last major behavioral outcome that we would like to highlight is that a substantial proportion of the patients with action naming deficits had normal naming of one, two, or all three of the object categories that were tested (animals, fruits/vegetables, and tools). Dissociations between impaired action naming and preserved object naming have been reported in numerous previous studies, and the opposite type of dissociation is also well-attested (for reviews see Mätzig et al., 2009; Vigliocco et al., in press). Hence the findings reported here are by no means new. Nonetheless, they are valuable insofar as they reveal the extent to which the patients' naming impairments are specific to the domain of actions.

4.2. Major neuroanatomical outcomes

4.2.1. Associations between impaired performances and lesion sites across the six tasks—

On the basis of our own previous neuropsychological research utilizing the Naming, Picture Attribute, and Picture Comparison tasks, we predicted that deficits on not only those three tasks, but also on the other three tasks—Word-Picture Matching, Word Attribute, and Word Comparison, all of which require verb comprehension—would be strongly linked with damage to the following left-hemisphere regions: the IFG, the inferior precentral and postcentral gyri, the SMG, the pMTG, and the white matter underlying all of these areas. The complex pattern of results that emerged is consistent with most, but not all, of these predictions. The most salient finding is that, as expected, the left IFG was significantly associated with all six tasks. We also obtained evidence for a connection between poor performance on all six tasks and lesions in the left inferior precentral gyrus, including the lateral sector that is likely to be the hand-related portion of the motor homunculus (for a historical perspective see Graziano, 2009; for a recent high-resolution fMRI study see Meier et al., 2008). To our surprise, the left SMG was not reliably linked with all six tasks; however, our prediction did receive partial support, since this cortical region turned out to be linked with four tasks—specifically, Naming, Word Comparison, Picture Attribute, and Picture Comparison. As for the pMTG, although it was not associated with all six tasks, it was nevertheless associated with five of them, the sole exception being the easiest task in the battery—Word-Picture Matching.

Additional support for our predictions, and further insight into the neural underpinnings of lexical and conceptual knowledge of actions, comes from the lesion sites of cases 1172, 1709, and 1808—three of the four patients who failed all six tasks.[5] The fact that both

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[5] We will not discuss the lesion of the fourth patient who failed all six tasks—namely, 1699—because this patient was clearly a neuroanatomical "outlier," with damage completely outside all of the areas implicated in our group results.

1172's and 1709's lesions were centered in the left IFG constitutes powerful evidence that this structure plays a key role in the neurocognitive network that subserves the processing of action words and concepts. It is also worth emphasizing that both patients' lesions extended superiorly into the lateral portion of the precentral sulcus and the adjacent posterior portion of the middle frontal gyrus—an area that is generally considered to be a hand-related sector of the premotor cortex. Turning to 1808, his left frontal lobe was completely spared, but he had a focal lesion in the left temporal lobe, specifically in the pMTG and underlying white matter. Taken together, these findings from 1172, 1709, and 1808 support the hypothesis that both the left IFG and the left pMTG are essential for lexical and conceptual knowledge of actions, since damage to either region by itself can be, in some cases, sufficient to disrupt that knowledge.

Another notable outcome of our neuroanatomical analyses is that they revealed a number of interesting patterns involving correspondences between, on the one hand, certain combinations of tasks, and on the other, certain combinations of lesion sites. Some of these patterns are as follows. First, the three most difficult tasks—Naming, Word Comparison, and Picture Comparison—were associated with the most extensive amounts of left frontal and parietal damage, and two of those tasks—Naming and Word Comparison—were also associated with the most extensive amounts of left pMTG damage. These correspondences may reflect a general tendency for the most challenging tasks to place greater computational demands on the core components of the neurocognitive circuitry underlying the controlled processing of action words and concepts. Second, and as a somewhat narrower form of the first pattern, the two tasks that involve three-way "comparison" judgments—Word Comparison and Picture Comparison—were linked with larger amounts of the left frontal lobe than the two tasks that involve two-way "attribute" judgments—Word Attribute and Picture Attribute. Analogous to the first pattern, this could be a manifestation of the greater difficulty of the former tasks, especially with respect to executive control operations. Third, the four tasks that include pictures of actions as stimuli—Naming, Word-Picture Matching, Picture Attribute, and Picture Comparison—were much more strongly associated with ventral occipito-temporal regions than the two tasks that only involve words as stimuli—Word Attribute and Word Comparison. One interpretation of this pattern is that, in contrast to the latter tasks, the former ones require accurate visual processing of the shape, color, and texture features of statically depicted actions, and those features are well-established as depending on the ventral "what" stream (for reviews see Giese & Poggio, 2003; Martin, 2009; Kemmerer, 2010; for further discussion see section 4.2.2.2).

4.2.2. Possible functional roles of left frontal, temporal, and parietal regions in processing lexical and conceptual knowledge of actions

4.2.2.1. Frontal regions: The left IFG includes BA44 and BA45, which together constitute Broca's area. The left IFG includes BA47 as well, and because this structure has also been implicated in linguistic processing, Hagoort (2005) lumps it together with BA44 and BA45 to form what he calls "Broca's complex." As we expected, impaired performance on each of the six tasks was strongly linked with damage to all three sectors of the left IFG. Several different theories are currently being debated regarding the functional-anatomical details of how the left IFG supports language (e.g., Hagoort, 2005; Thompson-Schill, 2005; Grodzinsky & Amunts, 2006; Koechlin & Jubault, 2006; Schubotz & Fiebach, 2006; Lindenberg et al., 2007; Bornkessel-Schlesewsky et al., 2009). Here we restrict our discussion to three ways in which this region may contribute to the processing of lexical and conceptual knowledge of actions: selecting appropriate representations from competing co-activated alternatives; mapping verb meanings onto verb forms; and understanding certain aspects of actions, especially goal-related features.

One way in which the left IFG may contribute to performing the various tasks in our battery involves executive function, or what is sometimes called cognitive control. Although the six tasks clearly differ with respect to the specific computational demands that they impose on the participant, they all require the participant to search semantic memory strategically and focus attention on certain concepts rather than others. Recent studies employing diverse techniques suggest that in such situations two different kinds of cognitive control processes are subserved by two different sectors of the left IFG. In particular, according to the "two-process model" (Badre & Wagner, 2007), the anterior sector (BA47) guides the top-down retrieval or activation of semantic content stored elsewhere in the brain (Wagner et al., 2001; Badre et al., 2005; Bunge et al., 2005; Gough et al., 2005; Sabb et al., 2007), and the middle sector (BA45), perhaps together with the posterior sector (BA44), operates on the products of retrieval to select appropriate representations from among competitors (Thompson-Schill et al., 1998; Fletcher et al., 2000; Badre et al., 2005; Moss et al., 2005; Bedny et al., 2008; Schnur et al., 2009). Consistent with this distinction, an fMRI study by Gold et al. (2006) showed that when the meanings of concrete nouns are processed, left BA47 is involved in "strategic semantic facilitation" whereas left BA45 is involved in "strategic semantic inhibition." Furthermore, an fMRI study by Kemmerer et al. (2008) showed that both sectors of the left IFG are reliably recruited when participants make subtle semantic similarity judgments about triads of verbs—a task that is analogous in some ways to the Word Comparison task in the present study. These considerations suggest that many of the patients who failed various combinations of the tasks in our battery may have had impairments affecting the kinds of cognitive control operations that are putatively subserved by the left IFG. At the same time, however, it is important to bear in mind that all six tasks dissociated from each other in at least some patients. Thus, further research is needed to explore how different sorts of task-specific processes may depend on the left IFG in different ways.

Although the "cognitive control" hypothesis regarding the left IFG applies equally to the processing of nouns and verbs, other evidence suggests that the left IFG may contribute somewhat disproportionately to the latter. The current investigation converges with several previous studies in demonstrating that although brain-damaged patients with action naming deficits do not always have lesions in the left IFG, they frequently do, and in fact that is the most common site of injury (for reviews see Mätzig et al., 2009; Vigliocco et al., in press). For instance, as already noted, Tranel et al. (2001, 2008) found that the left IFG was the region of maximal lesion overlap in patients with impaired naming of static and dynamic actions. Even more interesting, however, is that many of those patients, as well as many of the patients in the current investigation, had normal naming of various categories of concrete objects. Similarly, in a study with acute stroke patients, Hillis et al. (2002b) found that left IFG dysfunction was implicated more in defective action naming than in defective object naming. In addition, significantly worse action than object naming has been observed in patients with a number of neurodegenerative diseases that affect, among other regions, the left IFG, including progressive nonfluent aphasia (Cotelli et al., 2006; Hillis et al., 2002a, 2004, 2006; see also Cappa et al., 1998), corticobasal degeneration (Cotelli et al., 2006; Silveri & Ciccarelli, 2007), and a variant of amyotrophic lateral sclerosis (motor neuron disease) that includes the predominantly frontal form of frontotemporal dementia (Bak et al., 2001; Bak & Hodges, 2004; Hillis et al., 2004, 2006). Finally, a few functional neuroimaging studies with healthy participants have revealed significantly greater left IFG engagement during action naming than during object naming (Tranel et al., 2005; Berlingeri et al., 2008); this is not, however, a consistent finding (Damasio et al., 2001; Saccuman et al., 2006; Liljestrom et al., 2008; Siri et al., 2008; for reviews see Berlingeri et al., 2008; Vigliocco et al., in press). Taken together, these different sources of data provide some support for the notion that the left IFG contributes more to action naming than object naming, or at the least, plays a disproportionately important role in action naming.

Pursuing this line of thinking a step further, there is also increasing evidence that the left IFG may play a critical role in directly representing certain aspects of action concepts. Here we found that damage to the left IFG was significantly linked not only with impairment on the one task that requires action verb production—specifically, Naming—but also with impairment on the three tasks that require action verb comprehension—specifically, Word-Picture Matching, Word Attribute, and Word Comparison. This finding supports the idea that the left IFG may be essential for understanding at least some of the semantic features that are typically encoded by action verbs, and it adds to previous studies that have revealed verb comprehension deficits in patients with various neurogenerative diseases that, as noted above, include left IFG pathology (Rhee et al., 2001; Bak et al., 2001; Bak & Hodges, 2003, 2004; Cotelli et al., 2006; Hillis et al., 2006).

Apart from the present study, we are only aware of two other large-scale neuropsychological studies that have investigated the lesion correlates of impaired verb comprehension in stroke patients—namely, the studies by Hillis et al. (2002b) and Kalénine et al. (in press) that we mentioned toward the end of the Introduction. Hillis et al. (2002b) found that of 23 patients who exhibited impaired action naming, 11 also exhibited impaired verb comprehension, as measured by a word-picture verification task. Among those 11 patients, infarct and/or hypoperfusion was found most frequently in the left superior temporal gyrus, including Wernicke's area. Unlike in the current study, the left IFG was not significantly linked with difficulties understanding verbs. However, it is noteworthy that all of the patients in Hillis et al.'s study were acute (tested within 24 hours post-onset), whereas all of the patients in our study were chronic. Kalénine et al. (in press) reported data from 43 left-hemisphere stroke patients who were asked to match action verbs (e.g., *hammering*) with videoclips under the following conditions: in the semantic task, the incorrect videoclip on each trial involved a semantically related action (e.g., sawing); and in the spatial task, the incorrect videoclip on each trial involved an error of body posture or movement amplitude/timing. Analyses using voxel-based lesion-symptom mapping indicated that poor performance on the semantic task was most significantly associated with damage to the pMTG, and that poor performance on the spatial task was most significantly associated with damage to the inferior parietal lobule. Neither task turned out to be linked with the IFG. This lack of IFG involvement in action knowledge is certainly an intriguing finding, but it is clearly at odds with the results of the present study, and it is also hard to reconcile with a number of other recent investigations, as described below.

Importantly, the present study replicated and extended Tranel et al.'s (2003) finding that left IFG damage is strongly associated with impairment on the two tasks in the battery that probe action knowledge in non-verbal formats—specifically, Picture Attribute and Picture Comparison. This dovetails nicely with a growing literature that, ever since the seminal discovery of mirror neurons roughly 20 years ago (de Pellegrino et al., 1992), has implicated the IFG, and especially BA44, in not only the production but also the perception of actions, especially hand actions (for a review see Grafton, 2009). Evidence that left BA44 is normally engaged during the perception of hand actions comes from a number of studies with healthy subjects, including studies using fMRI (e.g., Kilner et al., 2009), TMS (e.g., Pobric & Hamilton, 2006), and MEG (e.g., Nishitani & Hari, 2000). And evidence that the same region may in fact be causally necessary for understanding perceived hand actions comes not only from Tranel et al.'s (2003) study and the current investigation, but also from several other neuropsychological studies (Saygin et al., 2004; Saygin, 2007; Moro et al., 2008; Pazzaglia et al., 2008; Fazio et al., 2009). Interestingly, a number of researchers have argued that BA44 may be more sensitive to the goals than the kinematics of bodily actions (Hamzei et al., 2003; Johnson-Frey et al., 2003; Gazzola et al., 2007a, 2007b; Hamilton & Grafton, 2007, 2008; Tunik et al., 2008; Schubotz & von Cramon, 2009; see also Grafton, 2009). Following this lead, Kemmerer and Gonzalez Castillo (2010) explored the idea that left BA44 may play an especially important role in representing goal-related aspects of verb meanings and associated clausal constructions. However, this remains a very speculative line of inquiry.

At this point, we would like to shift our focus to a different region of the left frontal lobe that was significantly linked with impairment on all of the tasks comprising our battery—specifically, the lateral precentral gyrus and the rostrally adjacent posterior middle frontal gyrus. As noted above, this general region has traditionally been associated with the control of hand actions (Graziano, 2009). Moreover, a number of studies employing fMRI (e.g., Buccino et al., 2001), TMS (e.g., Aglioti et al., 2008), MEG (e.g., Caetano et al., 2007), and the lesion method (e.g., Serino et al., 2010) suggest that, like the IFG, this region also contributes to the perception of hand actions—with an emphasis, however, on kinematics rather than goals. In addition, and of direct relevance to the current investigation, there is mounting evidence that the same region is engaged when subjects read or hear verbs denoting hand actions (for reviews see Pulvermüller, 2005, 2008; Willems & Hagoort, 2007; Hauk et al., 2008; Fernandino & Iacoboni, 2010; Kemmerer & Gonzalez Castillo, 2010). Some of this evidence is as follows.

First, as shown in **Figure 5**, evidence that action verbs induce somatotopically organized activation patterns in leg/foot-related, arm/hand-related, and lip/tongue-related primary motor and premotor cortices comes from several fMRI studies (for partially conflicting data see Tomasino et al., 2007; Postle et al., 2008). Second, evidence that these activation patterns are triggered quite rapidly, sometimes as fast as 150-250 ms post-verb-onset, comes from studies using MEG (Pulvermüller et al., 2005b) and electrophysiology (Pulvermüller et al., 2000, 2001; Hauk & Pulvermüller, 2004; Shtyrov et al., 2004; Boulenger et al., 2008; van Elk et al., 2010). And third, evidence that the activation patterns are functionally relevant to verb comprehension comes from TMS studies showing that stimulation of the pertinent motor areas can either facilitate (Pulvermüller et al., 2005a) or disrupt (Gerfo et al., 2008) semantic processing, depending on the protocol (see also Oliveri et al., 2004; Buccino et al., 2005; Glenberg et al., 2008; for partially conflicting data see Tomasino et al., 2008; Papeo et al., 2009). Further evidence that the frontal motor regions in question play a causal role in understanding action verbs comes from an important neuropsychological study involving patients with ALS (Grossman et al., 2008). In general, however, research on “semantic somatotopy” has suffered from a dearth of neuropsychological data. The current investigation helps to fill this gap, because even though our battery of tasks did not employ a well-controlled set of hand-action verbs, all of the tasks did have a preponderance (roughly 70%) of hand-related stimuli, and the results revealed that hand-related primary motor and premotor cortices in the left hemisphere were among the regions that were most reliably damaged in the patients who failed those tasks. Thus, our study provides additional support for the hypothesis that understanding action verbs requires simulating those actions in one's own motor system. We hasten to add, however, that in order for this hypothesis to be rigorously evaluated, it will be necessary to conduct further studies that explore more directly whether—and, if so, exactly how—interfering with the operations of the body-part-specific regions of the primary motor and/or premotor cortices affects the processing of the corresponding body-part-specific motor features of verb meanings.

4.2.2.2. Temporal regions: The left pMTG was implicated in all of the tasks except Word-Picture Matching. A number of fMRI studies have reported significant engagement of this region during the processing of action verbs and sentences, compared to various baseline conditions (verbs: Damasio et al., 2001; Grossman et al., 2002; Kable et al., 2002, 2005; Noppeney et al., 2005; Tranel et al., 2005; Bedny et al., 2008; Kemmerer et al., 2008; Pirog Revill et al., 2008; Pulvermüller et al., 2009; sentences: Tettamanti et al., 2005; Wallentin et al., 2005; Chen et al., 2008; Tyler et al., 2008; Deen & McCarthy, 2010; Saygin et al., in press). These findings are often interpreted as evidence that the left pMTG—together with the left posterior superior temporal sulcus (pSTS), which was also included in our lesion maps—subserves the visual manner-of-motion features of action concepts. This view is motivated in large part by independent evidence that the pMTG and pSTS receive direct input from the motion-related area hMT+ and respond strongly to the visual perception of complex movement patterns, including those of people (for reviews see Allison et al., 2000; Giese & Poggio, 2003; Beauchamp & Martin, 2007; Blake & Shiffrar, 2007).

However, another possibility—one that is not necessarily incompatible with the first—is that the left pMTG/pSTS region represents more schematic aspects of event structure. Some of the most compelling evidence for this view comes from an fMRI study by Bedny et al. (2008) in which participants made semantic similarity judgments involving four types of words: action verbs (e.g., *run*), non-action verbs (e.g., *think*), action-related animate nouns (e.g., *cat*) and non-action-related inanimate nouns (e.g., *rock*). The investigators found that the signals in the left pMTG/pSTS were equally high for verbs like *run* and *think*, and equally low for nouns like *cat* and *rock* (for similar findings see Grossman et al., 2002; however, for contradictory data see Tettamanti et al., 2005). This finding raises the possibility that the left pMTG/pSTS may represent relatively austere properties of verb meaning—i.e., properties that are shared by both action and non-action verbs and that contribute to the content of event structure templates, such as information about agency, argument structure, force-dynamic relations between entities, etc. Several other studies also support this possibility (e.g., Bornkessel et al., 2005; Grewe et al., 2007; Wu et al., 2007). Moreover, the left pMTG/pSTS region has been implicated in a number of additional neurocognitive capacities that are relevant to the representation of events, including visuospatial perspective-taking, mental state attribution, and multisensory integration (Beauchamp et al., 2008; Heberlein, 2008; Hein & Knight, 2008; Perner & Leekam, 2008). Considering all of these factors, it may ultimately turn out that the posterolateral temporal area at issue here contributes to the processing of several different aspects of action concepts, including, but not limited to, the visual manner-of-motion features of action verbs. Future research will undoubtedly shed more light on this complex issue.

Shifting now to the posterior ventral temporal cortex and underlying white matter, the first thing to note is that we did not initially predict this region to be significantly associated with impairment on any of the tasks. Nevertheless, it did turn out to be implicated, albeit with variable hemispheric asymmetries, in the four tasks that include pictures of actions as stimuli—Naming (mostly left hemisphere), Word-Picture Matching (mostly right hemisphere), Picture Attribute (mostly left hemisphere), and Picture Comparison (mostly right hemisphere). This finding may reflect the fact that successful performance on these tasks depends on the ability to extract the movement patterns implied by the statically portrayed action stimuli. In this context, it is worthwhile to consider a neurophysiologically plausible computational model of motion perception which posits two parallel, hierarchical, interactive processing streams, one called the “motion pathway” and the other called the “form pathway” (Giese & Poggio, 2003; for empirical support see Peuskens et al., 2005). Whereas the motion pathway includes the pMTG/pSTS, the form pathway includes the posterior ventral temporal cortex, and its function is to recognize, by means of “snapshot neurons,” learned sequences of human postures. This raises the possibility that many of the patients who performed poorly on the tasks with pictorial stimuli may have had deficits in retrieving stored visual knowledge about the sequences of body configurations that uniquely characterize various kinds of human movement patterns. Again, further research is needed to explore this issue in greater detail.

Finally, we would like to comment briefly on some theoretical implications of the fact that none of our tasks were significantly linked with the anterior temporal lobes (ATLs), even though we had effective coverage of those regions. A growing body of literature suggests that the ATLs may operate as domain-general semantic hubs that bind together and organize modality-specific fragments of conceptual information distributed throughout the brain (e.g., Patterson et al., 2007; Lambon Ralph & Patterson, 2008; Lambon Ralph et al., 2010; Binney et al., in press; Visser et al., in press). So far, despite the fact that this approach makes claims about domain generality, it has focused almost entirely on object concepts. For instance, very few studies have carefully investigated the status of action concepts in semantic dementia (SD), which affects predominantly, but by no means exclusively, the left ATL. Consistent with the theory, there is some evidence that SD patients have reduced lexical decision accuracies for action verbs (Pulvermüller et al., 2009a) as well as impaired production and comprehension of action verbs (Cotelli et al., 2006; Yi et al., 2007). However, there is also some evidence that SD patients have relatively well-preserved understanding of action verbs, with accuracies exceeding 90% (Robinson et al., 2009). Although the current study did not focus on SD, it did include a large number of patients with damage to the left ATL, usually due to surgical intervention to alleviate epileptic seizures. Contrary to the domain-general semantic hub theory, our results suggest that the left ATL does not play an essential role in the processing of action concepts, since the patients with left ATL resections or lesions were not reliably impaired on any of the tasks.

4.2.2.3. Parietal regions: Damage to the left anterior SMG was significantly associated with impairment on four tasks—Naming, Word Comparison, Picture Attribute, and Picture Comparison. This cortical area has rich connections with both the ventral premotor cortex and the pMTG (Ramayya et al., in press). It is traditionally thought to contribute to a wide range of cognitive capacities, but here we will focus on just a few functions that are related to the higher-order processing of actions. The left SMG has been strongly linked with the planning of complex visually guided actions, especially those that involve the skilled manipulation of tools to mechanically transform objects in specific ways (for reviews see Glover, 2004; Lewis, 2006; Culham & Valyear, 2007; Johnson-Frey, 2007). Although the precise functional contribution of the left SMG to tool knowledge and use is controversial, some studies of patients with apraxia due to lesions encompassing the left SMG suggest that this cortical area may play an important role in processing spatial interactions between parts of the agent's body, parts of the manipulated tool, and parts of the affected object (Goldenberg, 2009; Goldenberg & Spatt, 2009). This view is consistent with other evidence that the left SMG is essential for understanding categorical spatial relationships (Tranel & Kemmerer, 2004; Wu et al., 2007; Amorapanth et al., 2010). Interestingly, there is also growing evidence that the left SMG is engaged during the observation of other people's actions, regardless of whether those actions are object-directed (e.g., Bonda et al., 1996; Buccino et al., 2001), non-object-directed (e.g., Calvo-Merino et al., 2006; Cross et al., 2006; Lui et al., 2008), or statically portrayed as pictograms (Assmus et al., 2007). Turning to the linguistic representation of action, Tettamanti et al. (2005) showed that, relative to listening to transitive sentences describing abstract events (e.g., *I appreciate sincerity*), listening to transitive sentences describing concrete object-directed actions (e.g., *I grasp the knife*) engaged the left SMG. These results converge with the findings of several other fMRI studies (Noppeney et al., 2005; Saccuman et al., 2006; Liljeström et al., 2008; den Ouden et al., 2009). More generally, however, very little research has directly addressed the question of how the left SMG contributes to the production and comprehension of linguistically encoded actions. The current study helps to fill this gap, since it demonstrates that impaired lexical and conceptual knowledge of actions—including actions involving tool use, which were well-represented in our tasks—is often associated with damage to the left SMG.

4.3. Conclusion—In sum, this study sheds new light on the neural substrates of lexical and conceptual knowledge of actions by reporting extensive neuropsychological and neuroanatomical data for an unusually large group of brain-damaged patients with lesions distributed throughout the left and right cerebral hemispheres. 61 of the 226 patients who were studied failed at least one of the six tasks in the battery, and those 61 impaired patients exhibited a wide range of associations and dissociations across the various tasks, thereby demonstrating that the capacity to efficiently and flexibly process action words and concepts depends on a number of distinct neurocognitive operations. Furthermore, sophisticated analyses of the lesions of 147 of the 226 patients revealed that lexical and conceptual knowledge of actions is mediated by a network of left-lateralized brain regions that include the IFG, the ventral precentral and postcentral gyri, the SMG, the pMTG, and posterior ventral temporal areas. Taken together, these findings enrich our theoretical understanding of the complex neural underpinnings of action knowledge, and they expand our clinical understanding of the many ways in which that knowledge can be disrupted by brain injury.

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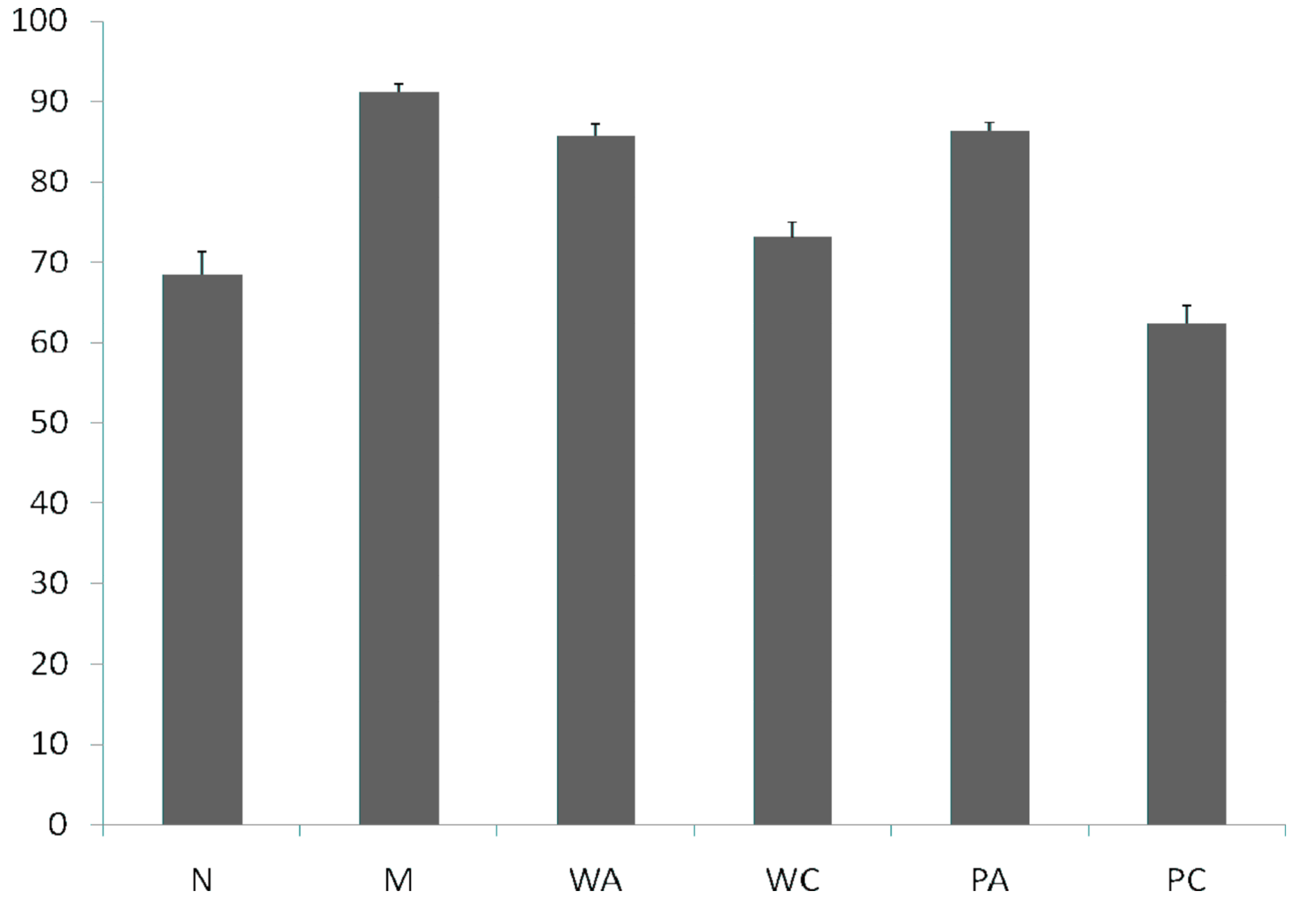

Figure 1.

Behavioral results across the six tasks, for the 61 patients who failed one or more of the tasks. Bars indicate mean percent correct and standard errors. N = Naming; M = Word-Picture Matching; WA = Word Attribute; WC = Word Comparison; PA = Picture Attribute; PC = Picture Comparison.

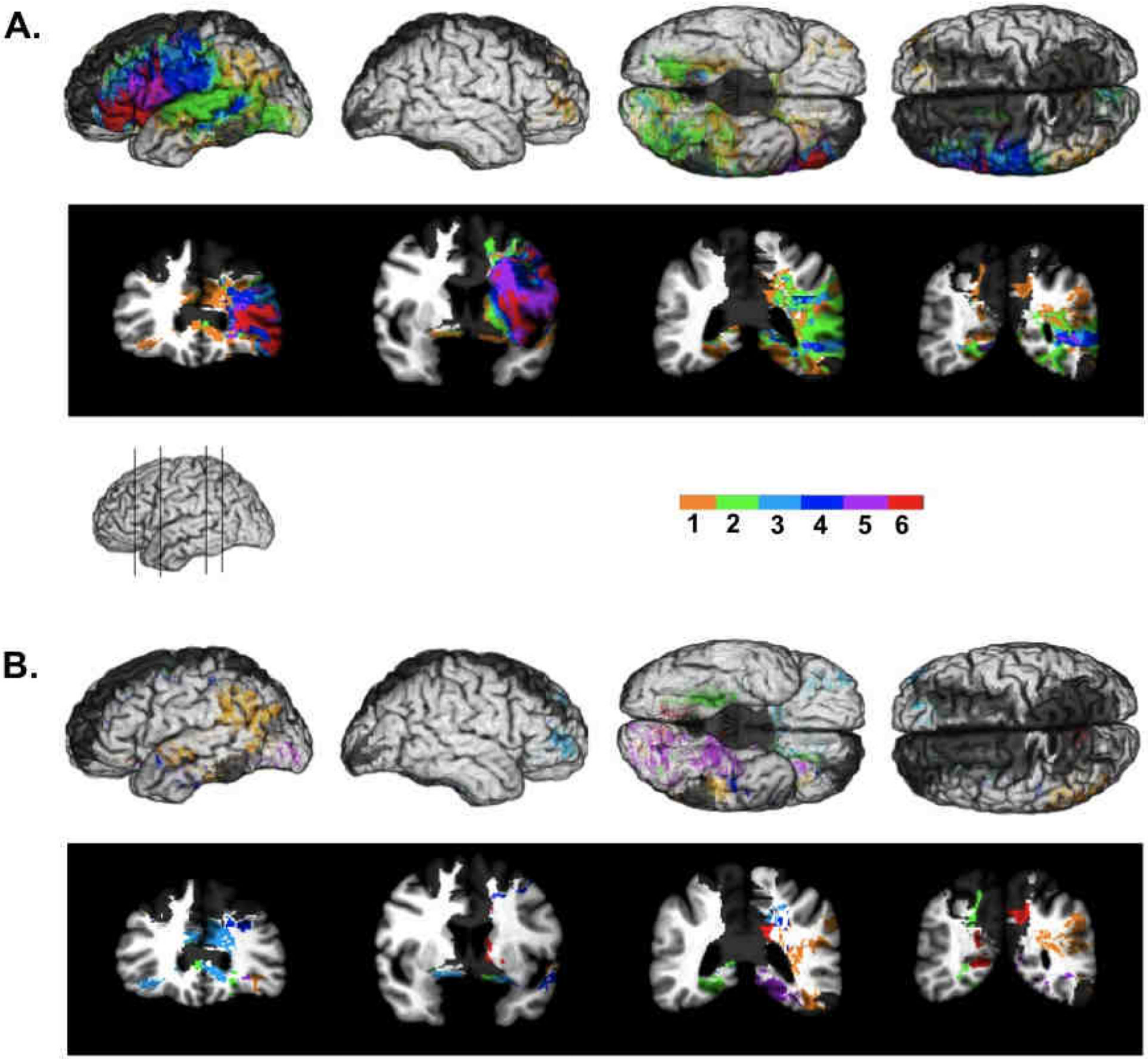

Figure 2.

Conjunction/disjunction analysis of significant effects across the six tasks. **A.** Number of tasks with significant effects in regions where effective coverage was observed for all six tasks. *Upper tier*: From left to right, left lateral, right lateral, ventral, and dorsal aspects of the cortex. *Lower tier*: Coronal slices (radiological convention). The location of the sections is indicated below, with vertical lines on the reference brain, displayed in the same order from left to right as the order of the coronal slices. Dark gray areas on brain images indicate regions where effective coverage was not observed for all six tasks. The color bar indicates the color code corresponding to the number of tasks associated with significant effects. **B.** Regions where significant effects were found for only one of the tasks in regions where effective coverage was observed for all six tasks. Same display principles as above. Color coding is as follows: orange = Naming; green = Word-Picture Matching; light blue = Word Attribute; dark blue = Word Comparison; purple = Picture Attribute; red = Picture Comparison. (See text.)

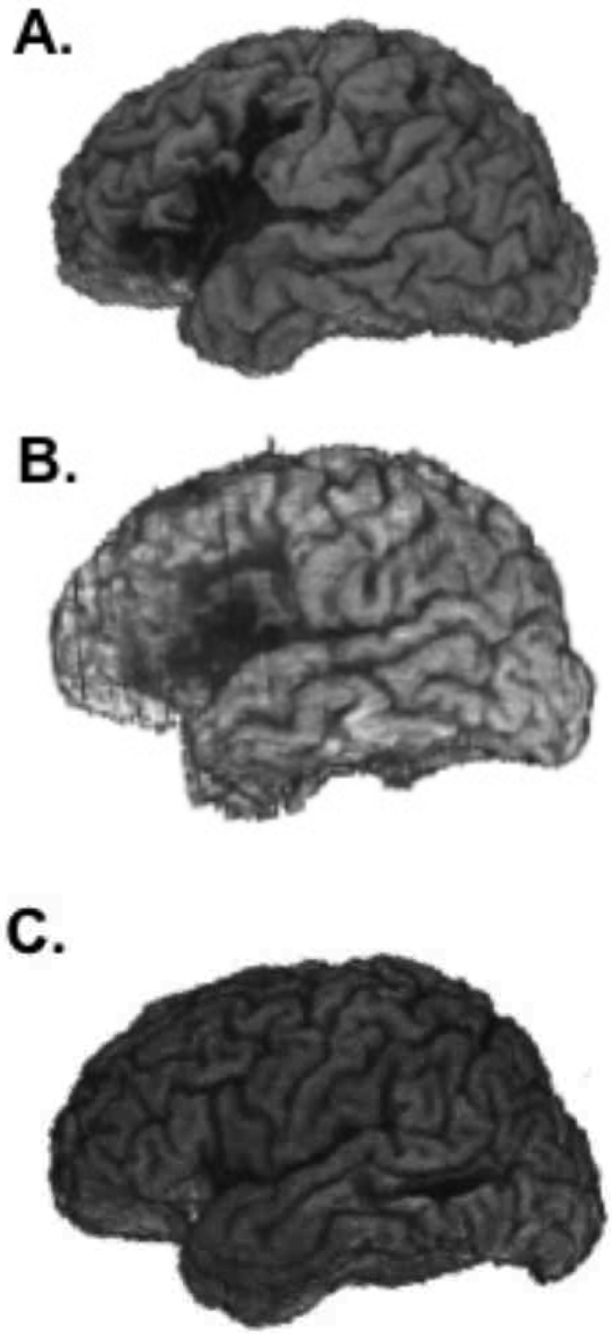

Figure 3.

Location of damage of participants with impairments on all six tasks. **A.** Case 1172, lateral left hemisphere aspect. **B.** Case 1709, lateral left hemisphere aspect. **C.** Case 1808, lateral left hemisphere aspect (*left*), and ventral aspect (*right*).

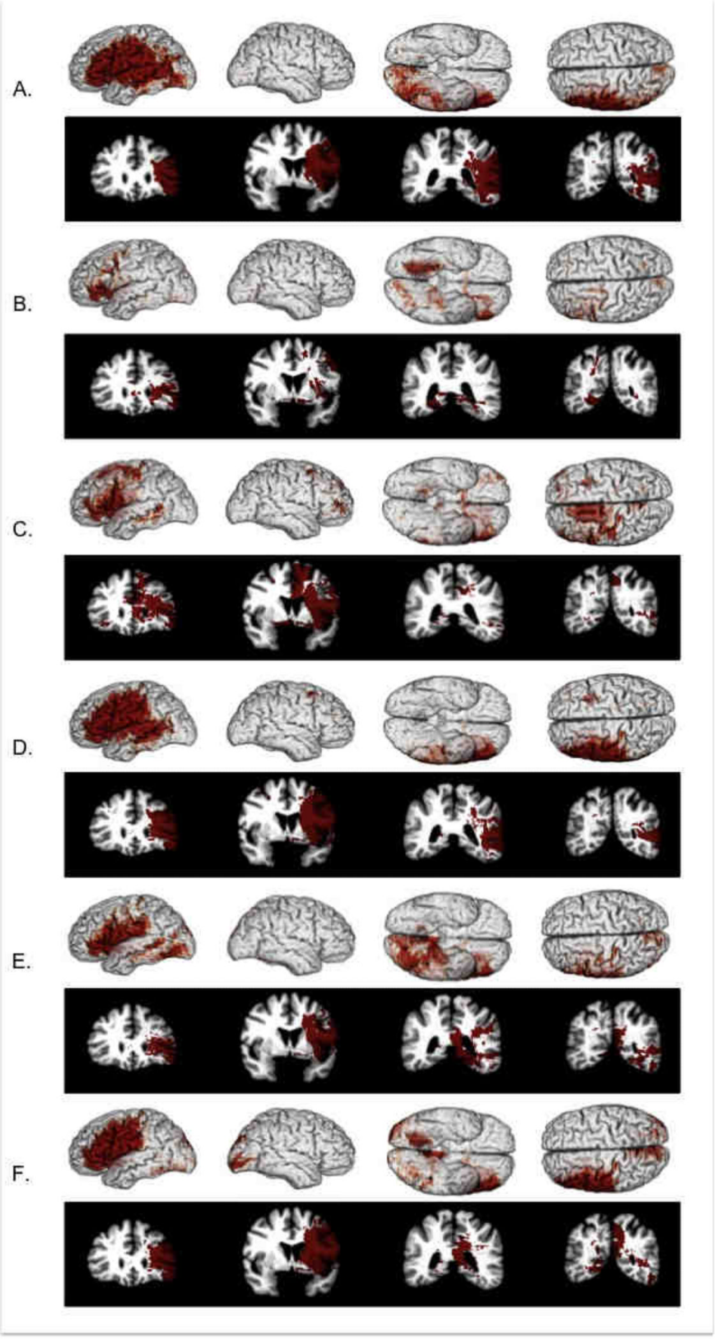

Figure 4.

Regions with significant effects for each individual task. For each task, the *upper tier* shows, from left to right, the left lateral, right lateral, ventral and dorsal aspects of the cortex, and the *lower tier* shows coronal slices (radiological convention). The location and order of the sections for the slices is the same as in Figure 2A. **A**: Naming; **B**: Word-Picture Matching; **C**: Word Attribute; **D**: Word Comparison; **E**: Picture Attribute; **F**: Picture Comparison. Significant effects are in red. See text for details.

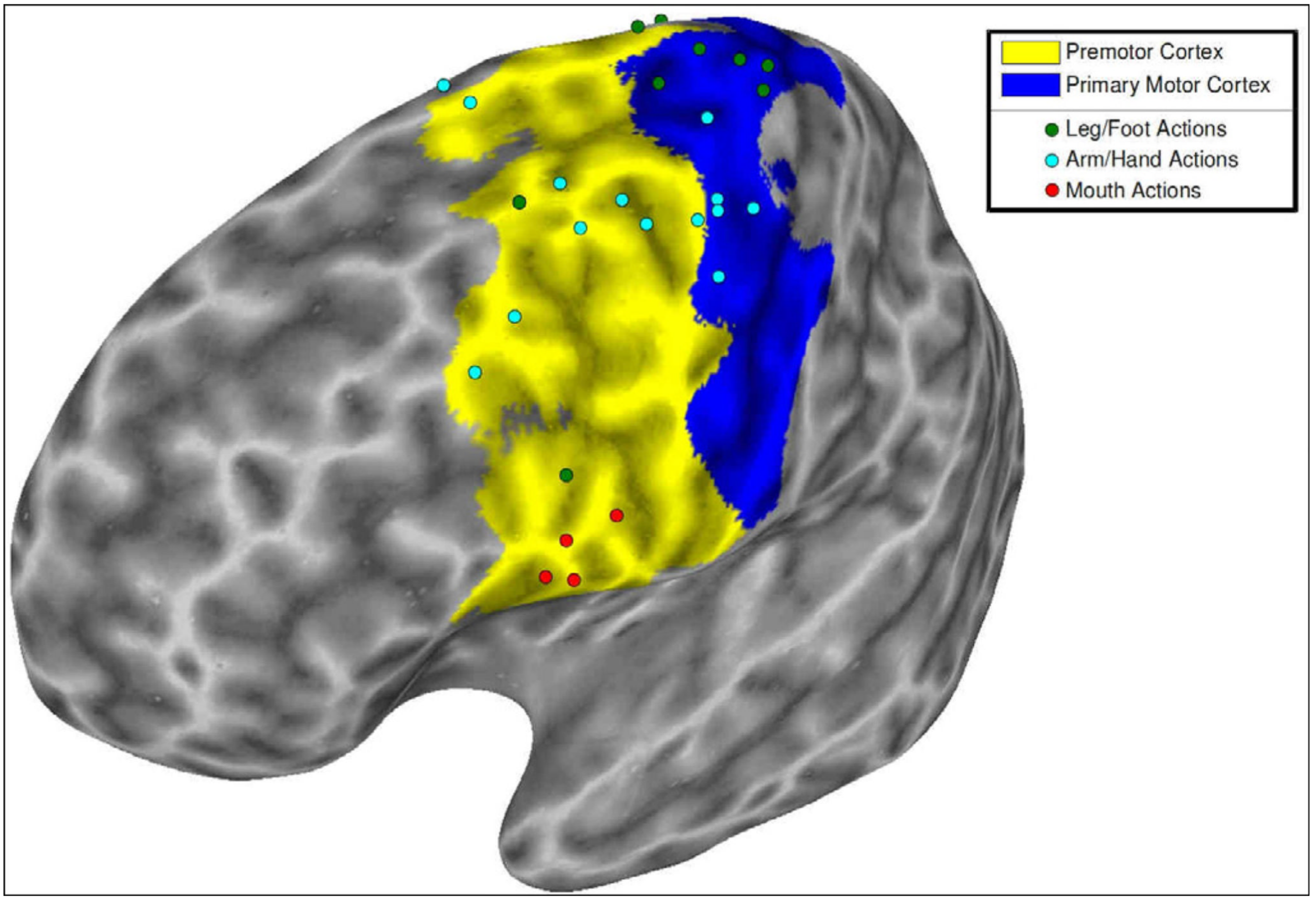

Figure 5.

Activation peaks in left primary motor and premotor cortices reported by some of the fMRI studies that have probed the neural substrates of the motor features of verbs and sentences encoding leg/foot actions, arm/hand actions, and mouth actions. Activations are plotted on a color-coded inflated 3D brain with definitions for the primary motor cortex (dark blue) and premotor cortex (yellow) from Mayka et al.'s (2006) Human Motor Area Template (HMAT). Specifically, the primary motor cortex shown here corresponds to M1 in the HMAT, and the premotor cortex corresponds to the combination of ventral (PMv) and dorsal (PMd) premotor areas in the HMAT. The activation peaks are drawn from the following sources: Hauk et al. (2004), with corrections reported by Kemmerer & Gonzalez Castillo (2010); Tettamanti et al. (2005); Aziz-Zadeh et al. (2006); Rüschemeyer et al. (2007); Kemmerer et al. (2008); Beilock et al. (2008); Boulenger et al. (2009); Pulvermüller et al. (2009b); Raposo et al. (2009); Willems et al. (2010); and Desai et al. (2010). The precise coordinates of all the activation peaks depicted in the figure are available from the first author upon request. The figure was created and kindly provided by Javier Gonzalez Castillo.

Table 1

Percent correct and *z*−scores for all patients impaired on one or more of the six tasks (*N* = 61). Scores classified as significantly below normal are highlighted in both bold and italic font (n.a. = data not available). Patients whose data were originally reported by Kemmerer et al. (2001a) have asterisks after their case numbers. Patients whose lesion data are included in Study 2 are marked by grey shading. Patients impaired on all six tasks are presented in the first block of rows (with the end of a block defined by a solid horizontal line); patients impaired on five tasks are presented in the second block; patients impaired on four tasks are presented in the third block; and so on.

Case	Naming		W−P Matching		W−Attribute		W−Comparison		P−Attribute		P−Comparison	
	%	*z*	%	*z*	%	*z*	%	*z*	%	*z*	%	*z*
1172*	***33***	***−10.4***	***72***	***−4.4***	***79***	***−4.4***	***59***	***−3.7***	***82***	***−2.0***	***25***	***−7.1***
1709*	***9***	***−15.2***	***65***	***−5.9***	***58***	***−10.2***	***39***	***−6.1***	***67***	***−5.1***	***46***	***−4.5***
1808*	***57***	***−5.6***	***78***	***−3.1***	***77***	***−4.9***	***64***	***−3.0***	***78***	***−2.9***	***21***	***−7.5***
1699*	***64***	***−4.2***	***68***	***−5.2***	***74***	***−5.8***	***52***	***−4.5***	***71***	***−4.3***	***33***	***−6.1***
129	n.a.	n.a.	***67***	***−5.5***	***74***	***−5.8***	***39***	***−6.1***	***65***	***−5.6***	***46***	***−4.5***
868*	***40***	***−9***	90	−0.5	***76***	***−5.2***	***57***	***−3.9***	***75***	***−3.5***	***58***	***−3.1***
1232*	***56***	***−5.8***	***81***	***−2.4***	***85***	***−2.7***	***70***	***−2.3***	***69***	***−4.7***	75	−1.0
3297	***69***	***−3.2***	88	−0.9	***82***	***−3.6***	***36***	***−6.5***	***81***	***−2.2***	***29***	***−6.6***
615*	***66***	***−3.8***	88	−0.9	***87***	***−2.2***	***61***	***−3.4***	***82***	***−2.0***	75	−1.0
1076*	***31***	***−10.8***	***83***	***−2.0***	***66***	***−8.0***	***66***	***−2.8***	83	−1.8	88	0.5
1362*	87	0.4	***80***	***−2.6***	***47***	***−13.3***	***39***	***−6.1***	88	−0.8	***42***	***−5.0***
1575*	***59***	***−5.2***	***81***	***−2.4***	***85***	***−2.7***	80	−1.1	83	−1.8	***33***	***−6.1***
1726*	***62***	***−4.6***	97	1.1	***87***	***−2.2***	***70***	***−2.3***	88	−0.8	***46***	***−4.5***
1976	***64***	***−4.2***	***77***	***−3.3***	***74***	***−5.8***	n.a.	n.a.	88	−0.8	***47***	***−4.4***
1978	***62***	***−4.6***	84	−1.8	***85***	***−2.7***	***70***	***−2.3***	83	−1.8	***40***	***−5.3***
2061	***75***	***−2***	100	1.7	***85***	***−2.7***	***66***	***−2.8***	92	0.1	***62.5***	***−2.5***
2127	82	−0.6	97	1.1	***81***	***−3.8***	***59***	***−3.7***	***82***	***−2.0***	***67***	***−2.0***
2607	***75***	***−2***	96	0.8	89	−1.6	***70***	***−2.3***	***82***	***−2.0***	***62.5***	***−2.5***
3135	***26***	***−11.8***	87	−1.1	***56***	***−10.8***	***57***	***−3.9***	***68***	***−4.9***	79	−0.6
983*	***56***	***−5.8***	86	−1.3	89	−1.6	73	−1.9	***81***	***−2.2***	***58***	***−3.1***
1033*	***59***	***−5.2***	87	−1.1	***84***	***−3.0***	***66***	***−2.8***	89	−0.6	92	1.0
1247*	***53***	***−6.4***	***81***	***−2.4***	92	−0.8	82	−0.8	***75***	***−3.5***	75	−1.0

Case	Naming		W−P Matching		W−Attribute		W−Comparison		P−Attribute		P−Comparison	
	%	z	%	z	%	z	%	z	%	z	%	z
1359*	***14***	***−14.2***	91	−0.2	89	−1.6	75	−1.7	***74***	***−3.7***	***63***	***−2.5***
1599*	***75***	***−2***	96	0.8	***84***	***−3.0***	75	−1.7	92	0.1	***50***	***−4.0***
1852*	***43***	***−8.4***	99	1.5	94	−0.2	***66***	***−2.8***	93	0.3	***50***	***−4.0***
1962*	***22***	***−12.6***	99	1.5	94	−0.2	***64***	***−3.0***	89	−0.6	***58***	***−3.1***
2722	***72***	***−2.6***	97	1.1	***85***	***−2.7***	***71***	***−2.2***	88	−0.8	87	0.4
2980	***56***	***−5.8***	93	0.2	***87***	***−2.2***	80	−1.1	90	−0.4	***43***	***−4.9***
3050	89	0.8	97	1.1	***85***	***−2.7***	***66***	***−2.8***	90	−0.4	***50***	***−4.0***
468*	80	−1	93	0.2	89	−1.6	***55***	***−4.2***	88	−0.8	***54***	***−3.6***
513*	***48***	***−7.4***	87	−1.1	92	−0.8	***66***	***−2.8***	86	−1.2	75	−1.0
1103*	***73***	***−2.4***	91	−0.2	90	−1.3	91	0.3	85	−1.4	***67***	***−2.0***
1130	88	0.6	94	0.4	***85***	***−2.7***	77	−1.4	87.5	−0.9	***62.5***	***−2.5***
1312*	***73***	***−2.4***	96	0.8	95	0.1	89	0.0	***81***	***−2.2***	83	−0.1
1504*	96	2.2	84	−1.8	***87***	***−2.2***	77	−1.4	94	0.5	***63***	***−2.5***
1951*	87	0.4	97	1.1	***87***	***−2.2***	80	−1.1	92	0.1	***67***	***−2.0***
2194	82	−0.6	93	0.2	***87***	***−2.2***	77	−1.4	89	−0.6	***62.5***	***−2.5***
2589	93	1.6	100	1.7	***62***	***−9.1***	98	1.1	92	0.1	***50***	***−4.0***
2762	***2***	***−16.6***	96	0.8	100	1.4	***70***	***−2.3***	92	0.1	87.5	0.5
3025	***57***	***−5.6***	94	0.4	97	0.6	89	0.0	***82***	***−2.0***	87.5	0.5
3351	90	1	96	0.8	***77***	***−4.9***	***68***	***−2.6***	83	−1.8	83	−0.1
414*	81	−0.8	94	0.4	***85***	***−2.7***	77	−1.4	83	−1.8	71	−1.5
1251	83	−0.4	99	1.5	95	0.1	89	0.0	96	0.9	***58***	***−3.1***
1379*	***72***	***−2.6***	99	1.5	95	0.1	95	0.8	96	0.9	96	1.5
1470*	***70***	***−3***	99	1.5	92	−0.8	89	0.0	92	0.1	96	1.5
1566	***70***	***−3***	96	0.8	94	−0.2	77	−1.4	97	1.1	71	−1.5
1584*	85	0	100	1.7	95	0.1	82	−0.8	97	1.1	***67***	***−2.0***
1733*	77	−1.6	99	1.5	95	0.1	77	−1.4	96	0.9	***58***	***−3.1***
1739	92	1.4	92	0.0	***87***	***−2.2***	75	−1.7	95	0.7	87	0.4
1772	87	0.4	96	0.8	92	−0.8	77	−1.4	85	−1.4	***53***	***−3.7***
1879*	***59***	***−5.2***	93	0.2	90	−1.3	80	−1.1	90	−0.4	83	−0.1

Case	**Naming**		**W−P Matching**		**W−Attribute**		**W−Comparison**		**P−Attribute**		**P−Comparison**	
	%	***z***	**%**	***z***	**%**	***z***	**%**	***z***	**%**	***z***	**%**	***z***
2308	84	−0.2	94	0.4	95	0.1	82	−0.8	85	−1.4	***58***	***−3.1***
2603	84	−0.2	96	0.8	94	−0.2	***64***	***−3.0***	94	0.5	83	−0.1
2710	96	2.2	99	1.5	95	0.1	100	1.4	99	1.5	***67***	***−2.0***
2771	94	1.8	93	0.2	97	0.6	91	0.3	87.5	−0.9	***67***	***−2.0***
2824	92	1.4	96	0.8	92	−0.8	93	0.5	89	−0.6	***62.5***	***−2.5***
2856	93	1.6	99	1.5	89	−1.6	87.5	−0.1	95	0.7	***57***	***−3.2***
3138	81	−0.8	94	0.4	97	0.6	82	−0.8	97	1.1	***50***	***−4.0***
3177	96	2.2	100	1.7	95	0.1	95	0.8	92	0.1	***58***	***−3.1***
3227	90	1	94	0.4	89	−1.6	77	−1.4	89	−0.6	***58***	***−3.1***
3341	93	1.6	99	1.5	92	−0.8	91	0.3	94	0.5	***58***	***−3.1***
Mean	68.5	−3.3	91.1	−0.2	85.8	−2.5	73.1	−1.9	86.4	−1.1	62.3	−2.6
S.D.	22.8	4.6	8.7	1.9	10.6	3.0	14.8	1.8	8.1	1.7	17.6	2.1
	34/60 impaired		11/61 impaired		31/61 impaired		27/60 impaired		17/61 impaired		42/61 impaired	

Table 2

Number of patients manifesting each of the 30 possible one-way dissociations between the six tasks. Each cell indicates how many patients obtained a normal *z*-score on the task indicated along the horizontal axis and an impaired *z*-score on the task indicated along the vertical axis, with at least a 2.0-point difference between the two scores.

	Normal Score					
	Naming	**W-P Matching**	**W-Attribute**	**W-Comparison**	**P-Attribute**	**P-Comparison**
Impaired Score						
Naming	−	24	14	11	16	13
W-P Matching	1	−	0	0	1	1
W-Attribute	11	18	−	1	12	5
W-Comparison	7	15	6	−	8	8
P-Attribute	0	7	4	4	−	5
P-Comparison	20	31	13	15	25	−

Table 3

Percent correct and *z*−scores for naming actions as well as three categories of objects (animals, fruits/vegetables, and tools), among all of the patients with action naming deficits (N = 34). Scores classified as significantly below normal are highlighted in both bold and italic font (n.a. = data not available). Patients whose lesion data are included in Study 2 are marked by grey shading. Patients impaired on all three object naming tasks are presented in the first block of rows (with the end of a block defined by a solid horizontal line); patients impaired on two object naming tasks are presented in the second block; and so on.

Case	**Actions**		**Animals**		**Fruits/Vegetables**		**Tools**	
	%	***z***	**%**	***z***	**%**	***z***	**%**	***z***
1172	***33***	***−10.4***	***50***	***−14.7***	***31***	***−17.1***	***61***	***−9.3***
868	***40***	***−9***	***68***	***−8.9***	***72***	***−6.0***	***79***	***−4.7***
3297	***69***	***−3.2***	***87.5***	***−2.6***	***75***	***−5.2***	***88***	***−2.4***
1076	***31***	***−10.8***	***22***	***−23.8***	***11***	***−22.5***	***10***	***−22.4***
1976	***64***	***−4.2***	***70***	***−8.3***	***59***	***−9.5***	***86***	***−2.9***
1978	***62***	***−4.6***	***57***	***−12.5***	***58***	***−9.8***	***52***	***−11.6***
2061	***75***	***−2***	***71***	***−8.0***	***83***	***−3.1***	***88***	***−2.4***
1033	***59***	***−5.2***	***51***	***−14.4***	***56***	***−10.4***	***70***	***−7.0***
1359	***14***	***−14.2***	***62***	***−10.9***	***52***	***−11.4***	***86***	***−2.9***
1852	***43***	***−8.4***	***55***	***−13.1***	***48***	***−12.5***	***49***	***−12.4***
2980	***56***	***−5.8***	***32***	***−20.5***	***24***	***−19.0***	***39***	***−14.9***
513	***48***	***−7.4***	***82***	***−4.4***	***84***	***−2.8***	***71***	***−6.7***
2762	***2***	***−16.6***	***0***	***−30.9***	***8***	***−23.3***	***3***	***−24.2***
3025	***57***	***−5.6***	***77***	***−6.0***	***80***	***−3.9***	***82***	***−3.9***
1470	***70***	***−3***	***74***	***−7.0***	***74***	***−5.5***	***85***	***−3.1***
1726	***62***	***−4.6***	90	−1.8	***80***	***−3.9***	***78***	***−4.9***
1962	***22***	***−12.6***	91	−1.5	***65***	***−7.9***	***77***	***−5.2***
1566	***70***	***−3***	***82***	***−4.4***	97	0.7	***89***	***−2.1***
1709	***9***	***−15.2***	***22***	***−23.8***	n.a.	n.a.	***24***	***−18.8***
1699	***64***	***−4.2***	***86***	***−3.1***	93	−0.4	99	0.5
983	***56***	***−5.8***	***75***	***−6.7***	88	−1.7	96	−0.3
1808	***57***	***−5.6***	92	−1.2	90	−1.2	***67***	***−7.7***
2127	***82***	***−2***	96	0.1	96	0.5	***84***	***−3.4***
2722	***72***	***−2.6***	97	0.4	96	0.5	***87***	***−2.6***
1232	***56***	***−5.8***	100	1.4	92	−0.6	96	−0.3
615	***66***	***−3.8***	98	0.7	97	0.7	98	0.2
1247	***53***	***−6.4***	98	0.7	95	0.2	99	0.5
1103	***73***	***−2.4***	98	0.7	96	0.5	92	−1.3
1599	***75***	***−2***	92	−1.2	n.a.	n.a.	94	−0.8
1312	***73***	***−2.4***	92	−1.2	n.a.	n.a.	92	−1.3
1575	***59***	***−5.2***	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
3135	***26***	***−11.8***	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

Case	Actions		Animals		Fruits/Vegetables		Tools	
	%	***z***	**%**	***z***	**%**	***z***	**%**	***z***
1379	***72***	***−2.6***	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
1879	***59***	***−5.2***	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Mean	54.2	−6.2	75.6	−6.5	71.4	−6.2	74.3	−5.9
SD	20.3	4.0	22.8	7.4	26.9	7.3	25.5	6.6
	34/34 impaired		19/30 impaired		17/27 impaired		22/30 impaired	