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Searching for the Elusive Neural Substrates of Body Part Terms: A Neuropsychological Study

David Kemmerer^{1,2} and Daniel Tranel²

¹Department of Speech, Language, and Hearing Sciences and Department of Psychological Sciences, Purdue University

²Department of Neurology, Division of Cognitive Neuroscience, University of Iowa College of Medicine

Abstract

Previous neuropsychological studies suggest that, compared to other categories of concrete entities, lexical and conceptual aspects of body part knowledge are frequently spared in brain-damaged patients. To further investigate this issue, we administered a battery of 12 tests assessing lexical and conceptual aspects of body part knowledge to 104 brain-damaged patients with lesions distributed throughout the telencephalon. There were two main outcomes. First, impaired oral naming of body parts, attributable to a disturbance of the mapping between lexical-semantic and lexical-phonological structures, was most reliably and specifically associated with lesions in the left frontal opercular and anterior/inferior parietal opercular cortices, and in the white matter underlying these regions (8 patients). Also, one patient with body part anomia had a left occipital lesion that included the “extrastriate body area” (EBA). Second, knowledge of the meanings of body part terms was remarkably resistant to impairment, regardless of lesion site; in fact, we did not uncover a single patient who exhibited significantly impaired understanding of the meanings of these terms. In the 9 patients with body part anomia, oral naming of concrete entities was evaluated, and this revealed that 4 patients had disproportionately worse naming of body parts relative to other types of concrete entities. Taken together, these findings extend previous neuropsychological and functional neuroimaging studies of body part knowledge, and add to our growing understanding of the nuances of how different linguistic and conceptual categories are operated by left frontal and parietal structures.

1. Introduction

Compared to all other kinds of objects, human bodies are special (Knoblich et al., 2006). We experience our own bodies not only through exteroceptive sensory channels (e.g., vision) but also, and more importantly, through interoceptive sensory channels (e.g., nociception). This continuous flow of multisensory input gives rise to what William James (1890, p. 242) called “the feeling of the same old body always there.” One of the most significant sources of this “feeling” is the *body schema*, which consists of a dynamic, on-line representation of the relative locations of one's body parts in space (Haggard & Wolpert, 2005). The body schema derives from the integration of many different types of signals (proprioceptive, vestibular, tactile, visual) and is a fundamental component of corporeal awareness and the self (Damasio, 1999; Goldenberg, 2005). Damage to this complex system can engender a wide range of bizarre disorders, including out-of-body experiences (Blanke & Arzy, 2005), supernumerary phantom

limbs (McGonigle et al., 2002), and somatoparaphrenia, i.e., disownership of body parts (Halligan et al., 1995).

We can only apprehend other people's bodies by means of exteroceptive sensory mechanisms, but this category of objects nevertheless has a privileged perceptual status. Much like images of human faces, images of human bodies rapidly capture the focus of attention when nothing is expected (Downing et al., 2004; Ro et al., 2007) and are recognized holistically via the configuration of their parts (Glia & Dehaene-Lambertz, 2005; Reed et al., 2003; Slaughter et al., 2004; Stekelenburg et al., 2004; Urgesi et al., 2007a). These perceptual processes may be mediated in part by the “extrastriate body area” (EBA), which is located in the inferior lateral portion of Brodmann area (BA) 19 (for a review see Peelen & Downing, 2007). The EBA responds preferentially to the sight of human bodies and non-facial body parts, regardless of whether they are stationary (Downing et al., 2001, 2006a, 2007; Morris et al., 2006; Peelen & Downing, 2005b; Peelen et al., 2006; Spiridon et al., 2006) or moving (Bartels & Zeki, 2004; Downing et al., 2006b; Kable & Chatterjee, 2006).¹ This area is also engaged during the planning, execution, and imagination of goal-directed movements, even in the absence of visual feedback, which suggests that it is involved not only in the visual perception of body parts, but also in the production of actions with different limbs (Astafiev et al., 2004; Jackson et al., 2006; see also Arzy et al., 2006, for data relating the EBA to the spatial localization of the self within the body). Perhaps relatedly, the left EBA does not discriminate between allocentric (other) and egocentric (self) views of body parts, but the right EBA responds more strongly to allocentric views (Chan et al., 2004; Saxe et al., 2006). In addition, the visual perception of human bodies and non-facial body parts elicits a distinctive electrophysiological component—the N190—that has been linked with the EBA using both source localization techniques (Thierry et al., 2006) and direct intracranial recordings (Pourtois et al., 2007). Furthermore, repetitive transcranial magnetic stimulation (rTMS) over the EBA interferes with the discrimination of bodily forms (Urgesi et al., 2004, 2007a, 2007b). As yet, however, the question of how body part knowledge is mapped in the EBA has not been carefully addressed using the lesion method.

Human bodies may also be special with regard to lexical and conceptual representation. In their extensive review of literature on category-specific deficits, Capitani et al. (2003; see especially Appendix D) observe that in comparison with other categories of concrete entities, body part knowledge tends to be spared in brain-damaged patients (see also Gainotti, 2004, for similar conclusions). Although previous studies suggest that this type of knowledge can be selectively impaired (e.g., Suzuki et al., 1997; Laiacina et al., 2006), the general trend is for it to be preserved. In fact, it is not uncommon for patients to exhibit normal, or only mildly defective, knowledge of body parts despite impaired knowledge of a wide range of other object categories (Coslett et al., 2002; Ferro & Santos, 1984; Forde et al., 1997; Riddoch & Humphreys, 1987; Zingeser & Berndt, 1988; see also Gainotti, 2004). This pattern has even been found when the stimulus items are matched across categories for nuisance variables like familiarity, frequency, and visual complexity (Shelton et al., 1998).

To gain deeper insight into these issues, we administered a battery of twelve tests that assess lexical and conceptual knowledge of body parts to 104 brain-damaged patients with lesions distributed throughout the telencephalon. In addition, for a subgroup of these patients who exhibited impaired naming of body parts ($N = 9$), we explored the selectivity of their deficits by evaluating their ability to name four other categories of objects (animals, fruits/vegetables,

¹Another region with body-specific response properties was recently found in the posterior fusiform gyrus, partially overlapping the “fusiform face area” (Peelen & Downing, 2005a; Peelen et al., 2006; Schwartzlose et al., 2005). This region, called the “fusiform body area” (FBA), is biased toward the perception of complete body images, whereas the EBA is biased toward the perception of body parts (Taylor et al., in press).

tools/utensils, and vehicles). Before describing these experiments, we discuss the semantic components of body part terms, review previous neuropsychological and functional neuroimaging studies that have begun to shed light on the neural bases of these terms, and present the specific hypotheses that motivated our own investigation.

1.1. Semantic Components of Body Part Terms

The neuropsychological literature contains many different treatments of body representations, with one of the most prominent contemporary approaches being Schwoebel and Coslett's (2005; see also Coslett et al., 2002; Schwoebel et al., 2001) distinction between the following three types of representations: (1) the *body schema*, which, as already noted, is “a dynamic representation of the relative positions of body parts ... that interacts with motor systems in the genesis of actions” (p. 543); (2) the *body structural description*, which is “a topological map of locations derived primarily from visual input that defines body part boundaries and proximity relationships” (p. 543); and (3) the *body image* or *body semantics*, which is “a lexical-semantic representation of the body including body part names, functions, and relations with artifacts” (p. 543). This taxonomy has received support from several converging lines of evidence. There are limitations, however, especially in regard to the third system. For example, because this system is referred to as *body semantics*, one might expect it to contain just the meanings of body part terms such as *arm*, *hand*, *nose*, and *ear*, but it apparently also contains the lexical-phonological forms of these terms. We feel that, in general, it is important to distinguish more clearly between these two aspects of words (for a review of pertinent neuropsychological research, see Hillis, 2001). In addition, Schwoebel and Coslett do not present a detailed decomposition of the meanings of body part terms. However, such a decomposition may help to advance our understanding of the neural substrates of this conceptual domain. It might also reveal that certain semantic features of body part terms—specifically, information about what a given part looks like, and information about where a given part is located—are closely related to the second system in Schwoebel and Coslett's framework, namely the *body structural description*.

Here we propose that body part terms encode complex semantic structures that have four main components: (1) information about the typical shape of the designated part; (2) information about the location of the designated part within the hierarchical spatial organization of the human body; (3) information about the characteristic function(s) of the designated part; and (4) information about the cultural associations of the designated part.² We briefly elaborate each of these semantic components below, noting in passing how they may map onto the types of representations postulated by Schwoebel and Coslett (2005).

The first semantic component of body part terms is shape, by which we mean geometric information about the canonical contours and boundaries of body parts. Given that the human body is a single object with a continuous surface, the purpose of a mereological (i.e., part-based) nomenclature is to allow speakers to refer to spatially restricted body segments. Current evidence suggests that, cross-linguistically, the most common principle of body segmentation is visual discontinuity (Majid et al., 2006). For instance, most languages rely on the visual discontinuities of joints to distinguish between different parts of the limbs (e.g., finger, hand, forearm, upper arm). The presence of a salient discontinuity, however, does not ensure that a language will use it as the basis for separate terms, and in fact a considerable amount of cross-linguistic variation has been documented in lexically based body segmentation systems (Brown, 2005a,b; Majid et al., 2006). This implies that the shape features of English body part terms constitute, at least to some extent, language-specific semantic knowledge. (The shape

²The meanings of body part terms may also include various kinds of “encyclopedic” information, but we do not address such knowledge in this study.

component of body part terms may correspond to the information about visual form that is assumed to be captured by the *body structural description* in Schwoebel and Coslett's (2005) model. However, in light of the cross-linguistic diversity just mentioned, it is likely that partially distinct sets of shape representations exist for linguistic and non-linguistic shape information.)

The second semantic component is spatial location within the structural framework of the human body at an appropriate level of scale (Brown, 1976; Anderson, 1978; Cruse, 1986, Chapter 7). It has been argued that the canonical spatial relations between body parts are stored in long-term memory according to categorical notions such as “on-top-of,” “left-side-connected,” and “in-center-of,” because this representational strategy can facilitate the visual perception of contorted bodies (e.g., a twisted athlete or dancer) by enabling knowledge of the relative locations of parts to guide the control of eye movements during object scanning (Kosslyn, 1987, 2006; Laeng et al., 2003; see also Jellema & Perrett, 2006).³ The overall configuration of the human body furnishes the spatial context for defining terms like *head*, *arm*, *leg*, and *torso*. At a smaller scale, the concept of an arm serves as the immediate spatial context for defining terms like *hand*, *forearm*, and *elbow*; and at an even smaller scale, the concept of a hand provides the essential context for defining terms like *palm*, *finger*, and *thumb*. Linguistic evidence for this type of hierarchical partonymic knowledge comes from the relative felicity of sentences with *have*. For instance, the sentences in (1) sound quite natural, whereas those in (2) sound increasingly odd (Cruse, 1979; Langacker, 1997, p. 119):

1. a. A body has two arms.
 b. An arm has an elbow and a hand.
 c. A hand has five fingers.
 d. A finger has three knuckles and a fingernail.
2. a. ? A body has two elbows.
 b. ?? An arm has five fingers.
 c. ??? An arm has five fingernails and fourteen knuckles.
 d. ??? A body has twenty-eight knuckles.

(The location component may correspond to the information about proximity relations that is represented by the *body structural description* in Schwoebel and Coslett's (2005) model. We would like to point out, however, that even though the shape and location components that we posit may both map onto the same system in Schwoebel and Coslett's (2005) framework, the distinction between them is quite important; in fact, as indicated below (see section 1.3), we hypothesize that these two semantic components have different neural substrates.)

The third semantic component is function (Tversky et al., 2002). Legs are not only long, vertically oriented limbs connected to the base of the trunk, but are also used for support and for various kinds of locomotion such as walking and running. Other body parts are also associated with particular functions—e.g., the eyes are for seeing, the ears are for hearing, the hands are for grasping (and for a variety of much more specific types of object manipulation), and so on. In some languages, many body part terms actually derive from expressions for

³Kosslyn (2006, p. 1521) expresses this point as follows, alluding to neuroanatomical hypotheses that we delineate more fully in section 1.3: “Consider the spatial relation between the forearm and upper arm when a person assumes different postures. If that relation is described as ‘connected by a hinge,’ the same spatial relation applies when the arm is bent a little bit, straight, or bent more than 90°—or when it is at any other angle. Thus, if the forearm and upper arm are described as ‘connected by a hinge’ (with the parts being recognized in the ventral system and the spatial relation produced in the dorsal system), outputs from the ventral and dorsal systems can produce the same descriptions for different contortions of the form....”

customary actions performed with the given parts—e.g., the Lao compound term *khaa3 phap1*⁴ refers to the back of the knee but literally means “fold leg” (Enfield, 2006). (The function component in our framework matches the information about function in Schwoebel and Coslett's (2005) *body image* or *body semantics*.)

The fourth and final semantic component involves what we call cultural associations. These include objects that are conventionally related to body parts in certain ways, such as articles of clothing, pieces of jewelry, and hygienic devices. In addition, we take this component to include the wide range of connotations—some positive, some negative—that are encoded by alternative terms for the same body parts, especially the genitals (see Pinker, 2007, chapter 7). (This component subsumes the information about links between body parts and artifacts that is represented by Schwoebel and Coslett's (2005) *body image* or *body semantics*.)

1.2. Previous Studies

The neural substrates of lexical and conceptual knowledge of body parts have proven to be elusive, not only because this particular linguistic domain appears to be relatively resistant to impairment by lesions, but also because it has not yet been carefully investigated with functional neuroimaging techniques. Moreover, of the neuropsychological and functional neuroimaging studies that have been conducted so far, many do not take into account the distinct semantic components outlined above, and some do not even distinguish clearly between accessing word meanings and accessing word forms. Capitani et al. (2003) and Gainotti (2004) provide useful reviews of the neuropsychological literature on body part terms, and Poeck and Orgass (1971), Denes (1999), Semenza (2001), Denburg and Tranel (2003), Goldenberg (2005) and Haggard and Wolpert (2005) provide broader surveys of various disorders of body representation. In what follows, we briefly summarize a number of neuropsychological case studies and group studies, as well as several functional neuroimaging studies, in order to lay the groundwork for the specific hypotheses that we elaborate in section 1.2. Whenever possible, we attempt to relate the findings of particular studies to the four semantic components described above.

We begin by noting that in the older literature there are a number of reports of patients with left temporoparietal lesions who exhibited impaired auditory comprehension of body part terms, often together with impaired auditory comprehension of words for certain categories of nonliving things. But some of these patients had preserved oral naming of body parts (Goodglass et al., 1986; McKenna & Warrington, 1978) or preserved comprehension of printed body part terms (Goodglass & Budin, 1988), indicating lexical rather than conceptual deficits, and other patients were not tested in sufficient detail to discriminate between lexical and conceptual deficits (Fujimori et al., 1993; Goodglass et al., 1966).

More recently, several studies point to temporal lobe involvement in the processing of body part terms. First, as a result of a lesion in the right posterior ventral occipitotemporal region, patient SM performed quite poorly at naming not only body parts but also several other categories of objects (Turnbull & Laws, 2000). The investigators argue that the lesion disrupted SM's stored knowledge of object structure (see also Vandenbulcke et al., 2006), and it is possible, but not certain, that the affected knowledge included the shape component of the meanings of body part terms. Second, following a large left temporal lobe lesion, patient JJ was impaired at spoken and written production and comprehension of not only words for body parts, but also words for a number of other object categories, including clothing, furniture, fruits/vegetables, and other foods (Hillis & Caramazza, 1991). JJ's errors involving body part terms were predominantly semantic paraphasias (e.g., treating an elbow as a knee, hand, or

⁴The numbers “3” and “1” indicate lexical tones.

wrist). Third, Dennis (1976) presents a detailed analysis of patient DLA who, following a left anterior temporal lobectomy at age 17, produced circumlocutions (e.g., hand → “end of your arm”) and semantic paraphasias (e.g., ankle → “toe”) when attempting to name body parts, and also made systematic location- and function-based semantic errors during comprehension tasks (e.g., pointing to her index finger when asked to point to her ring finger). The author argues for a “lexical selection” impairment, but a semantic disorder involving either the shape, location, or function components of body part terms cannot be ruled out. This case should be interpreted cautiously, however, because DLA performed in the borderline to mentally retarded range on standardized intelligence tests (verbal IQ = 75; performance IQ = 69). Fourth, a recent lesion study with a large cohort of brain-damaged patients included two body part tests that assessed functional and associative aspects of conceptual knowledge independently of lexical knowledge (specifically, matching body parts by function, and matching body parts with associated articles of clothing), and found that of the three patients who failed both tests, all had lesions confined to the left temporal lobe, and two had lesions in portions of BA 37⁵ and the underlying white matter (Schwoebel & Coslett, 2005). Fifth, a PET study found that, relative to silent naming of animals, faces, and maps, silent naming of body parts and manipulable man-made objects elicited greater activation in the left posterior middle/inferior temporal cortex (BA 21/37; Gorno-Tempini et al., 2000). Sixth, an fMRI study revealed activation in a large left “temporal occipitoparietal” region (BA 22/37/39) during a complex task involving reading, covert speaking, and semantic comparison of body part terms (Goldberg et al., 2006). It is noteworthy that the last three studies all implicate BA 37, since the inferior portion of this area lies just anterior to the EBA.

There are also several studies which suggest that the left parietal lobe contributes to the processing of body part terms. First, patient KE, who suffered a left frontoparietal lesion, was administered six tasks assessing spoken and written production and comprehension of words for 10 categories of concrete entities, and was found to be most impaired for body parts, clothing, and furniture, and least impaired for fruits/vegetables and other foods (Hillis et al., 1990). Across all six tasks, he made comparable rates and types of semantic errors, with strong item-to-item as well as test-retest consistency, suggesting that the impairment was conceptual in nature. Second, patient HT, who also suffered a predominantly left frontoparietal lesion, exhibited severely impaired comprehension of spoken and written body part terms, but normal comprehension of spoken and printed terms for clothing, furniture, tools, vehicles, parts of a house, fruits/vegetables, and animals (Suzuki et al., 1997). This case has frequently been cited as an illustration of selective impairment of body part concepts (Barbarotto et al., 2001; Coslett et al., 2002; Shelton et al., 1998; Schwoebel & Coslett, 2005). However, it is notable that when HT was told the names of articles of clothing and instructed to point to the corresponding body parts on himself, he had no difficulty whatsoever, suggesting that he may have had preserved knowledge of the associative component of the meanings of body part terms. Third, patient YOT, who suffered a left temporoparietal lesion, was given a variety of tasks requiring comprehension of nouns for many different categories of concrete entities, and was most severely impaired for body part terms (Warrington & McCarthy, 1987). Most of YOT's other affected categories fell under the rubric of “small manipulable objects,” while her preserved categories included foods and living things. Fourth, evidence suggesting that the location component of the meanings of body part terms depends on the left parietal lobe comes from an fMRI study that revealed activation in the left intraparietal sulcus when subjects were presented with 19 body part terms, in both spoken and printed forms and in both English and French, and had to judge for each item whether the designated body part was higher or lower than the shoulders when a person is standing (Le Clec'h et al., 2000). The same hypothesis is also supported by some cases of autotopagnosia. Such patients often have left parietal lesions,

⁵BA stands for Brodmann area, and we use the conventional numbering system.

and although they usually retain the ability to name body parts as well as the ability to link body parts with specific functions and cultural associations, they are impaired at pointing to their own body parts on verbal command, indicating difficulty in identifying the spatial locations of those parts. This deficit is sometimes attributed to a body schema disturbance involving somatosensory, especially proprioceptive, processing (e.g., Felician et al., 2003; Schwoebel et al., 2001). However, some autotopagnosic patients also appear to be impaired at generating mental images of the normal spatial arrangement of human body parts (Guariglia et al., 2002; see also DeRenzi & Scotti, 1970).

Finally, Laiacona et al. (2006) recently reported a detailed case study of patient FC, who suffered extensive damage to many cortical and subcortical structures supplied by the left middle cerebral artery. Across a series of carefully designed tasks involving both word production and word comprehension, FC manifested disproportionately impaired semantic knowledge of body part terms relative to other kinds of object nouns that were well-matched for various nuisance factors. Moreover, FC's deficit for body part terms was most severe for the subcategory of limbs. Another notable discovery is that, despite his defective knowledge of limb semantics, FC's knowledge of action semantics appeared to be preserved, since he was not impaired at using his arms/hands to perform gestures related to object use or action imitation, nor was his action naming significantly worse than his naming of non-body-part objects. These findings provide evidence for the independent status (in this case, the selective preservation) of the function component of the meanings of body part terms. More generally, Laiacona et al.'s study constitutes a valuable addition to the neuropsychological literature; however, FC's large lesion prevents very precise or specific inferences about the neural substrates of body part terms.

1.3. Hypotheses

Against this background, we formulated the following specific hypotheses regarding the neuroanatomical bases of body part terms:

Hypothesis 1. During oral word production tasks such as picture naming, the process of mapping the meanings of body part terms onto the corresponding lexical-phonological forms depends on left frontoparietal or temporoparietal cortices.⁶—This hypothesis is motivated by many of the studies reviewed above (Goldberg et al., 2006; Gorno-Tempini et al., 2000; Hillis et al., 1990; Hillis & Caramazza, 1991; Suzuki et al., 1997; see also Gainotti, 2004, who presents a meta-analysis suggesting that the left frontoparietal region may be recruited during body part naming).

Hypothesis 2. The shape component of the meanings of body part terms depends on posterior ventrolateral temporal cortices, including BA 37, anterior to the EBA, in both left and right hemispheres—This hypothesis is suggested not only by many of the aforementioned studies (Goldberg et al., 2006; Gorno-Tempini et al., 2000; Hillis & Caramazza, 1991; Turnbull & Laws, 2000), but also by growing evidence that, for nouns that refer to various categories of concrete entities, such as animals and tools, the visually based shape components of the designated objects are mediated by the ventral temporal cortex, with increasingly complex combinations of shape features being integrated by increasingly anterior neural structures, and with different categories of objects exhibiting some degree of anatomical segregation (e.g., Bright et al., 2007; Chao et al., 1999; Price et al., 2003; Tranel et al., 1997; for recent reviews see Kemmerer, in press; Martin, 2007; Thompson-Schill et al., 2006).⁷

⁶We do not address written word production in this study.

Hypothesis 3. The location component of the meanings of body part terms depends on the left inferior parietal lobule—This hypothesis is motivated by several previous studies (Hillis et al., 1990; Le Clec'h et al., 2000; Paillard, 1980; Suzuki et al., 1997; Warrington & McCarthy, 1987), and receives additional indirect support from a growing literature suggesting that the representation of categorical spatial relations—which, as already noted, are the type relevant to body part configurations—depends predominantly on the left inferior parietal lobule (for reviews see Jager & Postma, 2003; Laeng et al., 2003; for recent studies see Postma & Laeng, 2006).

Hypothesis 4. The functional and associative components of the meanings of body part terms depend on the left temporal lobe, and the former component also relies to some extent on somatotopically mapped frontoparietal circuits that contribute to conceptual knowledge of the types of actions performed by certain body parts such as the mouth, arms/hands, and legs/feet—Evidence for left temporal lobe involvement in both functional and associative components of body part terms comes mainly from Schwoebel and Coslett's (2005) lesion study. Concerning the functional component, the proposal that frontoparietal circuits may also be important is motivated by studies focusing on action concepts (e.g., Assmus et al., 2007; Buccino et al., 2001; Hauk et al., 2004; Pobric & Hamilton, 2006; Pulvermüller et al., 2005a,b; Tettamanti et al., 2005; Tranel et al., 2003b).

This paper presents a lesion study aimed at exploring in greater detail the neural correlates of the production, comprehension, and semantic analysis of English body part terms. In particular, we addressed the hypotheses elaborated above by administering a battery of twelve tests to 104 patients with focal, stable damage to the left or right hemispheres.

2. Methods

2.1. Participants

The participants were 104 patients with left ($N = 63$), right ($N = 33$), or bilateral ($N = 8$) hemisphere brain damage, selected from the Patient Registry of the University of Iowa's Division of Behavioral Neurology and Cognitive Neuroscience. All gave informed consent in accordance with the Human Subjects Committee of the University of Iowa and federal regulations. The distribution of lesions allowed probing of many regions in the left and right hemispheres, helping to assess which brain regions are and are not crucial for performance on tasks of body part processing. By sampling many different brain regions, we could determine whether our main hypotheses were supported, and also whether there might be other brain regions that are important for processing body part information.

The patients' lesions were caused by either cerebrovascular disease ($N = 51$), surgical treatment of benign tumor ($N = 10$), arteriovenous malformation ($N = 3$), or subdural hematoma ($N = 5$), temporal lobectomy ($N = 30$), anoxia/ischemia ($N = 2$), traumatic brain injury ($N = 2$), or herpes simplex encephalitis ($N = 1$). Patients had to have evidence of left-hemisphere language dominance, as determined from neurological, Wada, and/or neuropsychological testing. Handedness, measured with the Geschwind-Oldfield Questionnaire (Oldfield, 1971) which has a scale ranging from full right-handedness (+100) to full left-handedness (−100), was

⁷See also Kiani et al. (2007), who recorded the responses of a large number (>600) of neurons in monkey ventral temporal cortex to a large number (>1000) of natural and artificial object images. The investigators found that the cells have complex activation patterns, or population codes, that capture the hierarchical organization of object forms, with an overarching division between animate and inanimate objects, and multiple nested subdivisions within the global category of animate objects, including faces—further split into primate and nonprimate faces—and bodies—further split into human bodies, 4-limb animal bodies, other animal bodies (insects, fish, reptiles), and hands.

distributed as follows: 88 patients were fully right-handed (+90 or greater); 7 were primarily right-handed (3 @ +80, 2 @ +55, 1 @ +50, 1 @ +40); 5 were fully left-handed (-90 or lower); and 4 were primarily left-handed (3 @ -80, 1 @ -30). All patients have been extensively characterized neuropsychologically and neuroanatomically, according to standard protocols (H. Damasio & Frank, 1992; Frank et al., 1997; Tranel, 2007). None of the patients had generalized intellectual deficits or generalized cognitive decline. On the Wechsler Adult Intelligence Scale-III, the entire group had mean IQ scores as follows: Verbal IQ, $M = 100.1$ ($SD = 17.8$); Performance IQ, $M = 101.3$ ($SD = 13.5$); Full Scale IQ, $M = 101.3$ ($SD = 14.1$) (all of these IQ scores are in the average range).

None of the patients had difficulty attending to or perceiving visual stimuli at basic level (as determined by detailed neuropsychological assessment). Some of the patients with left hemisphere lesions were recovered aphasics. Some of our hypotheses are specifically aimed at language-related left hemisphere structures, and we thus tried to include patients with lesions to these regions provided the patients could cooperate with the experiments. Accordingly, some of the patients had moderately severe residual aphasia, including both Broca-type and Wernicke-type profiles. However, none of the patients had residual aphasia of such a degree so as to preclude their comprehension of the experimental tasks. We excluded patients who could not comprehend the tasks, or who had any difficulty understanding the content of the queries used in the tasks (1 patient with severe global aphasia was excluded on this basis, prior to forming the group of 104 noted above).

All data, including standard neuropsychological measures, neuroanatomical data, and the experimental tasks, were obtained in the chronic phase, when patients were at least 3 months post lesion onset. In regard to the experimental tasks for body part processing, the average time at which patients were tested was 6.2 years ($SD = 5.8$) post lesion onset, with a range of 0.5 to 37 years (and all but 5 patients were tested a year or more after lesion onset).

A comparison group of normal subjects was also studied. These were 60 persons who were selected so as to be free of neurological or psychiatric disease. They participated in the experiments on a voluntary basis, and were compensated financially for their time. The normal comparison (NC) group and the brain-damaged (BD) group had the following general demographic characteristics: female/male gender ratio (NC = 28/32; BD = 48/56); average age in years (NC $M = 31.2$, $SD = 9.9$; BD $M = 51.6$, $SD = 13.6$); average educational level in years (NC $M = 16.2$, $SD = 2.3$; BD $M = 13.9$, $SD = 2.5$); preponderance of right-handedness (NC = 92% right-handed; 8% non-right-handed; BD = 91% right-handed; 9% non-right-handed); and racial composition (NC = 90% white; 10% nonwhite; BD = 92% white; 8% nonwhite). Overall, the NC group is somewhat younger and better educated than the BD group; otherwise, the groups are demographically similar (we note that both groups were drawn from a rural Midwestern population whose overall demographic characteristics are comparable to those of the study group).

2.2. Stimuli and Procedures

A battery of twelve tests was administered to each subject. All of these tests evaluate lexical and conceptual knowledge of human body parts, with four requiring production of body part terms, seven requiring comprehension of body part terms, and one requiring comparison of pictures of body parts but not lexical processing of body part terms.

2.2.1. Production Tests—Each of the four production tests requires retrieval of the phonological output forms of the same 30 words (or synonyms for them), which refer to body parts distributed across the major corporeal regions in the following manner: head ($N = 13$): *head, face, neck, chin, cheek, forehead, ear, earlobe, eye, eyelash, nose, mouth, lip*; torso ($N = 3$): *chest, belly/stomach/abdomen, back*; upper extremities ($N = 8$): *shoulder, arm, elbow*,

wrist, hand, finger, knuckle, fingernail; lower extremities (N = 6): *leg, thigh, knee, ankle, foot, toe*.

Test 1: Name own body parts (visual input): The examiner points to 30 of the subject's body parts, and the task is to produce the colloquial spoken name for each one.

Test 2: Name own body parts (tactile input): The examiner touches 30 of the subject's body parts while the subject is blindfolded, and the task is to produce the colloquial spoken name for each one.

Test 3: Name examiner's body parts: The examiner points to 30 of his/her own body parts, and the task is to produce the colloquial spoken name for each one.

Test 4: Name isolated body parts: The subject is shown 30 pictures of isolated body parts, and the task is to produce the colloquial spoken name for each one. The pictures consist of a mixture of photographs and line drawings, and each one includes not only the relevant body part but also its immediate spatial context—e.g., the picture of a cheek shows the right profile of a man's face with a black circle around the cheek. (See Figure 1A.) (Due to equipment failure, this test had data available from 72 of the 104 patients.)

We assume that all four of the production tests bear on Hypothesis 1, since all of them require access to the phonological output forms of body part terms. In addition, we assume that all four tests bear on Hypotheses 2, 3, and 4, since they also require access to the complex semantic structures of body part terms. The tests vary, however, with respect to which semantic components are most important. (See Table 1). Specifically, Tests 1, 3, and 4 depend more on the shape and location components (addressed by Hypotheses 2 and 3, respectively) than on the function component (addressed by Hypothesis 4), and Test 2 places the most emphasis on the location component (addressed by Hypothesis 3).

2.2.2. Comprehension Tests—The first six comprehension tests evaluate, in different ways, knowledge of the shape, location, and function components of body part terms. The last comprehension test assesses knowledge of how these terms are sometimes applied to the parts of inanimate objects.

Test 5: Point to own named body parts: The examiner says the names of 30 body parts (the same terms as in Tests 1-4), and the subject's task is to point to the corresponding parts of his/her own body. Failure on this type of test is the major symptom of autotopagnosia (e.g., Felician et al., 2003).

Test 6: Point to examiner's named body parts: The examiner says the names of 30 body parts (the same terms as in Tests 1-4), and the subject's task is to point to the corresponding parts of the examiner's body. Failure on this type of test is the major symptom of heterotopagnosia (e.g., Felician et al., 2003).⁸

Test 7: Word-picture matching: This test is made up of 25 sets of three pictures. The task is to choose which picture in each set best represents the meaning of a printed body part term.

⁸It is noteworthy, however, that pure heterotopagnosia—a very rare disorder—is more subtle than this. For instance, when heterotopagnosic subjects fail to point to the named body parts of other people, their errors usually involve self-referencing, i.e., pointing to the corresponding body parts on themselves, while simultaneously making odd statements like “Your mouth ... is my mouth” which suggest a disturbance of self-other differentiation (Degos et al., 1997). Moreover, they can accurately point to the named body parts of inanimate human images, such as dolls, and they can also accurately reach out and grasp the named body parts of other people, suggesting that they are only impaired when the task involves pointing to the named body parts of an animate, conscious person who has his/her own visuospatial perspective on the subject's gestural behavior (Degos et al., 1997; Felician et al., 2003).

For each set, one picture shows the target body part (e.g., a forehead), another picture shows a distractor body part that is related to the target with respect to either shape, position, or function (e.g., a cheek), and the third picture shows a distractor body part that is unrelated to the target (e.g., an elbow). (See Figure 1B.) The pictures are the same ones that are used in Test 4. The subject is told to ignore whether the pictures are color or black-and-white, and whether they are photographs or line drawings.

Test 8: Word-picture verification: The subject is shown 30 pictures of isolated body parts (just like in Test 4), each of which is associated with a single printed body part term. The task is to indicate whether or not the term accurately refers to the depicted body part. For example, in one item the word is *shoulder* and the picture shows a man's shoulder with a circle around it. (See Figure 1C.) (Due to equipment failure, data from this test were available from 72 of the 104 patients.)

Test 9: Locations of body parts: The subject is asked 10 questions about the relative spatial positions of body parts and must answer “Yes” or “No” for each one. Examples: “Is the elbow a part of the arm?” “Is the head connected to the waist?” Unlike Test 5 and Test 6, this test does not require the subject to point to named parts of either his/her own body or the examiner's body. Instead, it probes knowledge of the location component of body part terms in a somewhat more abstract manner.

Test 10: Functions of body parts: The subject is asked 6 questions about the characteristic functions of particular body parts. Examples: “What is the nose for?” “What do the feet do?” Acceptable answers included one-word responses (e.g., “smelling”) or short phrases (e.g., “help you walk”) that matched responses given by normal participants.

Test 11: Body part terms applied to the parts of inanimate objects: The subject is shown 20 pictures of inanimate objects, and in each picture a specific part of the object is highlighted by an arrow or circle. For each item, the picture is presented together with three printed body part terms, and the task is to indicate which term is conventionally used to refer to the highlighted part of the object. Examples (with the correct term underlined): the teeth/claws/face of a comb; the head/back/foot of a hammer; the arm/leg/foot of a chair; the mouth/nose/face of a cave; the nose/head/foot of an airplane. (See Figure 1D.) Although this test involves fixed linguistic collocations, it nevertheless provides a useful measure of the subject's knowledge of how English body part terms are sometimes applied to the parts of inanimate objects.⁹

These seven comprehension tests have varying degrees of relevance to Hypotheses 2, 3, and 4, which involve, respectively, the shape, location, and function components of body part terms. (See Table 1). Tests 5, 6, 7, and 8 address all three proposals, but especially Hypotheses 2 and 3. In addition, Test 9 bears specifically on Hypothesis 2, and Test 10 bears specifically on Hypothesis 3. We acknowledge, however, that these two tests do not provide detailed assessments of all of the knowledge under investigation. Finally, although Test 11 does not bear directly on the hypotheses, it is nevertheless uniquely valuable insofar as it taps into the subject's familiarity with certain linguistic conventions which stipulate how words that are typically used to designate parts of human bodies can also be used to refer to parts of inanimate

⁹This test was motivated in part by the fact that in some languages body part terms are used much more frequently and productively than in English to designate the parts of inanimate objects, and the choice of terms is determined in a rule-governed fashion by visuospatial analyses of axial and contour features. Perhaps the best-studied language of this type is Tzeltal, in which even an object as seemingly non-descript as a stone may be assigned a “face,” a “nose,” an “ear,” a “back,” a “belly,” or any of about fifteen other quasi-metaphorical body parts—e.g., an *s-jol* “head” is a protrusion that is located at one end of the major axis of an object and that has a gently curved, circular outline with only minor concavities on either side (Brown, 2006; Levinson, 1994; see also Heine, 1997).

objects, reflecting similarities of shape, location, and function that were originally detected, and incorporated into the language, by speakers from past generations.

2.2.3. Non-Linguistic Test—The last test was designed to probe conceptual knowledge of body parts independently of lexical-phonological processing of body part terms.

Test 12: Odd one out: This test is comprised of 20 sets of three pictures. For each set, two of the pictures show body parts that are related with respect to either position or function (e.g., a back and a chest, which are both parts of the torso), whereas the third picture shows a body part that is unrelated to the other two (e.g., a leg). The task is to indicate which picture is unrelated to the other two. The pictures are the same ones that are used in Test 4. (See Figure 1E.) The subject is told to ignore whether the pictures are color or black-and-white, and whether they are photographs or line drawings. This test bears on Hypotheses 2, 3, and 4. (See Table 1.)

2.3. Data Quantification

2.3.1. Neuropsychological Data Analysis—Our analyses of the neuropsychological data reflected the design characteristics and processing requirements of the tests. For the four production tests, we used a three-stage approach to the data analysis. The goal of the first stage was to determine which BD patients were impaired on which tests. For each test, the responses given by both groups of subjects—the BD group and the NC group—were scored as correct or incorrect. (For each of the 4 production tests, every item but one had a single body part term as the correct answer; the exception was the stomach region, for which we accepted “abdomen,” “belly,” and “stomach” as correct answers.) For each subject and each test, a percent correct score was calculated by dividing the number of correct responses by the number of items on the test, and multiplying by 100. Then, for each test, the mean and standard deviation from the NC subjects were used to establish a cutoff score—i.e., a level above which the BD patients' scores were considered to be unimpaired, and below which they were considered to be impaired (with scores right at the cutoff being treated as unimpaired). Cutoff scores were set at -2 standard deviations below the mean for the NC group, following standard convention in neuropsychology.

The goal of the second stage of data analysis was to maximize the reliability of our classification of BD patients as having or not having impairments in body part naming, by combining data across all of the production tests. For each subject in each group, a Composite Production score was calculated by dividing the number of correct responses across all four production tests by the total number items in those tests ($N = 120$, or $N = 90$ for those subjects who did not receive Test 4), and multiplying by 100. The mean and standard deviation from the NC group were again used to establish a cutoff score, and BD patients were classified as impaired if they were more than 2 standard deviations below the cutoff.

The goal of the third stage of data analysis was to document the types of errors committed by the BD patients whose Composite production scores were classified as impaired. To this end, these patients' errors were categorized according to the following taxonomy: semantic (either location-based, e.g., thigh → “calf,” or function-based, e.g., elbow → “knee”), phonological, omission, or “other” (e.g., definitions of body parts, or verbs denoting actions performed by body parts).

Turning to the seven comprehension tests, the data went through two stages of analysis, corresponding to the first two stages for the production tests. Initially, to determine which BD patients were impaired on which tests, we applied a cutoff of -2 standard deviations below the mean for the NC group. (Due to near-perfect mean scores and minimal variability in the NC group, we moved the cutoff score to $> 94\%$ for Tests 5, 6, 7, 8, and 9, and for the Composite

Comprehension score described below. As we show in section 3.2., however, even with the cutoff set so high, failures were extremely rare in the BD group.) Then, to maximize the reliability of our characterization of the status of body part knowledge comprehension in the BD patients, we calculated Composite Comprehension scores based on the total number of items across all seven tests ($N = 151$, or $N = 121$ in the patients who did not receive Test 8), and compared the scores of individual BD patients with the Composite Comprehension mean for the NC group.

Finally, the data for the non-linguistic Odd One Out test were quantified by conducting an analysis like the first stage for the production and comprehension tests. In short, percent correct scores were calculated for all subjects, and scores for BD patients were classified as impaired if they were more than 2 standard deviations below the mean for NC subjects.

2.3.2. Neuroanatomical Data Analysis—The neuroanatomical analysis was based on magnetic resonance (MR) data obtained in a 1.5 T scanner with an SPg sequence of thin (1.5 mm) and contiguous T_1 weighted coronal cuts. The data were reconstructed in three dimensions using Brainvox (Frank et al., 1997). (The analysis was based on CT data in a few patients in whom magnetic resonance could not be performed due to metal in the body or claustrophobia.) Anatomical characterization of the lesions and their placement relative to neuroanatomical landmarks was performed with Brainvox, using a standard method (H. Damasio, 2005). To address the main hypotheses, we performed a lesion overlap analysis of the patients from the BD group who were defective on a particular measure (as it turned out, we performed this analysis for the Composite Production index). This analysis overlaps in common brain space all of the lesions of patients who have a defect on a particular measure. The overlap map is color coded, so that differing degrees of overlap (greater or fewer patients with lesion at a particular voxel) are indicated by different colors.

3. Results

3.1. Production Tests

The behavioral group results for the production tests are shown in Table 2A. The NC subjects performed well on all four tests, with scores close to or above the 90% mark, and a Composite Production score of 93.4%. In the BD patients, failures on the four tests were not frequent, with the exception of Test 2, which had an overall failure rate of 21/104 patients (20%). However, of the 21 failures on Test 2, 9 scores were at 90%, just below the cutoff, and if these are omitted, the failure rate becomes only 11.5%. None of the other production tests had an appreciable failure rate: for Test 1, the rate was 4/104 or 3.8%; for Test 3, the rate was 7/104 or 6.7%; and for Test 4, the rate was 7/72 or 9.7%. For the Composite Production index, the failure rate was 10/104, or 9.6%. Of these 10 patients with an overall impaired Composite Production index, 9 had left hemisphere lesions and 1 had a right hemisphere lesion.

Table 3A presents the individual test scores for the 9 left hemisphere patients with overall Composite Production scores that fell in the impaired range. These results illustrate the different aspects of body part naming that tended to be defective in these patients. As can be seen, most of the patients manifested dissociations across the tests; however, most of the individual test scores that were classified as normal were actually very close to the cutoff for impairment (within two percentage points). In addition, we conducted an error analysis of these 9 patients' response protocols. Two of the patients (1760 and 2762) committed almost exclusively omission errors. For the other 7 patients, by far the most common errors (over 90% in most cases) were location-based semantic paraphasias.

As noted, of the 10 patients with impaired Composite Production scores, one had a right hemisphere lesion (caused by infarction) that was mainly in the angular gyrus, extending

superiorly into the supramarginal gyrus. The other 9 had left hemisphere lesions distributed as follows:

- Subject 1726 suffered a cerebrovascular accident (CVA) that damaged the cortex and underlying white matter in the posterior inferior frontal cortex (BA 45,44) and extended deep into the basal ganglia; the lesion also affected the insula, and tapered back to include part of the supramarginal gyrus (BA 40).
- Subject 1760 suffered a CVA that damaged a large portion of the inferior frontal cortex (BA 45,44,6,4) and subjacent white matter; the lesion also affected the insula, as well as the cortex and white matter in the inferior postcentral gyrus (BA 3,1,2), inferior parietal lobule (BA 40,39), and posterior superior temporal region (BA 22).
- Subject 1783 suffered a CVA that damaged the cortex and underlying white matter of the left inferior frontal operculum, in the heart of Broca's area including BA 45 and 44, and extending slightly posteriorly into inferior BA 6.
- Subject 1962 suffered a CVA that damaged most of the cortex and white matter in the inferior parietal lobule (BA 40,39) and posterior superior temporal cortex (BA 22); there is an additional, smaller area of damage in the left frontal operculum (BA 44). This patient's lesion is depicted in two previous publications—Kemmerer and Tranel (2003) and Kemmerer, Tranel, and Manzel (2005).
- Subject 1978 suffered a CVA that damaged the lower half of the lateral frontal cortex (BA 9,46,45,44,6,4) and subjacent white matter, extending into the basal ganglia; the lesion also encompassed the lower two thirds of the postcentral gyrus (BA 3,1,2) and part of the supramarginal gyrus (BA 40), as well as the underlying white matter.
- Subject 2127 suffered a CVA that affected predominantly two regions of the white matter in the left hemisphere: one region is in the territory superior and lateral to the frontal horn and anterior body of the lateral ventricle, subjacent to the middle and inferior frontal gyri; and the other, smaller region is near the posterior body of the lateral ventricle, subjacent to the terminus of the sylvian fissure. There is minor cortical involvement in the left frontal operculum.
- Subject 2762 suffered a traumatic brain injury that damaged the cortex, but very little white matter, in the posterior inferior frontal gyrus (BA 44,6,4), the inferior postcentral gyrus (BA 3,1,2), the anterior supramarginal gyrus (BA 40), most of the superior temporal gyrus (BA 22), and a small portion of the posterior middle temporal gyrus (BA 21/37). This patient's lesion is depicted in Kemmerer, Chandrasekaran, and Tranel (2007).
- Subject 2890 suffered a CVA that damaged the ventral aspect of visual association cortices, including BA 19 and 18, and underlying white matter, just behind but not including the posterior temporal region (BA 37). The lesion, which is depicted in Figure 2, includes the area that has been termed EBA in the functional neuroimaging literature. It also extends into the mesial occipital region in primary visual cortex (BA 17).
- Subject 3025 suffered left temporoparietal damage following rupture and surgical treatment of a left middle cerebral artery aneurysm. The lesion includes the middle and superior temporal gyri posteriorly, including the heart of Wernicke's area (posterior BA 22). It extends superiorly into the angular and supramarginal gyri in the inferior parietal region. There is also extension anteriorly into the white matter underneath the left frontal operculum.

The lesion overlap for seven of these patients is shown in Figure 3. (The lesion of subject 3025 was not available for the overlap analysis, and the EBA lesion in subject 2890 was not included

in the lesion overlap analysis.) The lesion overlap is color coded, and the areas of greatest overlap are shown in blue (all 7 patients), blue-green (6 patients), green (5 patients) and so forth according to the color bar on the Figure. As the Figure shows, the area of greatest overlap in the cortex is in the mid-portion of the left inferior frontal operculum, just at the junction between BA 45 and BA 44. The coronal sections in the Figure show that there is maximal overlap (all 7 patients) in the white matter underneath the inferior frontal operculum, extending posteriorly until about the transition from frontal to parietal lobe (i.e., at the level of the Rolandic sulcus). Up to four patients have lesion overlap in the cortex and underlying white matter in the anterior part of the inferior parietal operculum, tapering to three patients in the supramarginal gyrus (BA 40). (The addition of subject 3025 would add to both the frontal opercular overlap and the inferior parietal overlap for the group; see her lesion description above.) To summarize, the maximal lesion overlap for patients with impaired body part naming was right in the heart of Broca's area, in the cortex of BA 45/44 and the underlying white matter, with a second, less substantial focus of overlap in the anterior/inferior parietal operculum.

It is also important to examine the specificity of the lesion findings. Were there patients in the BD sample who had lesions that overlapped the critical zones specified above (especially corresponding to the blue and blue-green colors in Figure 3), and who were normal (unimpaired) on the body part naming tests? To address this issue, we searched through our dataset for BD patients who had left hemisphere lesions that encroached into the inferior frontal opercular and/or anterior/inferior parietal opercular regions, and who were not part of the impaired group enumerated above in connection with Figure 3. This search turned up two such cases. These patients had lesions that involved the left frontal operculum, one minimally and the other fairly extensively, and both patients had normal body part naming (Composite Production scores of 100% and 97%, respectively). These cases can be considered “false negatives,” inasmuch as they had lesions that involved the critical region for body part naming as revealed by the lesion overlap map in Figure 3, but did not manifest impaired body part naming. Overall, then, in regard to the left frontal operculum, we have 7 patients with impaired performance and lesions to that region, and 2 patients with unimpaired performance and lesions to that region. This yields a balance of 5 (7 minus 2), which happens to satisfy the criterion that we have set previously for associating a lesion site with a performance deficit (see H. Damasio et al., 2004). Thus, we can conclude that there is reasonable specificity in our lesion-deficit finding regarding the left frontal operculum and impaired body part naming.

The same issue is pertinent to our finding in patient 2890—that is, what is the specificity of this result? We searched our database for other cases with lesions that encroached into the left EBA region, and found two: one had a lesion mainly in BA 37, with slight extension posteriorly into ventral BA 19, and the other had a lesion mainly in the mesial ventral occipital region, with slight extension laterally into ventral BA 17/18. Both patients had normal Composite Production scores (92% and 89%, respectively); however, neither of these patients had significant damage to the EBA, and we are thus hesitant to classify them as “false negatives.” Although the EBA region is not well sampled in our dataset, the findings so far suggest that only extensive damage to this region per se will lead to a notable defect in body part naming.

3.2. Comprehension Tests

The behavioral group results for the comprehension tests are shown in Table 2B. The NC subjects performed well on all seven tests, achieving scores that were well above 90% correct in most cases, and their Composite Comprehension average was 99.7%. Failure on the comprehension tests in the BD patients was remarkably uncommon. On 3 tests, in fact, the failure rate was zero (Tests 6, 7, and 10). For Test 5, 1 patient failed, and for Tests 8 and 9, 3 patients failed, but in all cases, the mean performance scores of the patients who failed the tests according to the cutoff scores were not notably defective (scores near or above 90% correct).

Only on the comprehension of parts of inanimate objects (Test 11) was there an appreciable failure rate (6/104 patients, or 5.8%). In regard to the Composite Comprehension index, only 1 BD patient in the entire group of 104 had an impaired score; that patient happened to be the one with a left EBA lesion (2890), and, as shown in Table 3B, his composite was pulled down by a poor Test 11 performance, with 4 of the 7 comprehension tests showing perfect scores (100%).

3.3. Non-Linguistic Test

The behavioral group results for the Odd One Out test are shown in Table 2C. The NC subjects performed well on this test, at 98% correct. Of the 104 BD patients, 21 obtained scores that were classified as impaired ($M = 78.3\%$). Two of these patients had bilateral lesions—one mesial temporal and the other ventromedial prefrontal. Of the remaining 19 patients, 13 had left hemisphere lesions and 6 had right hemisphere lesions. The lesions were fairly widely distributed: (1) Left hemisphere: frontoparietal ($N = 6$); prefrontal/premotor ($N = 2$); anterior temporal/inferotemporal ($N = 3$); mesial temporal/occipitotemporal ($N = 1$); superior parietal ($N = 1$). (2) Right hemisphere: frontoparietal ($N = 2$); superior parietal ($N = 1$); anterior temporal/inferotemporal ($N = 2$); mesial temporal/occipitotemporal ($N = 1$). Among the 9 left hemisphere patients with impaired Composite Production of body part terms, 4 (1726, 1760, 1978, and 2127) were impaired on the Odd One Out test, as shown in Table 1C.

3.4. Naming of Other Concrete Entities

The findings reported above raise an important question about specificity: For the 9 left hemisphere patients with impaired Composite Production of body part terms, what is the status of their ability to orally name other categories of concrete entities? This question is especially important given that, as noted in the Introduction, a number of previous neuropsychological studies have documented dissociations between body part naming and other kinds of object naming (for reviews see Capitani et al., 2003, and Gainotti, 2004). To address this issue, we asked each of the 9 patients to orally name pictures of 281 concrete entities from the categories of animals ($N = 90$), fruits/vegetables ($N = 67$), tools/utensils ($N = 104$), and vehicles ($N = 20$) (for details regarding the stimuli, procedures, scoring, and normative data, see Damasio et al., 2004).¹⁰ The results are shown in Table 4, where they are depicted in a summary form that has a percent correct score for all of the concrete entities and the percent correct score for Composite Production for body part naming. (To avoid a confound of stimulus modality, Table 4 also shows, in parentheses, Composite Production scores that do not include the items from Test 2 involving tactile stimulation.) As can be seen, 4 of the 9 patients (1726, 1962, 2127, and 2890) are disproportionately impaired at naming body parts relative to other types of concrete entities. Specifically, given that the SDs on the concrete entity naming tests are around 4–5 percentage points (see H. Damasio et al., 2004), and the Composite Production body part score has an SD of 3.2 in normal subjects, difference scores that are around 2 or more standard deviations can be considered to indicate a significant discrepancy. Also, scores greater than 85% correct for concrete entities are within 2 SDs of normal, hence, in the current set of patients, the concrete entity naming performances of 1726, 1783, 2127, and 2890 can be considered normal. Thus, in 3 of the 4 patients with disproportionately impaired naming of body parts, the impairment is *restricted* to body part naming.

¹⁰The stimuli and target words used in this follow-up study were not matched with those used in the body part naming study according to nuisance variables like object familiarity, object complexity, word frequency, and age of word acquisition. In general, though, our normal comparison data indicate that the overall difficulty of the two sets of stimuli (body parts, other concrete entities) is very similar, with normal performances falling in the mid-90's percent correct. Thus, a direct comparison is valid.

4. Discussion

We investigated the neural substrates of lexical and conceptual knowledge of body part terms by first administering a multifaceted battery of tests to a large cohort of patients with widely distributed lesions, and then determining which aspects of body part knowledge were reliably impaired by lesions in specific brain areas. Below we discuss our major findings and their implications for the hypotheses outlined in the Introduction.

4.1. Producing Body Part Terms

Ten patients (one with a right hemisphere lesion) were found to have impaired oral naming of body parts, as indicated by the Composite Production index. We consider these naming deficits to be both valid and significant, because they reflect Composite Production scores that were generated for each patient by averaging performance across the 120 items (or 90 items for the 72 patients who did not receive Test 4) that together comprise probes that evaluate body part naming in different ways—specifically, naming one's own body parts from either visual or tactile input, naming the examiner's body parts from visual input, and naming pictures of isolated body parts. Moreover, we consider the naming deficits to constitute pure anomias, for the following reasons: first, none of the patients displayed impaired understanding of the meanings of body part terms, which rules out the possibility that the naming deficits may have been due to semantic disorders; and second, the patients' errors were almost entirely semantic paraphasias or omissions, which suggests that the cognitive disturbance involved the mapping from word meanings to word forms, as opposed to post-lexical processes. It is well-established that semantic paraphasias can arise from an impairment of lexical-phonological access; more precisely, when target word nodes are rendered relatively unavailable, semantically related ones that are engaged through a normal process of parallel activation can be produced instead (Caramazza & Hillis, 1990; for computer simulations see, among others, Rapp & Goldrick, 2000). It has also been argued that omissions can be caused by the inability of target word nodes to reach a critical threshold of activation, either because they are destroyed or because their top-down input is insufficiently strong (Laine et al., 1998; Ruml et al., 2000; for a computer simulation, see Dell et al., 2004).

Of the nine patients with left hemisphere lesions and impaired Composite Production of body part terms, eight had the greatest lesion overlap in the left inferior frontal operculum, and in the left anterior/inferior parietal opercular region. This finding provides partial support for Hypothesis 1, elaborated in the Introduction. The remaining patient—2890—had a left occipital lesion that included the EBA. This finding is intriguing, since it suggests that the left EBA might contribute in some way to the retrieval of body part terms, especially during naming tasks. The exact role(s) of the left EBA in body part naming are not clear, however, and further research is needed to investigate this topic in greater detail. It may be relevant, though, that the left but not the right EBA has been shown to respond equally to both egocentric (self) and allocentric (other) views of body parts (Chan et al., 2004; Saxe et al., 2006). This perspectival indifference of the left EBA squares well with the fact that subject 2890 failed both Test 2, which involves naming one's own body parts, and Test 3, which involves naming the examiner's body parts (in addition, 2890's scores on the other two naming tests, which differ in terms of the self/other contrast, were just barely above the cutoff).

In a follow-up study that investigated the specificity of body part naming deficits in the nine patients mentioned above, we found that four of the patients exhibited disproportionately worse naming of body parts than of other categories of concrete entities. Moreover, for 3 of these 4 patients, the object naming deficit was *restricted* to body parts. Most notably, this profile was manifested by subject 2890, whose lesion encompassed the left EBA. These findings contribute to the relatively small literature documenting patients with dissociations between impaired

naming of body parts and spared naming of other types of objects (for reviews see Capitani et al., 2003, and Gainotti, 2004).

4.2. Comprehending Body Part Terms

Because our study employed a broad-based lesion sampling approach, it allowed us to investigate, in a unique and powerful way, which brain regions are, and are not, crucial for good performance on the tests assessing comprehension of the language-specific meanings of body part terms. That is, by sampling many different brain regions, we could determine not only whether our main hypotheses were supported—in this case, Hypotheses 2, 3 and 4 about the neural correlates of the shape, location, and function components of body part terms—but also whether there might be other brain regions that are important for processing these aspects of semantic knowledge. It is therefore remarkable that in our group of 104 patients with widely distributed lesions, only one patient had a Composite Comprehension score that fell below the cutoff for impairment (and that score was 90%, which is not severely impaired by any means). We would like to point out that this finding is in keeping with previous research which has indicated that body part knowledge tends to be spared, even when other knowledge domains are disrupted (Coslett et al., 2002; Ferro & Santos, 1984; Forde et al., 1997; Laiacina et al., 2006; Riddoch & Humphreys, 1987; Shelton et al., 1998; Zingeser & Berndt, 1988; for reviews see Capitani et al., 2003, and Gainotti, 2004). However, it is quite surprising that such a large-scale lesion study did not uncover patients with substantial deficits in their understanding of body part terms. Below we discuss how this unexpected outcome might be explained, and we also consider its implications for Hypotheses 2, 3, and 4.

First, even though we used a large and diverse set of tests to assess comprehension of body part terms, the question naturally arises as to whether our measurement tools were sensitive enough to detect subtle semantic disorders in the patients. For example, some of the tests did not investigate in great detail the particular ability under consideration. Specifically, this was true of the “locations of body parts” test (9), which had 10 items, and the “functions of body parts” test (10), which had 6 items. It must be acknowledged that a lengthier and more demanding assessment of these abilities could turn up defects that might have been missed with our abbreviated assessment. In addition, it may not be trivial that many of the other comprehension tests yielded performances near or at 100% correct in the NC group. Nevertheless, most of the tests in the comprehension battery were fairly extensive, and the fact that we challenged the patients with a total of 151 items requiring comprehension of body part terms (or 121 items for patients who did not receive Test 8) provides some leverage for our conclusion that defects in comprehension were remarkably scarce. In short, while the lack of substantial comprehension impairments in the current study might be due in part to shortcomings of the measurement tools, it seems very unlikely that this would turn out to be the only important explanatory factor.

Second, compared to other categories of concrete entities, body parts are the most familiar, as reflected in the fact that the familiarity ratings for the body part items in the Snodgrass and Vanderwart (1980) picture set were 4.48 or higher (on a scale of 1 to 5, with 5 being “very familiar”), with an average of 4.66 for the category (compared to, for example, an average of 2.36 for the animal category and 4.16 for the kitchen utensils category). Previous neuropsychological studies have shown that familiarity can have a significant influence on the ability of patients to process concepts, with greater familiarity correlating with greater resistance to impairment (e.g., Funnell & Sheridan, 1992; Stewart et al., 1992). It is therefore possible that the lack of substantial comprehension deficits among the patients in the current study may have been due, at least to some extent, to the high degree of familiarity of the lexically encoded body part concepts on which we focused. On the other hand, a good number of the body parts terms used in Tests 5, 6, 7, and 8 were relatively infrequent (e.g., *earlobe*, *eyelash*,

knuckle, fingernail, none of which were in the set used in Snodgrass and Vanderwart). Furthermore, Shelton, Fouch, and Caramazza's (1998) patient IOC exhibited selectively preserved knowledge of body part terms, compared to a variety of other lexical-conceptual domains, even when the test items were equated not only for familiarity but also for word frequency and visual complexity. In fact, as the authors stated, "IOC commented that we included 'the easy ones' (body part pictures) in the tests so that she would not get discouraged, as she could not believe we would think anyone would perform poorly on those items ('everyone knows what a hand is')" (p. 342). These considerations suggest that although high familiarity may have been a "protective" factor in the current study, there are probably additional reasons why the meanings of body part terms are so resistant to impairment.

Finally, all of our patients were studied during the chronic epoch of recovery (on average, 6.2 years post lesion onset), and it is possible that some of them did have impaired comprehension of body part terms during the acute epoch, but then gradually regained comprehension through spontaneous processes of functional-anatomical reorganization. It is known that for many cognitive capacities, such as language, extensive neural reorganization can take place during the weeks or months after injury (e.g., Grafman & Litvan, 1999; Heiss et al., 1999; Thulborn et al., 1999; Warburton et al., 1999; Weiller et al., 1995; for recent reviews see Hillis, 2006a,b). Thus, it is conceivable that some of our patients with lesions to areas hypothesized to underlie certain semantic components of body part terms did have deficient understanding of those components immediately post-injury, but other areas subsequently "took over" those functions. (Only five of the patients in our dataset were tested with the body parts battery prior to one year post lesion onset, and none of the patients were tested within the first six months, thus precluding a definitive investigation of the chronicity variable.) Pursuing this line of thinking a bit further, it may be that the neural substrates of body part concepts are unusually "plastic" in the sense of being highly amenable to reorganization following damage. There may be several reasons for the resilience of this conceptual domain, including (1) the great importance of body representations for understanding both oneself and other people, and (2) the fact that, as we mentioned at the outset of this paper, body representations are extremely multimodal. If this conjecture is on the right track, it could account for why comprehension impairments for body part terms are only rarely observed in patients during the chronic period (see section 1.2). And taking this a step further, with regard to Hypotheses 2, 3, and 4, another way to test these hypotheses using the lesion method would be to study patients during the acute period, before functional-anatomical reorganization has taken place. Yet another approach would be to investigate the effects of transient "lesions" induced by repetitive transcranial magnetic stimulation (e.g., Urgesi et al., 2004, 2007a, 2007b).

In any event, our findings surely provide no indication that patients with brain damage, who are in the chronic epoch of recovery, have major defects in the comprehension of body part terms. Situating this finding in the context of the extant literature, it can be concluded with some certitude that knowledge of the meanings of body part terms is extremely resistant to brain damage, no matter the location of that damage. Interestingly, this finding has parallels with other domains of knowledge—for example, the finding that the recognition of facial expressions of happiness is essentially never impaired by brain damage (Adolphs et al., 2000).

4.3. Non-Linguistic Processing of Body Part Concepts

Twenty-one patients were impaired on the non-linguistic Odd One Out test. Although this test does not require the overt processing of body part terms in either the stimuli or the subject's responses, it does load heavily on a variety of other cognitive functions. The visual processing demands are significant because each item contains three pictures. Probably of even more importance, the "executive" processing demands are quite significant because the subject must

not only identify the relevant dimension of comparison—i.e., location or function—but also arrive at a correct decision as to which of the three depicted body parts differs from the other two along that dimension. These considerations help to account for why a relatively large number of patients had difficulty with the test. In particular, given the discussion in the preceding section, it seems highly probable that the patients who failed the Odd One Out test did so because of deficits involving various combinations of the multiple processing requirements of the experimental paradigm itself, as opposed to deficits involving body part concepts per se. This explanation of the behavioral results is consistent with the fact that the patients who failed the Odd One Out test had very heterogeneous lesion sites.

4.5. Conclusion

We have reported a neuropsychological study which found that of 104 patients with focal, stable lesions in the left or right hemispheres, ten had impaired naming of body parts. Nine of these patients had left hemisphere damage, with eight exhibiting maximal lesion overlap in the frontal opercular and anterior/inferior parietal opercular cortices, and one exhibiting an occipital lesion that encompassed the EBA. Four of the nine left hemisphere patients had disproportionately worse naming of body parts relative to other categories of concrete entities. Perhaps the most remarkable discovery, however, is that none of the patients with body part anomia manifested significant difficulty understanding the meanings of body part terms. In fact, we did not uncover a single patient with impaired conceptual knowledge of body parts. Possible explanatory factors that we have considered include the following: the fact that all of the patients were examined during the chronic rather than the acute epoch of recovery; the unusually high level of familiarity of body parts; and limitations of the measurement tools. In closing, we hope that this investigation will help inspire further research on the neural substrates of body part terms.

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A. Test 4: Name isolated body parts **B. Test 7: Word-picture matching**

forehead

C. Test 8: Word-picture verification

shoulder

D. Test 11: Body part terms applied to the parts of inanimate entities

teeth claws face

E. Test 12: Odd one out

location

function

Figure 1.

Examples of the types of stimuli used in five of the tests that probe lexical and conceptual knowledge of body parts. (A) Test 4: Name isolated body parts. The subject is asked to name the circled body part (cheek). (B) Test 7: Word-picture matching. The subject is asked to choose which picture represents a forehead. (C) Test 8: Word-picture verification. The subject is asked to decide whether the word *shoulder* correctly describes the circled body part. (D) Test 11: Body part terms applied to parts of inanimate entities. The subject is asked to determine which word—*teeth*, *claws*, or *face*—refers to the circled part of the comb. (E) Test 12: Odd one out. For each set of three pictures, the subject is asked to determine which body part is unrelated to the other two with respect to either location (top panel, with the leg being the correct answer) or function (bottom panel, with the ear being the correct answer). Note that the relevant

dimension of comparison is not provided by the examiner, but must be discovered by the subject.

Figure 2.

Lesion of subject 2890. The lesion is shown in an MR scan obtained 1.5 years after lesion onset, reconstructed in standard brain space. The left hemisphere lateral perspective is shown, along with coronal cuts (black lines, a-c) that depict the cortical and white matter extent of lesion (with left hemisphere on the right). The lesion encompasses the left EBA, located in the inferior lateral portion of Brodmann area 19.

Figure 3.

Lesion overlap map for seven patients with impaired Composite Production scores. The top panel depicts a lateral view of the left hemisphere, and the bottom panels show four coronal cuts (a, b, c, d) through the posterior frontal region (with left hemisphere on the right). The color bar codes the maximal overlap of lesions, with blue corresponding to greatest overlap (all 7 patients), blue-green to the next highest overlap (6 patients), green to the next highest overlap (5 patients), and so on.

Table 1

Indications of which tests bear on which hypotheses. Hypothesis 1 pertains to lexical access for naming body parts, and Hypotheses 2, 3, and 4 pertain to three distinct components of the meanings of body part terms: shape, location, and function. A single plus sign indicates minor relevance, and two plus signs indicate major relevance.

Tests	1. Lexical Access	2. Shape	3. Location	4. Function
A. Production Tests				
1. Name own body parts (visual input)	++	++	++	+
2. Name own body parts (tactile input)	++	+	++	+
3. Name examiner's body parts	++	++	++	+
4. Name isolated body parts	++	++	+	+
B. Comprehension Tests				
5. Point to own named body parts		++	++	+
6. Point to examiner's named body parts		++	++	+
7. Word-picture matching		++	++	++
8. Word-picture verification		++	++	+
9. Locations of body parts			++	
10. Functions of body parts				++
11. Parts of inanimate objects		?	?	?
C. Non-Linguistic Test				
12. Odd one out		++	++	++

Table 2

Group results (in percentage points) for 12 tests assessing lexical and conceptual knowledge of body parts. (A) Production tests. (B) Comprehension tests. (C) Non-linguistic test. In the two columns under “Impaired BD patients,” “N” indicates the number of patients, from the entire group of 104, whose score for the given test was below the cutoff, and “Mean (s.d.)” indicates the average percent correct and the standard deviation for the patients specified under “N.” *The Composite scores are based on the entire set of items that went into the score (not on an average of the various tests). **For these two tests, 72 of the 104 patients took the test. For all other tests, the total N is 104 patients. See text for more details.

Tests	NC subjects Mean (s.d.)	Cutoff	Impaired BD patients	
			N	Mean (s.d.)
A. Production Tests				
1. Name own body parts (visual input)	89.8 (6.6)	> 75	4	47.5 (29.7)
2. Name own body parts (tactile input)	97.2 (3.8)	> 90	21	78.7 (20.8)
3. Name examiner's body parts	95.1 (4.6)	> 84	7	62.9 (24.1)
4. Name isolated body parts**	91.6 (4.0)	> 82	7	61.9 (25.7)
Composite production*	93.4 (3.2)	> 86	10	63.4 (26.9)
B. Comprehension Tests				
5. Point to own named body parts	99.9 (0.4)	> 94	1	93.0 (-)
6. Point to examiner's named body parts	99.7 (1.1)	> 94	0	- (-)
7. Word-picture matching	99.8 (0.9)	> 94	0	- (-)
8. Word-picture verification**	99.6 (1.3)	> 94	3	91.0 (3.5)
9. Locations of body parts	100.0 (-)	> 94	3	86.7 (5.8)
10. Functions of body parts	98.9 (4.3)	> 89	0	- (-)
11. Parts of inanimate objects	92.4 (5.8)	> 79	6	70.8 (8.0)
Composite comprehension*	99.7 (0.6)	> 94	1	90.0 (-)
C. Non-Linguistic Test				
12. Odd one out	98.0 (3.7)	> 89	21	78.3 (8.4)

Table 3

Scores (in percent correct) on all 12 tests for the 9 BD patients with left hemisphere lesions and impaired Composite Production of body part terms. Scores in bold typeface are impaired. n/a = not administered.

Tests	BD patients with impaired Composite Production of body part terms								
	1726	1760	1783	1962	1978	2127	2762	2890	3025
A. Production Tests									
1. Name own body parts (visual input)	77	17	87	n/a	73	87	27	77	83
2. Name own body parts (tactile input)	83	23	83	n/a	63	87	17	77	83
3. Name examiner's body parts	77	27	90	n/a	67	83	30	73	90
4. Name isolated body parts	67	20	83	30	n/a	79	n/a	83	n/a
Composite production	76	22	86	30	68	84	24	77	86
B. Comprehension Tests									
5. Point to own named body parts	93	100	100	100	100	100	100	100	97
6. Point to examiner's named body parts	100	100	100	100	100	100	100	100	97
7. Word-picture matching	96	100	100	100	100	100	100	100	96
8. Word-picture verification	93	100	100	100	n/a	97	n/a	87	n/a
9. Locations of body parts	100	100	100	100	100	100	100	90	80
10. Functions of body parts	100	100	100	100	100	100	100	100	100
11. Parts of inanimate objects	80	80	70	100	95	75	85	55	90
Composite comprehension	96	97	96	100	99	96	98	90	95
C. Non-Linguistic Test									
12. Odd one out	75	80	90	100	80	60	100	95	90

Table 4

Contrast of naming of concrete entities and naming of body parts in the 9 patients with impaired Composite Production of body part terms. Scores are in percent correct, and correspond to all 281 concrete entities and the Composite Production scores for body parts. (To avoid a confound of stimulus modality, the body part naming scores in parentheses reflect the removal of the items in Test 2 involving tactile naming.) Differences of more than 8 percentage points (favoring concrete entities) indicate scores that are separated by around 2 or more standard deviations, suggesting disproportionate impairment in body part naming (patients 1726, 1962, 2127, and 2890).

Patient	Concrete Entities (CE)	Body Parts (BP)	Difference (CE minus BP)
1726	87	76 (74)	11 (13)
1760	24	22 (21)	2 (3)
1783	90	86 (87)	4 (3)
1962	73	30 (30)	43 (43)
1978	61	68 (70)	-7 (-9)
2127	93	84 (83)	9 (10)
2762	3	24 (28)	-21 (-25)
2890	93	77 (78)	16 (15)
3025	85	86 (86)	-1 (-1)