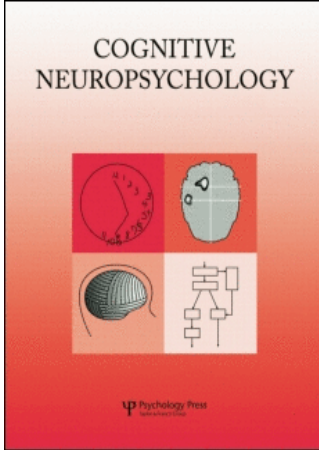


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### Searching for the elusive neural substrates of body part terms: A neuropsychological study

David Kemmerer<sup>ab</sup>, Daniel Tranel<sup>b</sup>

<sup>a</sup> Department of Speech, Language, and Hearing Sciences and Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA

<sup>b</sup> Department of Neurology, Division of Cognitive Neuroscience, University of Iowa College of Medicine, Iowa City, IA, USA

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# Searching for the elusive neural substrates of body part terms: A neuropsychological study

David Kemmerer

*Department of Speech, Language, and Hearing Sciences and Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA, and Department of Neurology, Division of Cognitive Neuroscience, University of Iowa College of Medicine, Iowa City, IA, USA*

Daniel Tranel

*Department of Neurology, Division of Cognitive Neuroscience, University of Iowa College of Medicine, Iowa City, IA, USA*

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, 1 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.

**Keywords:** Body parts; Embodied cognition; Broca’s area; Inferior parietal lobule; Extrastriate body area.

Compared to all other kinds of objects, human bodies are special (Knoblich, Thornton, Grosjean, & Shiffrar, 2006). We experience our own bodies not only through exteroceptive sensory channels

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Correspondence should be addressed to David Kemmerer, Department of Speech, Language, and Hearing Sciences, 1353 Heavilon Hall, Purdue University, West Lafayette, IN 47907–1353, USA (E-mail: kemmerer@purdue.edu).

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(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, online 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 (A. R. 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—that is, disownership of body parts (Halligan, Marshall, & Wade, 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, Bray, Rogers, & Childs, 2004; Ro, Friggel, & Lavie, 2007) and are recognized holistically via the configuration of their parts (Glia & Dehaene-Lambertz, 2005; Reed, Stone, Bozova, & Tanaka, 2003; Slaughter, Stone, & Reed, 2004; Stekelenburg & de Gelder, 2004; Urgesi, Calvo-Merino, Haggard, & Aglioti, 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 nonfacial body parts, regardless of whether they are stationary (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006a; Downing, Jiang, Shuman, & Kanwisher, 2001; Downing,

Wiggett, & Peelen, 2007; Morris, Pelphrey, & McCarthy, 2006; Peelen & Downing, 2005b; Peelen, Wiggett, & Downing, 2006; Spiridon, Fischl, & Kanwisher, 2006) or moving (Bartels & Zeki, 2004; Downing, Peelen, Wiggett, & Tew, 2006b; Kable & Chatterjee, 2006).<sup>1</sup> 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, Stanley, Shulman, & Corbetta, 2004; Jackson, Meltzoff, & Decety, 2006; see also Arzy, Thut, Mohr, Michel, & Blanke, 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, Peelen, & Downing, 2004; Saxe, Jamal, & Powell, 2006). In addition, the visual perception of human bodies and nonfacial 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, Peelen, Spinelli, Seeck, & Vuilleumier, 2007). Furthermore, repetitive transcranial magnetic stimulation (rTMS) over the EBA interferes with the discrimination of bodily forms (Urgesi, Berlucchi, & Aglioti, 2004; Urgesi et al., 2007a; Urgesi, Candidi, Ionta, & Aglioti, 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, Laiacona, Mahon, and Caramazza (2003; see especially Appendix D) observe that in comparison with other categories of concrete entities, body

<sup>1</sup> Another 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, Baker, & Kanwisher, 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, Wiggett, & Downing, 2007).

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., Laiacona, Allamano, Lorenzi, & Capitani, 2006; Suzuki, Yamadori, & Fujii, 1997), 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, Saffran, & Schwoebel, 2002; Ferro & Santos, 1984; Forde, Francis, Riddoch, Rumiati, & Humphreys, 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, Fouch, & Caramazza, 1998).

To gain deeper insight into these issues, we administered a battery of 12 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, 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.

### 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, Coslett, & Buxbaum, 2001)

distinction between the following three types of representation: (a) 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); (b) 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 (c) 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: (a) information about the typical shape of the designated part; (b) information about the location of the designated part within the hierarchical spatial organization of the human body; (c) information about the characteristic function(s) of the designated part; and (d) information about the cultural associations of the designated part.<sup>2</sup>

<sup>2</sup> The meanings of body part terms may also include various kinds of "encyclopaedic" information, but we do not address such knowledge in this study.

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, Enfield, & van Staden, 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, 2005b; 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 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 nonlinguistic shape information.)

The second semantic component is spatial location within the structural framework of the human body at an appropriate level of scale

(Anderson, 1978; Brown, 1976; Cruse, 1986, chap. 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-centre-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, Chabris, & Kosslyn, 2003; see also Jellema & Perrett, 2006).<sup>3</sup> 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, 1987, 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.*

<sup>3</sup> Kosslyn (2006, p. 1521) expresses this point as follows, alluding to neuroanatomical hypotheses that we delineate more fully in the section “Hypotheses”: “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. . . .”

(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 the section “Hypotheses”—we hypothesize that these two semantic components have different neural substrates.)

The third semantic component is function (Tversky, Morrison, & Zacks, 2002). Legs not only are 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—for example, 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 customary actions performed with the given parts—for example, the Lao compound term *kbaa3 phap1*<sup>4</sup> 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 jewellery, 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, chap. 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*.)

### 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 proposals that we elaborate in the section “Hypotheses”. 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, Wingfield, Hyde, & Theurkauf, 1986; McKenna & Warrington, 1978) or preserved comprehension of printed body part terms (Goodglass & Budin, 1988), indicating lexical rather than conceptual

<sup>4</sup> The numbers “3” and “1” indicate lexical tones.

deficits, and other patients were not tested in sufficient detail to discriminate between lexical and conceptual deficits (Fujimori, Yamadori, Imamura, Yamashita, & Yoshida, 1993; Goodglass, Klein, Carey, & Jones, 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 S.M. 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 S.M.'s stored knowledge of object structure (see also Vandenberghe, Peeters, Fannes, & Vandenberghe, 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 J.J. 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). J.J.'s errors involving body part terms were predominantly semantic paraphasias (e.g., treating an elbow as a knee, hand, or wrist). Third, Dennis (1976) presents a detailed analysis of patient D.L.A. 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 the shape, location, or function components of body part terms cannot be ruled out. This case should be interpreted cautiously, however, because D.L.A. 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 37<sup>5</sup> and the underlying white matter (Schwoebel & Coslett, 2005). Fifth, a positron emission tomography (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, Cipolotti, & Price, 2000). Sixth, a functional magnetic resonance imaging (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, Perfetti, & Schneider, 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 that suggest that the left parietal lobe contributes to the processing of body part terms. First, patient K.E., 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, Rapp, Romani, & Caramazza, 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 H.T., 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

<sup>5</sup> BA stands for Brodmann area, and we use the conventional numbering system.

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, Capitani, & Laiacona, 2001; Coslett et al., 2002; Shelton et al., 1998; Schwoebel & Coslett, 2005). However, it is notable that when H.T. was told the names of articles of clothing and was 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 Y.O.T., 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 Y.O.T.'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 participants 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 Clech et al., 2000). The same hypothesis is also supported by some cases of autotopagnosia. Such patients often have left parietal lesions, 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, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 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, Piccardi, Puglisi Allegra, & Traballes, 2002; see also DeRenzi & Scotti, 1970).

Finally, Laiacona et al. (2006) recently reported a detailed case study of patient F.C., 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, F.C. 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, F.C.'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, F.C.'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.

## 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.*<sup>6</sup> This hypothesis is motivated by many

<sup>6</sup> We do not address written word production in this study.

of the studies reviewed above (Goldberg et al., 2006; Gorno-Tempini et al., 2000; Hillis & Caramazza, 1991; Hillis et al., 1990; 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, Moss, Longe, Stamatakis, & Tyler, 2007; Chao, Haxby, & Martin, 1999; Price, Noppeney, Phillips, & Devlin, 2003; Tranel, Damasio, & Damasio, 1997; for recent reviews see Kemmerer, in press; Martin, 2007; Thompson-Schill, Kan, & Oliver, 2006).<sup>7</sup>

*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, Giessing, Weiss, & Fink, 2007; Buccino et al., 2001; Hauk, Johnsrude, & Pulvermüller, 2004; Pobric & Hamilton, 2006; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005a; Pulvermüller, Shtyrov, & Ilmoniemi, 2005b; Tettamanti et al., 2005; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003).

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 12 tests to 104 patients with focal, stable damage to the left or right hemispheres.

## METHOD

### Participants

The participants were 104 patients with left ( $N = 63$ ), right ( $N = 33$ ), or bilateral ( $N = 8$ )

<sup>7</sup> See also Kiani, Esteky, Mirpour, and Tanaka (2007), who recorded the responses of a large number (>600) of neurons in monkey ventral temporal cortex to a large number (>1,000) 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, four-limb animal bodies, other animal bodies (insects, fish, reptiles), and hands.

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 cerebrovascular disease ( $N=51$ ), surgical treatment of benign tumour ( $N=10$ ), arteriovenous malformation ( $N=3$ ), subdural haematoma ( $N=5$ ), 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 distributed as follows: A total of 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, Damasio, & Grabowski, 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 after lesion onset. In regard to the experimental tasks for body part processing, the average time at which patients were tested was 6.2 years ( $SD=5.8$ ) after 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 participants 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 was somewhat younger and better educated than the BD group; otherwise, the groups were 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).

## Stimuli and procedure

A battery of 12 tests was administered to each participant. All of these tests evaluate lexical and conceptual knowledge of human body parts, with 4 requiring production of body part terms, 7 requiring comprehension of body part terms, and 1 requiring comparison of pictures of body parts but not lexical processing of body part terms.

### *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 participant'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 participant's body parts while the participant 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.

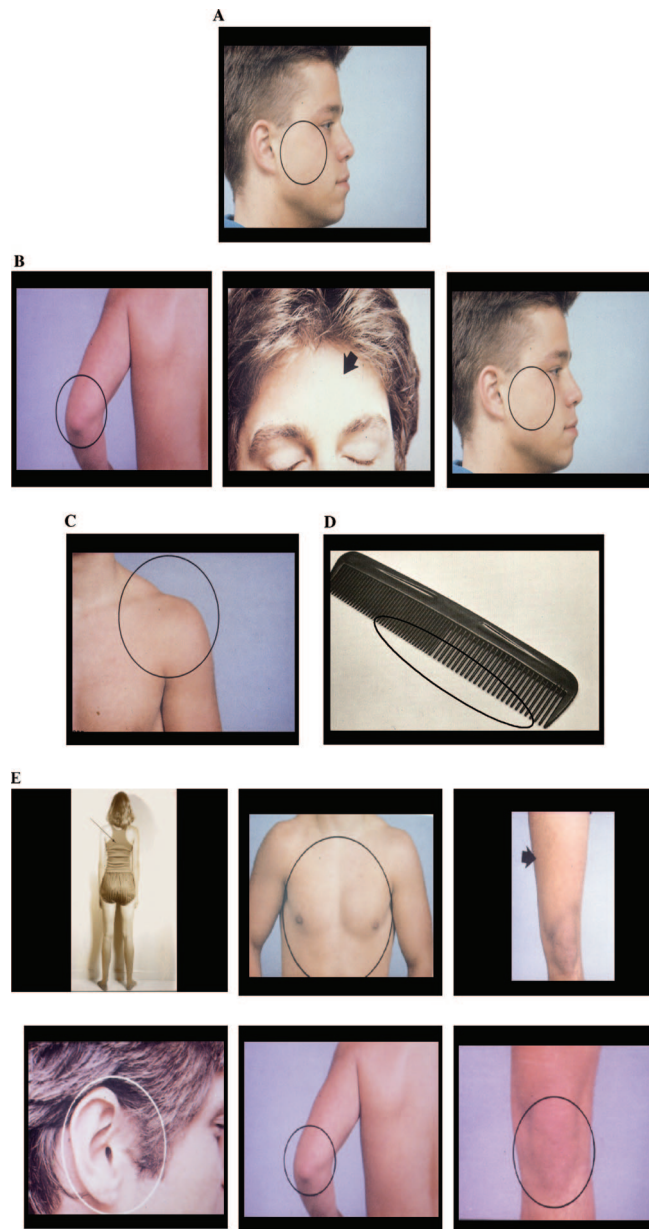
*Test 4: Name isolated body parts.* The participant is shown 30 pictures of isolated body parts, and the task is to produce the colloquial spoken name for each one. The pictures consist of a mixture of photographs and line drawings, and each one includes not only the relevant body part but also its immediate spatial context—for example, 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).

### *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 those in Tests 1–4), and the participant'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).



**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 participant is asked to name the circled body part (cheek). (B) Test 7: Word–picture matching. The participant is asked to choose which picture represents a forehead. (C) Test 8: Word–picture verification. The participant is asked to decide whether the word should correctly describes the circled body part. (D) Test 11: Body part terms applied to parts of inanimate entities. The participant 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 participant 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 participant. (To view a colour version of this figure, please see the online issue of the Journal.)

**Table 1.** *Indications of which tests bear on which hypotheses*

<i>Test</i>			<i>Hypothesis</i>				
			<i>1</i> <i>Lexical access</i>	<i>2</i> <i>Shape</i>	<i>3</i> <i>Location</i>	<i>4</i> <i>Function</i>	
A	Production	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	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	Nonlinguistic	12	Odd one out	++	++	++	

*Note:* 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.

*Test 6: Point to examiner's named body parts.* The examiner says the names of 30 body parts (the same terms as those in Tests 1–4), and the participant'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).<sup>8</sup>

*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. 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 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 as those that are used in Test 4. The participant is told to ignore whether the pictures are colour or black-and-white and whether they are photographs or line drawings.

*Test 8: Word-picture verification.* The participant 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.)

<sup>8</sup> It is noteworthy, however, that pure heterotopagnosia—a very rare disorder—is more subtle than this. For instance, when heterotopagnosic participants fail to point to the named body parts of other people, their errors usually involve self-referencing—that is, 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, Bachoud-Levi, Ergis, Petrissans, & Cesaro, 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 participant's gestural behaviour (Degos et al., 1997; Felician et al., 2003).

*Test 9: Locations of body parts.* The participant is asked 10 questions about the relative spatial positions of body parts and must answer “Yes” or “No” for each one. Examples include: “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 participant 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 participant is asked six questions about the characteristic functions of particular body parts. Examples include: “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 participant 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 participant’s knowledge of how English body part terms are sometimes applied to the parts of inanimate objects.<sup>9</sup>

<sup>9</sup>This 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 nondescript as a stone may be assigned a “face”, a “nose”, an “ear”, a “back”, a “belly”, or any of about 15 other quasi-metaphorical body parts—for example, 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).

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 3, and Test 10 bears specifically on Hypothesis 4. 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 participant’s familiarity with certain linguistic conventions that stipulate how words that are typically used to designate parts of human bodies can also be used to refer to parts of inanimate objects, reflecting similarities of shape, location, and function that were originally detected, and incorporated into the language, by speakers from past generations.

#### *Nonlinguistic 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 composed 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 as those that are used in Test 4. (See Figure 1E.) The participant is told to ignore whether the

pictures are colour or black-and-white and whether they are photographs or line drawings. This test bears on Hypotheses 2, 3, and 4. (See Table 1.)

## Data quantification

### *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 participants—the BD group and the NC group—were scored as correct or incorrect. (For each of the four 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 participant and each test, a percentage correct score was calculated by dividing the number of correct responses by the number of items on the test and multiplying by 100. Then, for each test, the mean and standard deviation from the NC participants were used to establish a cut-off score—that is, 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 cut-off being treated as unimpaired). Cut-off 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 participant 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 participants 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 cut-off score, and BD patients were classified as impaired if they were more than 2 standard deviations below the cut-off.

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  $\rightarrow$  “calf”, or function based, e.g., elbow  $\rightarrow$  “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 cut-off 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 cut-off score to  $> 94\%$  for Tests 5, 6, 7, 8, and 9, and for the composite comprehension score described below. As we show in the section “Comprehension tests”, however, even with the cut-off 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 nonlinguistic odd-one-out test were quantified by conducting an analysis like the first stage for the production and comprehension tests. In short, percentage correct scores were calculated for all participants, and scores for BD patients were classified as impaired if they were more than 2 standard deviations below the mean for NC participants.

*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<sub>1</sub> weighted coronal cuts. The data were reconstructed in three dimensions using Brainvox (Frank et al., 1997). (The analysis was based on computed tomography (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 colour coded, so that differing degrees of overlap

(greater or fewer patients with lesion at a particular voxel) are indicated by different colours.

**RESULTS****Production tests**

The behavioural group results for the production tests are shown in Table 2, Part A. The NC participants 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 cut-off, 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

**Table 2.** Group results for 12 tests assessing lexical and conceptual knowledge of body parts

Test	NC participants						Impaired BD patients		
	Mean	SD	Cut-off	N	Mean	SD			
A Production	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 <sup>b</sup>	91.6	4.0	>82	7	61.9	25.7	
		<i>Composite production<sup>a</sup></i>	<i>93.4</i>	<i>3.2</i>	<i>&gt;86</i>	<i>10</i>	<i>63.4</i>	<i>26.9</i>	
B Comprehension	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 <sup>b</sup>	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
			<i>Composite comprehension<sup>a</sup></i>	<i>99.7</i>	<i>0.6</i>	<i>&gt;94</i>	<i>1</i>	<i>90.0</i>	—
C Nonlinguistic	12	Odd one out	98.0	3.7	>89	21	78.3	8.4	

*Note:* Group results in percentages. NC = normal comparison. BD = brain-damaged. In the 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 cut-off, and "Mean" and "SD" indicate indicates the average percentage correct and the standard deviation for the patients specified under "N".

<sup>a</sup>The composite scores are based on the entire set of items that went into the score (not on an average of the various tests). <sup>b</sup>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.

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 3, Part A 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, many 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 cut-off for impairment (within 2 percentage points). In addition, we conducted an error analysis of these 9 patients' response protocols. A total of 2 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, 1 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:

- Participant 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).
- Participant 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).

**Table 3.** Scores on all 12 tests for the 9 BD patients with left hemisphere lesions and impaired composite production of body part terms

Tests		BD patients with impaired composite production of body part terms									
		1726	1760	1783	1962	1978	2127	2762	2890	3025	
A	Production	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
		<i>Composite production</i>	76	22	86	30	68	84	24	77	86
B	Comprehension	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
C	Nonlinguistic	11 Parts of inanimate objects	80	80	70	100	95	75	85	55	90
		<i>Composite comprehension</i>	96	97	96	100	99	96	98	90	95
		12 Odd one out	75	80	90	100	80	60	100	95	90

Note: Scores in percentages correct. BD = brain-damaged. Scores in bold typeface are impaired. n/a = not administered.

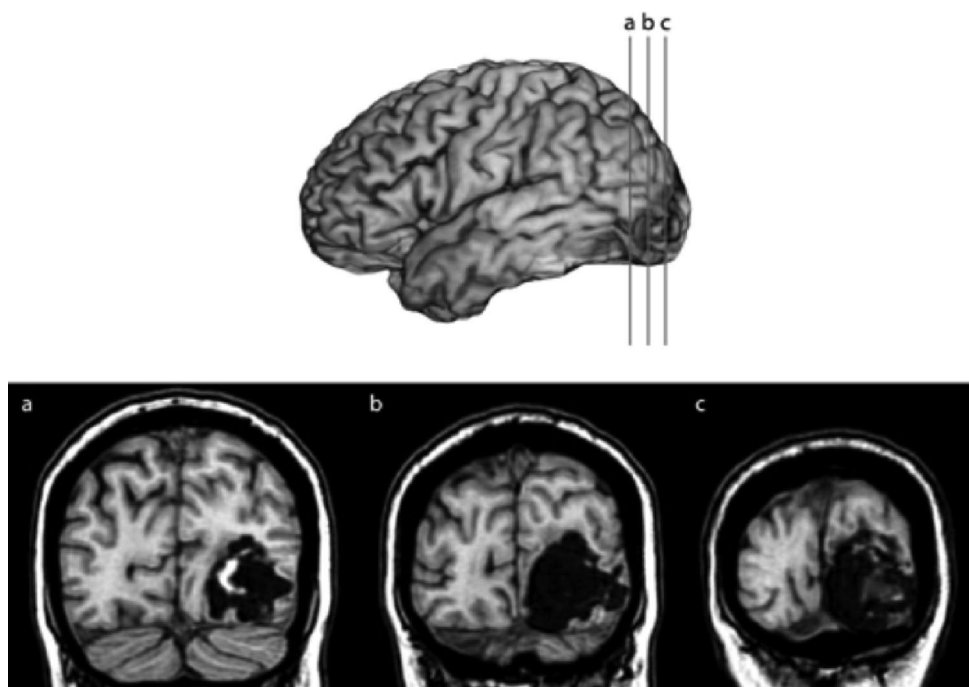
- Participant 1783 suffered a CVA that damaged the cortex and underlying white matter of the left inferior frontal operculum, in the heart of Broca's area including BA 45 and 44, and extending slightly posteriorly into inferior BA 6.
- Participant 1962 suffered a CVA that damaged most of the cortex and 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).
- Participant 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.
- Participant 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.
- Participant 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).
- Participant 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).

- Participant 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 7 of these patients is shown in Figure 3. (The lesion of participant 3025 was not available for the overlap analysis, and the EBA lesion in participant 2890 was not included in the lesion overlap analysis.) The lesion overlap is colour 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 colour bar on the figure. As the figure shows, the area of greatest overlap in the cortex is in the midportion 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 4 patients have lesion overlap in the cortex and underlying white matter in the anterior part of the inferior parietal operculum, tapering to 3 patients in the supramarginal gyrus (BA 40). (The addition of participant 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

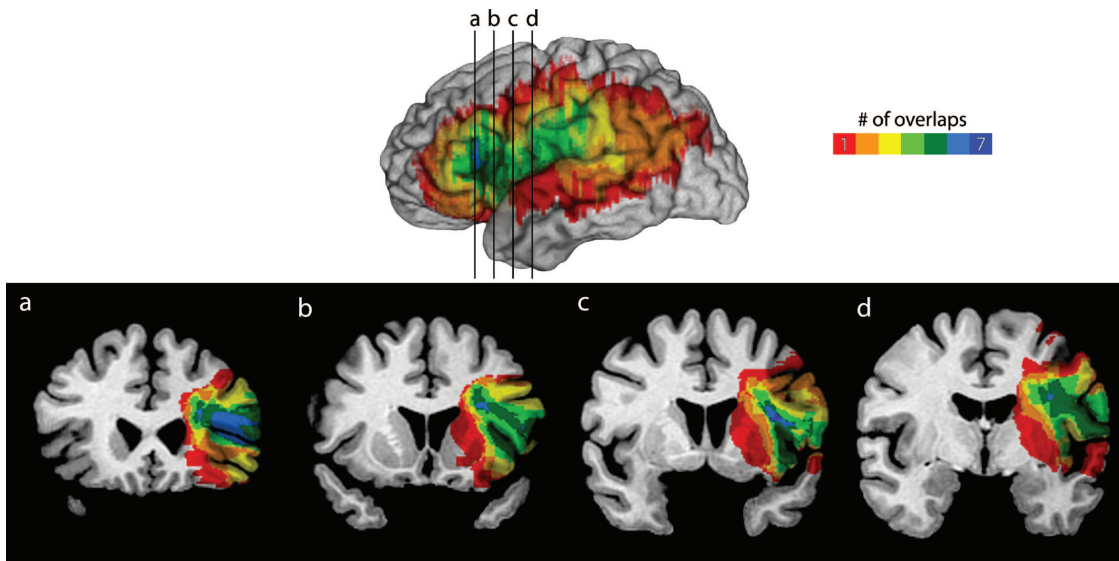


**Figure 2.** Lesion of participant 2890. The lesion is shown in a magnetic resonance (MR) scan obtained 1.5 years after lesion onset, reconstructed in standard brain space. The left hemisphere lateral perspective is shown, along with coronal cuts (black lines, a–c) that depict the cortical and white matter extent of lesion (with left hemisphere on the right). The lesion encompasses the left extrastriate body area (EBA), located in the inferior lateral portion of Brodmann area 19.

BD sample who had lesions that overlapped the critical zones specified above (especially corresponding to the blue and blue-green colours 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, Tranel, Grabowski, Adolphs, & Damasio, 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



**Figure 3.** Lesion overlap map for 7 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 colour 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. (To view a colour version of this figure, please see the online issue of the Journal.)

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.

### Comprehension tests

The behavioural group results for the comprehension tests are shown in Table 2, Part B. The NC participants 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 three 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 cut-off 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 3, Part B, his composite was pulled down by a poor Test 11 performance, with 4 of the 7 comprehension tests showing perfect scores (100%).

## Nonlinguistic test

The behavioural group results for the odd-one-out test are shown in Table 2, Part C. The NC participants performed well on this test, at 98% correct. Of the 104 BD patients, 21 obtained scores that were classified as impaired ( $M = 78.3\%$ ). Of these patients, 2 had bilateral lesions—1 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: (a) left hemisphere: frontoparietal ( $N = 6$ ); prefrontal/premotor ( $N = 2$ ); anterior temporal/inferotemporal ( $N = 3$ ); mesial temporal/occipitotemporal ( $N = 1$ ); superior parietal ( $N = 1$ ); (b) 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 3, Part C.

## 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 ( $N =$

**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

Patient	Concrete entities (CE)	Body parts (BP)	Difference (CE - 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)

*Note:* Scores are in percentage 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 (favouring 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).

104), and vehicles ( $N = 20$ ; for details regarding the stimuli, procedures, scoring, and normative data, see H. Damasio et al., 2004).<sup>10</sup> The results are shown in Table 4, where they are depicted in a summary form that has a percentage correct score for all of the concrete entities and the percentage 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 standard deviations on the concrete entity naming tests are around 4–5 percentage points (see H. Damasio et al., 2004), and the composite

<sup>10</sup> The 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-90s percentage correct. Thus, a direct comparison is valid.

production body part score has a standard deviation of 3.2 in normal participants, 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 standard deviations 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, of the 4 patients with disproportionately impaired naming of body parts (1726, 1962, 2127, 2890), the deficit is restricted to body parts for all but 1 (1962).

## 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.

### Producing body part terms

A total of 10 patients (1 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 postlexical 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, Tikkala, & Juhola, 1998; Ruml, Caramazza, Shelton, & Chialant, 2000; for a computer simulation, see Dell, Lawler, Harris, & Gordon, 2004).

Of the 9 patients with left hemisphere lesions and impaired composite production of body part terms, 8 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 participant 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 cut-off).

In a follow-up study that investigated the specificity of body part naming deficits in the 9 patients mentioned above, we found that 4 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 participant 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).

### 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 1 patient had a composite comprehension score that fell below the cut-off 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; Laiacona 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, Parkin, & Hunkin, 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*, *finger nail*, none of which were in the set used in Snodgrass and Vanderwart). Furthermore, Shelton et al.'s (1998) patient I.O.C. 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 after 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, Kessler, Thiel, Ghaemi, & Karbe, 1999; Thulborn, Carpenter, & Just, 1999;

Warburton, Swinburn, Price, & Wise, 1999; Weiller et al., 1995; for recent reviews see Hillis, 2006, 2007). 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 postinjury, but other areas subsequently "took over" those functions. (Only 5 of the patients in our dataset were tested with the body parts battery prior to 1 year after lesion onset, and none of the patients were tested within the first 6 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 (a) the great importance of body representations for understanding both oneself and other people, and (b) 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 the section "Previous studies"). 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 where the location of that damage is. 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, Damasio, Tranel, Cooper, & Damasio, 2000).

### Nonlinguistic processing of body part concepts

A total of 21 patients were impaired on the nonlinguistic odd-one-out test. Although this test does not require the overt processing of body part terms in either the stimuli or the participant'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 participant must not only identify the relevant dimension of comparison—that is, 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 behavioural results is consistent with the fact that the patients who failed the odd-one-out test had very heterogeneous lesion sites.

### CONCLUSION

We have reported a neuropsychological study that found that of 104 patients with focal, stable lesions in the left or right hemisphere, 10 had impaired naming of body parts. A total of 9 of these patients had left hemisphere damage, with 8 exhibiting maximal lesion overlap in the frontal opercular and anterior/inferior parietal opercular cortices,

and 1 exhibiting an occipital lesion that encompassed the EBA. A total of 4 of the 9 left hemisphere patients had disproportionately worse naming of body parts than naming of 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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