

# Evidence for Multiple, Distinct Representations of the Human Body

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## Abstract

■ Previous data from single-case and small group studies have suggested distinctions among structural, conceptual, and on-line sensorimotor representations of the human body. We developed a battery of tasks to further examine the prevalence and anatomic substrates of these body representations. The battery was administered to 70 stroke patients. Fifty-one percent of the patients were impaired relative to controls on at least one body representation measure. Further, principal components analysis of the patient data as well as direct comparisons of

patient and control performance suggested a triple dissociation between measures of the 3 putative body representations. Consistent with previous distinctions between the “what” and “how” pathways, lesions of the left temporal lobe were most consistently associated with impaired performance on tasks assessing knowledge of the shape or lexical-semantic information about the body, whereas lesions of the dorsolateral frontal and parietal regions resulted in impaired performance on tasks requiring on-line coding of body posture. ■

## INTRODUCTION

Consistent with classic accounts suggesting multiple representations of the human body (e.g., Pick, 1922; Head & Holmes, 1911–1912), recent evidence suggests that there are at least three distinct types of body representations. The first, termed the *body schema*, is a dynamic representation of the relative positions of body parts derived from multiple sensory and motor inputs (e.g., proprioceptive, vestibular, tactile, visual, efference copy) that interacts with motor systems in the genesis of actions (e.g., Schwoebel, Boronat, & Coslett, 2002). The second representation, termed the *body structural description*, is a topological map of locations derived primarily from visual input that defines body part boundaries and proximity relationships (e.g., Buxbaum & Coslett, 2001; Sirigu, Grafman, Bressler, & Sunderland, 1991). The third human body representation, which has been called the *body image* or *body semantics*, is a lexical-semantic representation of the body including body part names, functions, and relations with artifacts (e.g., Coslett, Saffran, & Schwoebel, 2002). Several converging lines of evidence support the psychological validity of and distinctions between these three types of human body representations.

### Body Schema: On-line Sensorimotor Representations

Several investigators have reported physiological data suggesting that efficient action may depend on coding

the relative positions of the fingers with respect to one another (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), as well as the relative positions of the eyes and head and the head and torso (Snyder, Grieve, Brotchie, & Andersen, 1998). Graziano, Cooke, and Taylor (2000) also demonstrated that the firing rate of individual neurons in parietal area 5 of monkeys was significantly influenced by both the orientation of the monkey's own, unseen, arm as well as the orientation of a visible fake or “dummy” arm. Firing rates, however, were only influenced when the dummy arm was presented in a position that suggested that it was part of the animal. For example, if the dummy arm was positioned so that its hand was closest to the monkey's shoulder or if the dummy right arm was shown extending from the monkey's left shoulder, no effect of the left/right orientation of the arm was observed. The authors suggested that these neurons, “could form the basis of the complex body schema that we constantly use to adjust posture and guide movement” (p. 1782).

In addition, recent models of motor control suggest that sensory and efference copy information may be integrated to allow for the on-line correction of motor errors as well as to generate a more accurate estimate of body posture (e.g., Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000; Desmurget et al., 1999; Wolpert, Ghahramani, & Jordan, 1995). Further, Buxbaum, Giovannetti, and Libon (2000) have recently examined a patient (B.G.) with primary progressive apraxia and argued that her apraxia may be attributable to impairments of the body schema. They state that, “Taken together, the evidence suggests that B.G.'s deficits in gesture pantomime, recognition, and imitation result

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primarily not from gesture representation integrity, access, or egress, but from deficits in dynamic coding of the intrinsic positions of the body parts of the self and others” (p. 184). Also of note, Lackner (1988) has demonstrated that vibration of the biceps muscle not only results in an apparent extension of the arm but also in the distortion of other body parts that the hand of the stimulated arm is contacting. For example, subjects reported an illusory extension of their nose when it was grasped by their right hand during stimulation of their right biceps muscle. This striking finding suggests the presence of an on-line representation of the relative positions of body parts (i.e., body schema).

Parsons and others have argued that the body schema underlies simulated movements of the body as well (Schwoebel, Boronat, et al., 2002; Schwoebel, Coslett, Bradt, Freidman, & Dileo, 2002; Schwoebel, Friedman, Duda, & Coslett, 2001; Coslett, 1998; Parsons, 1987, 1994). Data from a series of experiments examining the time required for subjects to determine the laterality of pictured hands suggest that participants confirm laterality judgments by imagining their hand moving from its current position into the orientation of a stimulus hand. Thus, response times depend on whether a participant’s own hand is palm-up or palm-down and its degree of angular disparity from the stimulus hand. Furthermore, the response times for such imagined movements reflect the human body’s biomechanical constraints on movement and are highly correlated with actual movement times. These findings suggest that the simulated hand movements rely on a dynamic internal representation of hand position, which may be derived from proprioceptive input as well as efference copy information (i.e., body schema).

Importantly, we have recently reported evidence suggesting a relationship between the representations underlying performance on the hand laterality task and the ability to produce spatially and temporally accurate movements (Schwoebel, Buxbaum, & Coslett, 2004). In a group of 55 unilateral left hemisphere stroke patients, multiple regression analyses demonstrated that performance on the hand laterality task was a significant predictor of performance on tasks requiring the production of meaningful gestures to command and imitation as well as tasks requiring the imitation of meaningless movements. This suggests that components of the body schema (i.e., representations derived from efference copy information) may, in part, underlie performance on tasks requiring both imagined and real actions. Functional neuroimaging findings further suggest that the performance of hand laterality judgments as well as explicit motor imagery are associated with activation in inferior and superior parietal areas as well as motor and premotor areas (e.g., Parsons, Fox, et al., 1995) and that these brain regions overlap substantially with the areas activated during actual move-

ments (e.g., Grezes & Decety, 2001; Jeannerod, 2001; Parsons & Fox, 1998; Gerardin et al., 1996). Consistent with these findings, Sirigu et al. (1995, 1996) have noted that although strong correlations between the times required to imagine and execute sequential finger movements are observed in normal subjects and patients with motor cortex damage, patients with parietal damage exhibit poor correlations, suggesting an impaired ability to accurately simulate action. Taken together, these findings suggest that both actual and mentally simulated movements may depend on the body schema and that the posterior parietal cortex may serve as an integral component of the neural substrates underlying body schema representations.

### **Body Structural Description: A Topological Map of the Body**

There is also evidence supporting the validity of the body structural description. Consistent with Pick’s (1922) original account of patients who were unable to point to named body parts on themselves or others (i.e., *autotopagnosia*), recent findings suggest that autotopagnosia may be attributable to a selectively impaired representation of the structure of the human body (here termed *body structural description*). In contrast to the body schema, which appears to be derived from multiple sensory and motor inputs, the body structural description is postulated to be derived primarily from visual input (Buxbaum & Coslett, 2001; Sirigu et al., 1991). Buxbaum and Coslett (2001) observed an autotopagnosic patient (G.L.) with diffuse left hemisphere damage who was impaired relative to controls when asked to point to named or visually identified body parts on himself or others and when asked to match pictured body parts across changes in viewing angle. However, G.L. performed perfectly when asked to point to parts of animals and inanimate objects. These findings suggest that G.L.’s ability to access structural descriptions of human body parts may be selectively disrupted. Several lines of evidence suggest that he did not exhibit a disruption of the on-line sensory-motor representation of the body. For example, the maximum distance between G.L.’s thumb and finger while reaching to grasp objects varied with the size of the objects and were not significantly different from the preparatory grips of a normal control subject. G.L. also performed flawlessly when required to point to objects taped to the examiner’s body.

### **Body Image: Semantic and Lexical Representations of the Body**

Recent findings also argue for a third distinct body representation (i.e., *body image*) that represents semantic and lexical information about the human body,

such as body part names, associations between body parts and artifacts, and the functions of body parts. For example, Sirigu et al. (1991) reported a selective preservation of the body image in an autotopagnosic patient with diffuse cerebral atrophy. This patient performed at chance, despite being able to view her own body, when asked questions that required her to verbally indicate the spatial relationships between body parts (e.g., “Is the wrist next to the forearm?”), but performed normally when asked about body part functions (e.g., “What is the mouth for?”). Buxbaum and Coslett (2001) also noted that G.L., an autotopagnosic patient, performed perfectly when asked to point to body parts on himself that were associated with items of clothing or grooming tools (e.g., he was shown a picture of a shoe and asked to point to the part of his body with which it was most closely associated) suggesting that his semantic knowledge of body parts was preserved.

We have also recently observed a patient (A.D.) with selective preservation of body part semantic information despite impaired comprehension of words from other categories (Coslett et al., 2002). For example, when asked to point to named pictures of body parts and non-body part stimuli that were matched for frequency and familiarity, A.D. correctly identified all 12 body parts and 4 of 8 stimuli from other categories. A similar pattern of performance was also observed on comprehension and oral reading tasks (see also Shelton, Fouch, & Caramazza, 1998). In contrast, Suzuki, Yamadori, and Fujii (1997) reported a patient with Broca’s aphasia and left hemisphere infarctions, which included the frontal operculum, who exhibited impaired body part name comprehension despite preserved comprehension of words from other semantic categories and a preserved ability to point to visually identified body parts on himself (i.e., he was not autotopagnosic). For example, when asked to point to a named picture among distracters from the same category, he correctly identified 2 of 10 body parts, but identified 8 of 10 or better for all 10 of the other categories tested.

To our knowledge, there has been no large-scale investigation of the putative human body representations discussed above and there is no information available concerning the prevalence of disorders of body knowledge. Further, although there is substantial evidence concerning the psychological validity and anatomic bases of the body schema and there is strong evidence from single-case reports suggesting functional distinctions between the 3 putative body representations, relatively little is known about the anatomic bases of the body structural description and body image representations.

To explore the psychological validity of the 3 putative body representations and to define the prevalence and anatomic bases of disorders of body knowledge, we

examined the performance of 70 patients with single-hemisphere stroke and 18 age-matched normal controls on a battery of tasks developed to assess the body schema, body structural description, and body image. As described in detail in the Methods section, we developed multiple tasks to assess each of the body representations. Tasks designed to assess the body schema included the hand imagery/action task (for ipsilesional and contralesional hands), which is similar to that described by Sirigu et al. (1996) and the hand laterality task (for ipsilesional and contralesional hands) developed by Parsons (1987). Tasks designed to assess the body structural description required subjects to point on their own bodies to parts that matched pictured body parts (localization of isolated body parts), to point to parts of a mannequin that corresponded to the location on their own bodies where a tactile stimulus was presented (localization of tactile input), and to point to 1 of 3 pictured body parts that is closest on the body surface to a target body part (matching body parts by location). Tasks assessing the body image required subjects to point to 1 of 3 pictured body parts that was most similar in function to a target body part (matching body parts by function) and to point to 1 of 4 pictured body parts that was most closely associated with a pictured item of clothing or tool (matching of body part to clothing and objects).

## RESULTS

### Examining Relations between Tasks

First, a principal components analysis of the patient data from each of the theoretically motivated tasks was performed. This analysis was stimulated by the fact that we have developed an account of body knowledge that posits three distinct types of representations: the body schema, body structural description, and body image. Thus, tasks designed to assess a particular body representation would be expected to be more strongly correlated with one another than with tasks designed to assess a different representation (i.e., the tasks would form a factor). In contrast, if our account is incorrect in that a single, undifferentiated representation underlies all aspects of body knowledge, one would predict that one factor would emerge from the analysis, or that if discrete factors were identified, the tasks would either segregate in a random fashion or not segregate into distinct factors at all. Thus, the factor analysis provides an important test of our account.

Principal component extraction with varimax rotation was performed with SPSS (Chicago, IL) to examine the relations between performance on the 9 body representation measures. The appropriateness of principal component analysis for the observed correlations was suggested by a value of .70 resulting from the Kaiser–Meyer–Olkin measure of sampling adequacy (Tabachnick

& Fidell, 1989). Examination of an initial scree plot and residual correlation matrices suggested 4 components (e.g., 4 components resulted in 7 residual correlations  $> .05$ ; 3 factors resulted in 17 residuals  $> .05$ ). The factors accounted for a substantial amount of variance in each of the variables, as indicated by the communalities in Table 1, suggesting that the variables are well defined by the 4-factor solution.

First, it should be noted that the factor analysis strongly supported the claim derived in large part from a series of single-case and small group studies that discrete and dissociable body representations may be identified. For example, support for the claim that the body structural description represents a distinct representation comes from the fact that the three tasks assessing the body structural description exhibited substantial internal con-

sistency; the first factor (sum of squared loadings, or SSLs = 2.49) was primarily defined by the three body structural description tasks. Additionally, the two tasks assessing the body image comprised factor 4 (SSL = 1.73).<sup>1</sup>

Contrary to our expectations, the tasks designed to assess the body schema (hand laterality and hand imagery/action tasks with both the right and left hands) did not load onto the same factor. The hand laterality judgment with the contralesional and ipsilesional hands constituted the second component (SSL = 1.75), whereas the hand imagery/action task with the contralesional and ipsilesional hands constituted the third component (SSL = 1.75). Indeed, a striking double dissociation between the two body schema tasks was observed. Twenty-six subjects performed abnormally (i.e., below the range of scores for normal controls) on either the hand laterality or hand imagery/action task; 9 could not perform the hand imagery/action task with the contralesional hand because of hemiplegia. Of the 17 subjects for whom data on both tasks is available, only 1 performed abnormally on both tasks. As indicated in Figure 1, 8 of 16 patients performed abnormally on the hand laterality task, but normally on the hand imagery/action task,  $t(7) = 3.03$ ,  $p < .02$ , and 8 of 16 performed abnormally on the hand imagery/action task, but normally on the hand laterality task,  $t(7) = 8.62$ ,  $p < .001$ . The possible implications for this surprising finding will be discussed further in the Discussion.

**Table 1.** Component Loadings (C1–C4), Communalities, and Percent of Variance Accounted for Principal Component Extraction with Varimax Rotation

Task	C1	C2	C3	C4	Communalities
<i>Body schema</i>					
Hand imagery/ action ipsilesional	-.210	-.181	<b>.888</b>	.007	.871
Hand imagery/ action contralesional	.103	-.009	<b>.912</b>	-.168	.880
Hand laterality ipsilesional	.122	<b>.908</b>	-.124	.193	.892
Hand laterality contralesional	.318	<b>.845</b>	-.200	.133	.873
<i>Body structural description</i>					
Localization of isolated body parts	<b>.825</b>	.170	-.021	.241	.768
Localization of tactile input	<b>.899</b>	.155	-.115	.134	.864
Matching body parts by location	<b>.630</b>	.300	-.111	.616	.879
<i>Body image</i>					
Matching body parts by function	.231	.142	-.108	<b>.920</b>	.932
Matching body parts to clothing/objects	.415	.356	-.180	<b>.682</b>	.876
Percent variance	28	21	19	19	

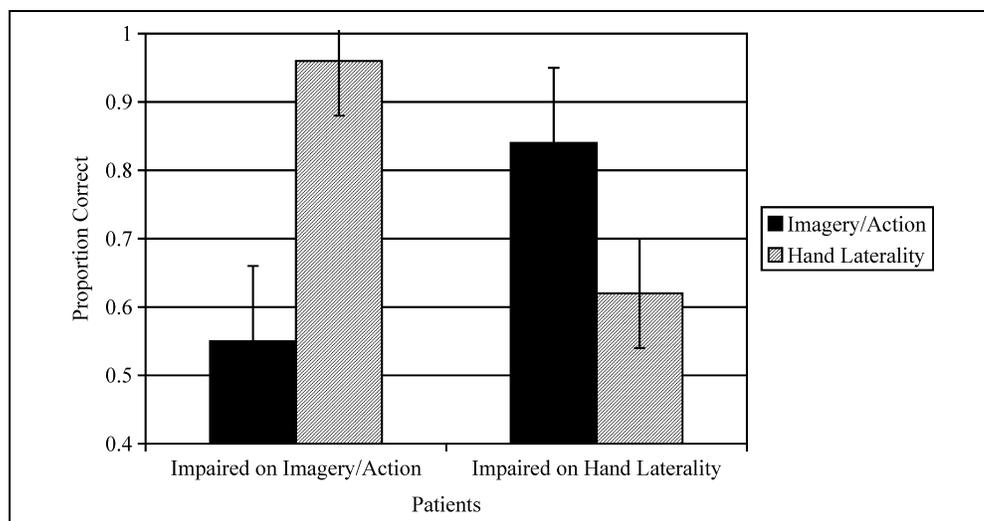
Numbers in **bold** indicate strong component loadings.

### Examining Selective Body Representation Deficits

We next examined whether there were selective deficits on the body schema, body structural description, and/or body image tasks by comparing the performance of all 70 patients to the performance of the control group. First, mean scores were calculated for the body structural description (3 tasks) and body image (2 tasks) measures; these measures, along with performance on the hand laterality (ipsi- and contralesional hands) and hand imagery/action tasks (ipsi- and contralesional hand) were then compared with control performance. Patient scores that fell below the range of scores for the normal controls were considered impaired.

As indicated in Table 2, several interesting observations emerged from this comparison. First, like the principal component analysis described above, the analysis of the performance of individual subjects suggests that the body schema, body structural description, and body image are dissociable representations. Seven subjects exhibited an impairment on the hand imagery/action task but performed normally on all other body representation measures. Similarly, 6 subjects performed abnormally on only the hand laterality task

**Figure 1.** Mean proportions correct for the hand imagery/action and hand laterality tasks for patients ( $n = 16$ ) exhibiting dissociations between performance on these tasks. Error bars indicate standard deviations.



and two subjects abnormally only on the body structural description measure. Finally, three subjects were impaired only on the body image measure.<sup>2</sup>

### Examining Anatomic Bases of Body Representations

Finally, analyses of the anatomic underpinnings of body representation disorders were performed using imaging studies obtained for clinical purposes. CT and/or MRI examinations demonstrating the relevant lesion were examined for 64 of the subjects. Seven had exclusively subcortical lesions; thus, studies demonstrating an infarct involving the cortex were available for 57 subjects (28 with no body representation deficits, 29 with one or more body representation deficit).

Representations underlying the body image and body structural description are lateralized to the left hemisphere. Thus, 15 of 16 subjects who were impaired on the body image measure (sometimes in conjunction with body structural description and/or body schema deficits) and 16 of 18 subjects who were impaired on the body structural description measure had left hemisphere lesions (both  $p < .05$ ). In contrast, impaired performance on the hand laterality and hand imagery/action tasks were not clearly lateralized; there was a tendency for deficits on the hand imagery/action task to be associated with left hemisphere lesions (7/9,  $p = .18$  by Sign Test). Ten of the 17 subjects exhibiting impairment on the hand laterality task exhibited left hemisphere lesions.

Furthermore, although it has been suggested in previous reports that subjects with right hemisphere lesions exhibit a deficit on the hand imagery/action (e.g., Sirigu et al., 1995) and hand laterality (Coslett, 1998) tasks for the contralateral hand only, we observed that deficits on both the hand imagery/action and hand laterality tasks were strikingly symmetric. That is, subjects with brain

lesions exhibited deficits of similar magnitude with both the ipsi- and contralesional hands. Thus, for patients with left hemisphere lesions ( $n = 45$ ), performance was similar for both the ipsilesional ( $M = .76$ ,  $SD = .16$ ) and contralesional ( $M = .76$ ,  $SD = .15$ ) hands on the hand imagery/action task and for the ipsilesional ( $M = .84$ ,  $SD = .19$ ) and contralesional ( $M = .85$ ,  $SD = .20$ ) hands on the hand laterality task. Similarly, for patients with right hemisphere lesions ( $n = 25$ ), performance was equivalent for both the ipsilesional ( $M = .80$ ,  $SD = .16$ ) and contralesional ( $M = .80$ ,  $SD = .17$ ) hands on the hand imagery/action task and for the ipsilesional ( $M = .84$ ,  $SD = .16$ ) and contralesional ( $M = .84$ ,  $SD = .18$ ) hands on the hand laterality task. This symmetry was also observed regardless of whether we examined (1) all subjects with brain lesions ( $n = 70$ ); (2) all subjects with any body representation deficit ( $n = 36$ ); or (3) subjects with deficits restricted to the hand laterality ( $n = 6$ ) or hand imagery/action tasks ( $n = 7$ ).

Analyses of the distribution of lesions are also of interest. Each imaging study was coded by a behavioral neurologist who was blind to the behavioral data with respect to involvement (yes/no) of the following brain regions: dorsolateral frontal (DLF) lobe, frontal lobe excluding DLF, parietal lobe, temporal lobe, insula, occipital lobe, and subcortical structures. Lesions involving the DLF and/or parietal lobe were significantly more frequent in subjects with body representation deficits as compared with subjects without body representation deficits (25/29 vs. 12/28, respectively, Fisher's Exact Test,  $p = .001$ ). Significant differences were not found for other brain regions. These data must be interpreted with caution, however, as the lesions in the former group may be larger. Subjects with body representation deficits sustained damage to a significantly larger number of coded body regions than subjects without these deficits (3.14 vs. 2.3,  $p = .0126$ ).

**Table 2.** Mean Proportions Correct for Normal Controls (Range in Parentheses) and Patients (Indicated by Initials) with Selective Deficits on the Body Representation Tasks

Tasks	Image/Act	Laterality	Structural description	Image
Normals	.82 (.63–.97)	.87 (.68–1)	.97 (.90–1)	.87 (.73–.97)
<i>Selective impairment on hand imagery/action task</i>				
B.A.	<b>.47</b>	.92	.97	.95
W.D.	<b>.37</b>	1	1	.93
W.G.	<b>.39</b>	.96	.99	.89
F.J.	<b>.56</b>	1	1	.93
S.M.	<b>.52</b>	.99	.99	.95
L.G.	<b>.60</b>	.94	.96	.74
D.J.	<b>.62</b>	.89	1	.87
<i>Selective impairment on hand laterality task</i>				
B.R.	.67	<b>.50</b>	1	.90
G.M.	.91	<b>.63</b>	.99	1
B.S.	NA	<b>.61</b>	1	.96
S.J.	.88	<b>.66</b>	.99	.96
B.J.	.84	<b>.63</b>	.97	.73
G.E.	NA	<b>.54</b>	.97	.73
<i>Selective impairment on body structural description task</i>				
M.G.	.80	1	<b>.89</b>	.79
C.J.	NA	.93	<b>.88</b>	.73
<i>Selective impairment on body image task</i>				
M.T.	.81	.93	.93	<b>.61</b>
B.D.	NA	.99	.97	<b>.66</b>
F.E.	.84	.93	.90	<b>.71</b>

Proportions in **bold** indicate impaired performance (i.e., scores below the range of scores for normal controls).

Analyses also suggest that the specific body representations may be localizable. Imaging data were available for 13 of the 16 subjects with body image deficits. For 12 of the 13 subjects, the lesion involved the temporal lobe. Similarly, imaging data were available for 15 subjects with body structural description deficits; again, the temporal lobe was the most common site of injury (12/15 subjects); there was a trend for involvement of the temporal lobe to be more frequent than damage to the parietal lobe in subjects with body structural description deficits (12/15 vs. 6/15, Fisher's Exact test,  $p = .064$ ).

As previously noted, data from functional imaging (e.g., Parsons, Fox, et al., 1994; see Grezes & Decety, 2001) as well as studies of patients with cerebral lesions (e.g., Schwoebel, Boronat, et al., 2002; Sirigu et al., 1996) are consistent with the hypothesis that the body schema is dependent on the DLF and posterior parietal cortex. Based on these data, we predicted that subjects who were impaired on the hand imagery/action and hand laterality tasks would exhibit infarction in the DLF cortex, the parietal cortex, or both regions. This prediction was confirmed. Scans revealing a cortical lesion were available for 12 subjects with impaired performance on the hand laterality task; in all instances the lesion involves the DLF cortex ( $n = 5$ ), the parietal cortex ( $n = 4$ ), or both ( $n = 3$ ). Scans revealing a cortical lesion are available for 6 subjects with impaired performance on the hand imagery/action task; again, for all subjects, the lesion involved either the parietal lobe ( $n = 2$ ) or DLF ( $n = 4$ ).

Finally, a lesion overlap analysis was performed. To this end, lesions identified on CT or MRI were drawn on a brain template using the MRICro software package ([www.icn.ucl.ac.uk/groups/jd/mricro/mricro.html](http://www.icn.ucl.ac.uk/groups/jd/mricro/mricro.html)) by a behavioral neurologist who was naïve with respect to the behavioral data. Using this software package, the imaging data from patients with isolated deficits of the body structural description (2 patients), body image (3 patients), hand laterality task (6 patients), and hand imagery/action task (7 patients) were superimposed, and regions of infarction common to at least 50% of patients were identified. Although both patients with isolated body structural description deficits exhibited lesions involving the left temporal lobe, there was no overlap of the region of infarction. All three subjects with body image lesions had suffered temporal lesions; as shown in Figure 2, the lesion involved portions of Brodmann's area 37 as well as underlying white matter in 2 subjects. For 4 of 7 subjects with isolated deficits on the hand imagery/action task, the lesion involved inferior portions of Brodmann's area 40 on the left side (see Figure 3). Finally, the lesion involved subcortical white matter underlying Brodmann's area 40 and primary sensory cortex on the right in 4 of 7 subjects with isolated deficits of hand laterality task (see Figure 4).

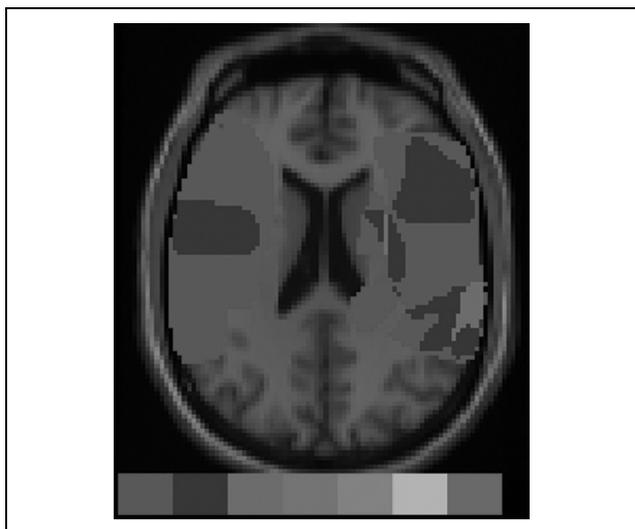
## DISCUSSION

First, it should be noted that the principal component analysis of the data from this large group of patients strongly supports the claims derived in large part from a series of single-case and small group studies. Thus, consistent with previous accounts suggesting distinct representations of structural and lexical-semantic information about the human body (Coslett et al., 2002; Buxbaum & Coslett, 2001; Schwoebel, Coslett, & Bux-

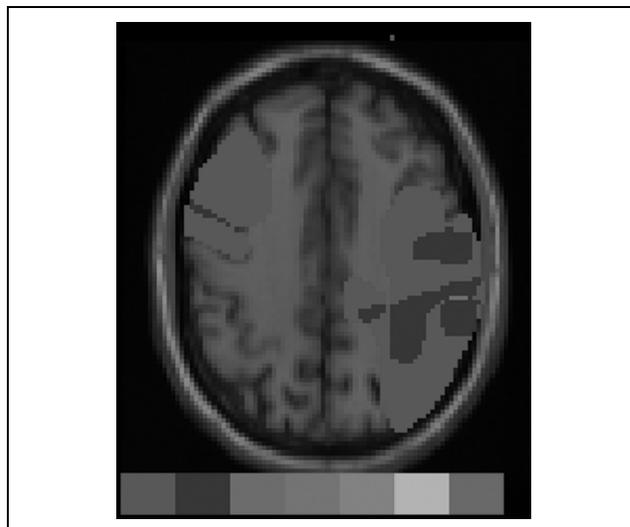


**Figure 2.** Lesion overlaps for subjects with selective impairment on body image tasks.

baum, 2001; Coslett, 1998; Suzuki et al., 1997; Sirigu et al., 1991; Ogden, 1985), principal components analysis suggested that two different components may best characterize the pattern of performance on the body structural description and body image tasks. This pattern of performance was also consistent with the double dissociation observed between the body structural description and body image measures when patient performance was directly compared with that of controls. Taken together, these findings strongly suggest that structural and lexical-semantic information about the human body may be maintained as 2 functionally distinct representations.



**Figure 3.** Lesion overlaps for subjects with selective impairment on hand imagery/action task.



**Figure 4.** Lesion overlaps for subjects with selective impairment on hand laterality task.

The anatomic substrates of these representations were also consistent with the findings of previous single-case and neuroimaging studies. Thus, just as the present data suggest that body structural description and body image representations are lateralized to the left hemisphere, previous cases of autotopagnosia (Buxbaum & Coslett, 2001; Schwoebel, Coslett, & Buxbaum, 2001; Sirigu et al., 1991; Semenza, 1988; Ogden, 1985) and relatively selective deficits in the comprehension of body parts (Suzuki et al., 1997; Fujimori, Yamadori, Imamura, Yamashita, & Yoshida, 1993; Hillis & Caramazza, 1991; Goodglass & Budin, 1988; Warrington & McCarthy, 1987; McKenna & Warrington, 1978; Dennis, 1976; Yamadori & Albert, 1973) have all involved patients with left hemisphere lesions. Furthermore, although localization of the body structural description and body image substrates has been difficult in previous case reports because of the extensive nature of the lesions, the present data suggest that damage to the left temporal lobe is most consistently associated with impaired performance on these measures. Interestingly, Downing, Jiang, Shuman, and Kanwisher (2001) recently reported an fMRI investigation in which a region in the right and left lateral occipito-temporal cortex was associated with greater activity when normal subjects performed a 1-back task while viewing pictures of human bodies and body parts as compared with inanimate objects and nonhuman mammals. Although it is interesting to speculate that this activity may have involved body structural description coding, it may also have involved distinguishing humans and other animals and objects at a more abstract level. Furthermore, neither this study nor our analysis of temporal lobe lesions allows for the discrimination of the

difference between temporal regions associated with body structural description and body image representations. Thus, the present study represents an initial step toward localizing the specific substrates underlying these representations.

Our analysis of the body schema yielded a surprising finding. We observed a double dissociation between performance on the hand imagery/action and hand laterality tasks. We are unaware of previous reports of such a dissociation and did not anticipate it. There are a number of potential explanations for this discrepancy. For example, the hand laterality task involves implicit processing of on-line body information whereas the hand imagery/action task requires explicit judgments or movement. Additionally, the tasks differ with respect to the part of body involved; the hand laterality task may involve rotation of the entire arm whereas the hand imagery/action task involves imagined movements of the hand/fingers only. Thus, further research will be necessary to better understand the dissociation between these tasks.

Despite the above dissociations, several similarities between the hand imagery/action and hand laterality tasks were observed. First, we consistently observed bilateral deficits on both tasks. Previous findings regarding this observation are inconsistent. Thus, Coslett (1998) reported that neglect was associated with a unilateral, contralesional deficit on the hand laterality task. Sirigu et al. (1996), on the other hand, reported 2 patients with left parietal lesions who exhibited bilateral deficits on the hand imagery/action task and 2 patients with a right hemisphere lesion who exhibited only a contralesional deficit. More recently, however, several investigators have reported subjects with unilateral brain lesions for whom performance with the ipsilesional and contralesional hands did not differ (e.g., Tomasino, Rumiat, & Umiltà, 2003). The explanation for the discrepant findings is not clear at present but may relate, at least in part, to differences in task demands or lesion localization.

Second, although no clear lateralization was observed for either task, deficits on both tasks were associated with lesions of the DLF and/or parietal cortices. This localization is consistent with previous functional imaging studies of the hand laterality task (Parsons & Fox, 1998; Parsons, Fox, et al., 1995), the hand imagery/action task (Gerardin et al., 1996), and motor imagery tasks more generally (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; see Grezes & Decety, 2001). Thus, although performance on the hand laterality and hand imagery/action tasks strongly dissociate, they both are associated with lesions involving the DLF and/or parietal lobe; the anatomic basis for the dissociation is, at present, not clear.

To our knowledge, the present investigation represents the first large-scale investigation of body representations. The findings are largely consistent with

previous accounts based on single-case or small group studies. More specifically, we observed a triple dissociation among measures of the body schema, body structural description, and body image, suggesting that knowledge of the human body may consist of functionally dissociable representations. We also note that the lesion localization for the different body representations reported here is consistent with accounts that distinguish between processes and brain regions mediating the recognition and knowledge of the world and representations critical for spatial localization and action (Goodale & Milner, 1992; Mishkin, Ungerleider, & Macko, 1983); as described in the Introduction, the body structural description and body image are representations encoding form and lexical-semantic knowledge of the body, whereas the body schema is integral to action. Viewed in this context, then, it is not surprising that the body structural description and body image are impaired by temporal lesions whereas impairments of the body schema are associated with lesions involving the DLF and/or parietal lobes.

Lastly, we note that the incidence of disorders of body representations is surprisingly high; 51% of an unselected group of patients with stroke were impaired relative to controls on at least one measure. Thus, although disorders of body representations are often considered to be rare and have received surprisingly little attention, they appear to occur with a frequency that is comparable to that of classical neurologic disorders such as aphasia or neglect. Given that such impairments are likely to substantially disrupt everyday activities for these patients, further exploration of human body knowledge may have important theoretical as well as clinical implications.

## METHODS

We examined 70 patients (36 women, age:  $M = 55$ ,  $SD = 11$ ) with neuroimaging-documented single-hemisphere stroke (45 with left hemisphere stroke). As we were interested in determining the prevalence and anatomic bases of disorders of body representation, subjects were not selected based on behavioral criteria or lesion location. In addition, we also tested 18 (17 women) age-matched normal control subjects (age:  $M = 47$ ,  $SD = 11$ ). The research was approved by the institutional review boards at the University of Pennsylvania, Temple University, and Moss Rehab Hospital; all subjects gave informed consent in accordance with the Declaration of Helsinki. Subjects were paid for the approximately 1-hr testing session.

All of the body representation tasks described below required nonverbal responses. Unless otherwise indicated, the stimuli for the body representation tasks consisted of color pictures of body parts displayed on the table in front of the subjects in their midline.

## Tasks Assessing the Body Schema

### *Hand Imagery/Action Task*

This task is similar to that described by Sirigu et al. (1996). Four movements ranging in difficulty from repetitive touching of the index and thumb to the independent extension of the index and little fingers were included. Subjects were tested with both hands independently in each of two conditions; hemiplegic subjects were tested with the ipsilesional hand only. In one condition, subjects were asked to imagine making a specified movement 5 times, as quickly and as accurately as possible; in the second condition, subjects were asked to execute the same movement 5 times. The examiner gave a verbal signal to initiate each trial and movement times were recorded with a stopwatch; for imagined movements, subjects indicated when they had completed the movement. Each imagined and executed movement was tested twice. For those subjects unable to produce the more difficult movements, easier movements were substituted so that all subjects were tested 8 times in both conditions with each hand. For both the ipsilesional and contralesional hands, the ratio of imagined to executed movement times was calculated.

### *Hand Laterality Task*

This task has been used extensively to investigate the body schema in normal (Parsons, Fox, et al., 1995; Parsons, 1987, 1994) and brain lesion (Tomasino, Rumiati, & Umiltà, 2003; Johnson, 2000; Coslett, 1998) subjects. Subjects were shown a picture of a hand and asked to indicate if the stimulus is the right or left hand. Pictures of hands were presented in the palm-up or palm-down condition and in 1 of 4 orientations: fingers pointing away, fingers pointing toward the subject, fingers pointing to the left, and fingers pointing to the right. There were 64 trials; subjects responded by moving their left or right hand. Hemiplegic subjects responded by pointing to the contralesional hand. For each subject, overall accuracy for the ipsilesional and contralesional hand was calculated.

## Tasks Assessing the Body Structural Description

### *Localization of Isolated Body Parts*

Pictures of 24 individual body parts were presented and subjects were asked to point to the same part of their own body.

### *Localization of Tactile Input*

On each of 20 trials, subjects were seated with their eyes closed when the investigator touched one part of their bodies with a brush, which, in preliminary testing, was demonstrated to provide a suprathreshold

stimulus at all sites to be assessed. Subjects were asked to point to the corresponding location on a large mannequin.

### *Matching Body Parts by Location*

On each of 24 trials, a target body part was visually presented and subjects were asked to point to 1 of 3 pictured body parts that was closest on the body surface to the target body part.

## Tasks Assessing the Body Image

### *Matching Body Parts by Function*

The stimuli for this task were exactly the same as for the matching body parts by location task described above. Subjects selected 1 of the 3 pictured body parts that was most closely related in terms of function—that is, “things that they do”—to the target body part. Foils included a body part in close proximity on the body’s surface to the pictured body part, as well as an unrelated body part. For example, on one trial the target was an elbow; response options included a knee (the correct choice), a forearm, and a nose.

### *Matching of Body Part to Clothing and Objects*

On each of 20 trials, an item of clothing was displayed along with 4 body parts. Subjects were asked to point to the picture of the body part with which the item of clothing or accessory was most closely associated. Foils included conceptually related, unrelated, and contiguous body parts.

## Acknowledgments

This work was supported by NIH grant R01 NS37920 awarded to H.B.C.

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## Notes

1. We note that the third body structural description task (i.e., matching body parts by location) was complex, in that it had moderate loadings on both the body structural description and body image components, suggesting that performance on this task is influenced by both of these representations.
2. We also directly compared the performance of each of these patients to the control group using analysis of variance and modified *F* criteria, as suggested by Mycroft, Mitchell, and Kay (2002). The results were quite similar to those obtained with the cut-off at the lower range of normal controls.

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